





Plant traits controlling growth change in response to a drier climate

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Summary

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- Plant traits are increasingly being used to improve prediction of plant function, including plant demography. However, the capability of plant traits to predict demographic rates remains uncertain, particularly in the context of trees experiencing a changing climate.
- Here we present data combining 17 plant traits associated with plant structure, metabolism and hydraulic status, with measurements of long-term mean, maximum and relative growth rates for 176 trees from the world's longest running tropical forest drought experiment.
- We demonstrate that plant traits can predict mean annual tree growth rates with moderate explanatory power. However, only combinations of traits associated more directly with plant functional processes, rather than more commonly employed traits like wood density or leaf mass per area, yield the power to predict growth. Critically, we observe a shift from growth being controlled by traits related to carbon cycling (assimilation and respiration) in well-watered trees, to traits relating to plant hydraulic stress in drought-stressed trees.
- We also demonstrate that even with a very comprehensive set of plant traits and growth data on large numbers of tropical trees, considerable uncertainty remains in directly interpreting the mechanisms through which traits influence performance in tropical forests.

Introduction

Uncertainty concerning the net carbon balance of tropical ecosystems propagates to generate one of the greatest uncertainties in the global carbon budget (Tian *et al.*, 2020; Piao *et al.*, 2020). Tree growth is a key plant demographic rate and, jointly with losses from mortality and gains from growth, determines the carbon balance of tropical forests. Carbon gains from growth are sensitive to increasing temperatures and reductions in water availability, and this sensitivity is likely to lead to a continued decline in the net carbon sink of tropical forests over the coming decades (Jung *et al.*, 2017; Liu *et al.*, 2018; Y. Yang *et al.*, 2018; Hubau *et al.*, 2020; Sullivan *et al.*, 2020). The ecophysiological processes controlling growth rates, particularly within species-diverse tropical systems, are still poorly understood, preventing more robust predictions of how changes in climate may alter growth trajectories.

Plant functional traits are commonly used to predict plant and ecosystem function (Reich *et al.*, 1997; Poorter *et al.*, 2008; Kattge *et al.*, 2011; Diaz *et al.*, 2016; Kunstler *et al.*, 2016). This is largely because at large geographical scales, plant traits have been found to cluster and form trade-offs associated with leaf photosynthetic, wood density or plant life-history strategies (Wright *et al.*, 2004; Chave *et al.*, 2009; Patiño *et al.*, 2012; Adler *et al.*, 2014; Diaz *et al.*, 2016; Mencuccini *et al.*, 2019). However, considerable uncertainty remains concerning how plant traits are linked to plant demographic rates (Liu *et al.*, 2016; Falster *et al.*, 2018; J. Yang *et al.*, 2018).

Correlations between demographic rates and plant traits have focused on the leaf economic and the wood economic spectra (LES; WES; Wright *et al.*, 2004; Falster & Westoby, 2005; Poorter *et al.*, 2008; Chave *et al.*, 2009; Poorter *et al.*, 2014; Liu *et al.*, 2016; J. Yang *et al.*, 2018). Correlations of such traits with key demographic rates are often weak (Wright *et al.*, 2010; Paine

et al., 2015; J. Yang *et al.*, 2018) and inconsistent among individuals under different light conditions and, in particular, of different sizes (Falster *et al.*, 2018). This is potentially because the physiological processes for which these traits act as surrogates can change across scales. Common plant trait trade-offs observed at global scales across a broad range of plant functional types (PFT) often break down at local and regional scales or when only one PFT is considered (Messier *et al.*, 2017; Anderegg *et al.*, 2018). Hence, relationships observed at global scales (e.g. Kunstler *et al.*, 2016) are often not suitable for effective use at local scales.

Finding traits related to or directly controlling the physiology of productivity (e.g. growth) of plants is challenging. Traits that are more complex to measure, such as plant hydraulic or photosynthetic traits, may be more representative of a plant's functioning, but these more complex traits remain poorly sampled globally (Eller *et al.*, 2018a). Additionally, these 'mechanistic' traits may combine in multiple ways to maximise growth. Indeed, traits at the scale of an individual organ can be compensated for by changes in, for example, a tree's size, light availability or allocation shifts across tissues (Gibert *et al.*, 2016; Falster *et al.*, 2018; Y. Yang *et al.*, 2018). In turn, this requires simultaneous samples of several metabolic, water use and structural traits, particularly within diverse tropical ecosystems with complex vertical variations in canopy structure.

In tropical forests, size-modulated differences in growth and functional traits are important in the context of the changes in exposure, light availability and water demand which occur as a tree grows in size through the canopy (Grime, 1998; Falster & Westoby, 2005; Gibert *et al.*, 2016; Thomas & Vesk, 2017). However, whether changes in light environment and tree size affect the relationships between tree growth rates and plant traits has been poorly explored.

Understanding relationships between plant traits and growth is central to improving our mechanistic understanding of how plant physiology is linked to plant demographics. These relationships between plant physiology and demographic processes are often emergent properties of vegetation models (Fyllas *et al.*, 2014; Fisher *et al.*, 2015; Fyllas *et al.*, 2017). Variation in plant growth across different PFTs is controlled by PFT-specific parameters, which determine form and rates of processes controlling carbon production, allocation and use (Fyllas *et al.*, 2014, 2017; Harper *et al.*, 2016; Xu *et al.*, 2016; Powell *et al.*, 2018). Trait values and physiological mechanisms controlling growth are generally kept fixed during model runs (e.g. Harper *et al.*, 2016). However, increasing drought stress under future climate scenarios, both in terms of more frequent extreme events (Duffy *et al.*, 2015; Zhou *et al.*, 2019) and long-term declines in soil moisture availability (IPCC, 2019), can potentially change the key mechanisms controlling plant growth.

Large-scale field experiments offer a means to test how trait-growth relationships may change over long timescales. These experiments are often restricted to manipulating one climate variable at a time and are limited in spatial extent and replication, yet they provide vegetation models with data on responses to longer-term climatic change (e.g. multi-year to decadal; Estiarte *et al.*, 2016). Utilising the world's longest running tropical forest

drought experiment as a case study, we explore how the relationships between plant traits and growth rates change when trees are exposed to prolonged soil drought stress. This experiment caused extensive changes in canopy structure, which arose as a consequence of drought-induced mortality (da Costa *et al.*, 2010; Rowland *et al.*, 2015a), also allowing the influence of the changing tree light environment to be evaluated. We test the following: how well simple traits from the LES and WES control growth rates, relative to more complex traits related to plant metabolism and water transport; whether the key traits determining growth rates change from well-watered to drought-stressed conditions; and whether tree size and light environment influence growth rates more than phylogeny, either directly or via controls on other plant functional traits.

Methods

Experimental site

We used the Caxiuanã through-fall exclusion (TFE) experiment, located in eastern Amazonia (lat. 1°43'S, long. 51°27'W), as our focal study site. From 2010 to 2016 the rainfall at our site was on average 2365 mm yr⁻¹, mainly concentrated into a 6-month wet season (December–May). The experiment consists of two plots, a 1-hectare (ha) TFE, where a plastic panel structure has been used to exclude 50% of the canopy through-fall since 2002, and a corresponding control forest plot. This site provides several advantages for testing our hypotheses, because the TFE plot has experienced extensive mortality, opening up the forest canopy (Rowland *et al.*, 2015a) and reducing the light limitation on the understory, therefore providing a contrast between a forest which is likely to have a greater water limitation and one which is likely to be more light- than water-limited. Further details on the experimental set-up and results of the experiment to date are available (Fisher *et al.*, 2006; da Costa *et al.*, 2010; Rowland *et al.*, 2015b; Meir *et al.*, 2018).

Tree and trait sampling

In peak dry season (September and October) 2016 we sampled 176 trees of the most common genera on both plots – 86 trees on the control and 90 trees on the TFE (Supporting Information Table S1). These trees were selected to cover the most dominant genera which existed on both plots and, where possible, to have a distribution across different tree size classes (from 10 cm diameter at breast height (DBH, at 1.3 m), upwards) and with different canopy light conditions within genera and common species. In total 14 genera and 31 species were sampled. We sampled 17 traits, which are given in Table 1 along with the acronyms, a description and the mean plot-scale values (see Dataset S1 for the full dataset used in this study). We note that of the traits sampled, some may be more traditionally considered to be traits within the literature (e.g. leaf mass per area (LMA), leaf nitrogen content (N_{leaf}), leaf phosphorus content (P_{leaf}), maximum carboxylation capacity (V_{max}), maximum electron transport capacity (J_{max}), leaf respiration in the dark (R_{leaf}), branch wood density (ρ),

Table 1 List of all measured traits, descriptions, mean values, standard error vales and sample sizes for the control (C) and through-fall exclusion (D) plots.

Trait	Description	C value	D value	n trees
V_{cmax}	Max. carboxylation capacity ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	23.94 ± 0.90	22.48 ± 0.84	C = 84, D = 76
J_{max}	Max. electron transport capacity ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	45.75 ± 1.62	41.92 ± 1.68	C = 84, D = 76
R_{leaf}	Leaf respiration in the dark ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.62 ± 0.04	0.65 ± 0.03	C = 85, D = 86
Min g_s	Min. stomatal conductance ($\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.04 ± 0.00	0.03 ± 0.00	C = 83, D = 86
Max g_s	Max. stomatal conductance ($\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.11 ± 0.01	0.09 ± 0.01	C = 83, D = 76
R_{stem}	Stem CO ₂ efflux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.93 ± 0.07	0.97 ± 0.07	C = 74, D = 83
LMA	Leaf mass per area (g m^{-2})	63.68 ± 1.65	65.28 ± 2.16	C = 82, D = 75
N_{leaf}	Leaf nitrogen content (g g^{-1})	18.30 ± 0.55	17.51 ± 0.71	C = 66, D = 67
P_{leaf}	Leaf phosphorus content (g g^{-1})	0.40 ± 0.02	0.51 ± 0.02	C = 78, D = 84
ρ	Branch wood density (g cm^{-3})	0.66 ± 0.01	0.64 ± 0.01	C = 76, D = 80
Ψ_{pd}	Pre-dawn leaf water potential (MPa)	0.55 ± 0.03	0.69 ± 0.04	C = 85, D = 90
Ψ_{md}	Midday leaf water potential (MPa)	1.90 ± 0.06	2.00 ± 0.07	C = 85, D = 90
P_{50}	Xylem pressure for a 50% loss of conductance (MPa).	2.22 ± 0.15	2.44 ± 0.15	C = 52, D = 56
K_{s_max}	Max. lumen conductance ($\text{mol H}_2\text{O m MPa}^{-1} \text{ s}^{-1} \text{ m}^{-2}$)	190.84 ± 14.53	184.97 ± 15.00	C = 73, D = 71
PLC	Percentage loss of conductivity	14.03 ± 1.65	22.73 ± 2.24	C = 73, D = 72
SM_{P50}	Hydraulic safety margin, calculated from Ψ_{md} and P_{50} (MPa)	0.59 ± 0.11	0.80 ± 0.12	C = 52, D = 56
LA : SA	Leaf area to sapwood rea ratio	10321.61 ± 619.20	10479.86 ± 654.27	C = 63, D = 66

Additional details regarding the methods used for the trait collection are shown in Supporting Information Methods S1, and the full dataset is available as Dataset S1.

xylem pressure for a 50% loss of conductance (P_{50}), maximum lumen conductance (K_{s_max}), whereas others (e.g. pre-dawn leaf water potential (Ψ_{pd}), midday leaf water potential (Ψ_{md}) may be considered more as indicator variables which signal the current physiological status of the plant. As measurements occurred during peak dry season, we consider both Ψ_{pd} and Ψ_{md} to be important variables to consider in relation to growth. We consider Ψ_{pd} to be an integrated metric of rooting depth or minimum soil water availability (Bartlett *et al.*, 2016) and Ψ_{md} to represent the minimum annual Ψ (water potential) of the plant. Consequently, we then compute the plant hydraulic safety margin (SM_{P50}) as $P_{50} - \Psi_{md}$, assuming it represents the minimum average annual value (e.g. Choat *et al.*, 2012), and we also assume that our percentage loss of conductivity (PLC) value represents the maximum annual average. We therefore assume that these variables give an indicator of the maximum damage from embolism and hydraulic risk that the trees are adapted to tolerate, and we refer to them henceforth as ‘traits’ in this article. Furthermore, given that existing research at this site demonstrates that a large proportion (two thirds to three quarters) of stem respiration from our study trees is likely to be related to maintenance, rather than growth respiration (Rowland *et al.*, 2018), we consider stem CO₂ efflux (R_{stem}), standardised to a set temperature (as also done with R_{leaf} which is more broadly considered a plant trait), to be a key variable that could be influencing potential growth rates, possibly reflecting phloem transport and source/sink relationships. We acknowledge that the variables we call ‘traits’ herein are not all traits in the traditional sense. They are, however, standardised to estimate moments of their respective statistical distributions, much as it is done for variables within the LES and WES, and they therefore have a justifiable link to the controls of growth rates.

To sample these traits, three branches collected from the same tree were gathered each day. All branches were fully sunlit from the upper canopy if the tree received direct sunlight, or were top-

of-canopy branches if the trees were small or shaded. The first branch was cut between 04:30 h and 06:30 h and used to measure pre-dawn leaf water potential (Ψ_{pd}); following this, it was sealed in a large black plastic bag and returned to a lab 1 km away. Here it was re-hydrated for 24 h, re-cut underwater and used to measure hydraulic vulnerability curves to calculate the P_{50} value. To find the P_{50} value, the pneumatic method was used (Pereira *et al.*, 2016) – the branch samples were progressively dried out whilst percentage air discharge and leaf Ψ were measured to form the vulnerability curve (Fig. S1).

A second branch was cut between 10:00 h and 12:00 h. The leaves on this branch were used to measure maximum carboxylation capacity (V_{cmax}) and maximum electron transport rates (J_{max}), derived from an $A-C_i$ curves taken with a Li-Cor 6400 photosynthesis system (Li-Cor, Lincoln, NE, USA). On the same branch the Li-Cor 6400 was also used to measure R_{leaf} , minimal stomatal conductance (Min g_s) and maximum stomatal conductance (Max g_s). Samples were also taken to measure P_{leaf} , N_{leaf} and LMA.

A third branch, ≥ 2 m in length, was cut between 13:00 h and 14:00 h, and three leaves were used to measure Ψ_{md} . This branch was then sealed in a large black plastic bag and returned to the lab, where it was used to measure PLC and K_{smax} , both following a previously described method (Pereira & Mazzafera, 2012). A 1-cm diameter section from this branch was used to measure ρ , and leaf area to sapwood area ratio (LA : SA) was also measured on this branch. Leaf area was measured by scanning all leaves on the branch and quantifying their area using IMAGEJ software (v.1.6.0_20; Schneider *et al.*, 2012). We calculated LA : SA as total branch leaf area divided by basal sapwood area. Detailed methodologies for the collection of all of these traits can be found in Methods S1 and, for the hydraulic traits, in a study by Bittencourt *et al.* (2020), from where these data were taken. R_{stem} measurements were made in October 2016 using a gas analyser

attached to a closed-loop system in a 75 cm² area of each of our study trees. These data were taken from a study by Rowland *et al.* (2018), where a full methodology can be found (see also Methods S1 and Dataset S1). Growth rates were calculated for each tree using mean stem increment data, which was measured every three months using dendrometers, as presented in Rowland *et al.*, (2015a). Mean growth increment was calculated by averaging three-monthly growth rate data from 2010–2016 for each tree and then log-transforming these data. Finally, during the trait sampling period each tree was also given a light score from 1 to 5, as follows: score of 1, tree is in 100% shade; 2, tree is mostly shaded, receiving limited direct sunlight; 3, tree receives direct sunlight but remains partially shaded; 4, tree is top of canopy and receives substantial direct sunlight; 5, tree canopy is entirely sunlit, usually being an emergent tree or existing in a canopy gap. A detailed methodology for the collection of each trait is provided in Methods S1.

Analysis

All statistical analyses were carried out in R (v.3.4.1; R Core Team, 2014). For each trait in Table 1 outliers were removed by excluding data points that were greater than three standard deviations from the mean. The total number of data points, *n*, per trait for the control and the TFE are shown in Table 1. We note that *P*₅₀ has a lower value of *n* because some of the curves could not

be successfully completed in the field. Due to the lognormal distribution of our response variable and 9 of the 17 traits (Kock, 1966; Mitchel, 1968; Limbert *et al.*, 2001), these variables were log-transformed for all subsequent analyses (Table 2). To enable us to log transform our data, Ψ_{pd} , Ψ_{md} and *P*₅₀ values were converted to positive values.

Initially all traits were individually linearly correlated with mean growth across the whole year and during mid wet season (Jan–March) and mid dry season (Jul–Sep) separately for the control and drought plot trees, to evaluate the potential differences in the annual and seasonal controls on growth. Secondly, to explore the role of the interactions of tree size and tree light exposure in key trait–growth relationships, as well as to evaluate whether traits interacted to influence growth, we used structural equation modelling (Grace *et al.*, 2010, 2012) to model the mean growth separately for the trees in the control and drought plots. To avoid excluding trees for which one or more traits were not measured, we selected path analysis using the Full Information Maximum Likelihood algorithm for our statistical analysis, as it allows for missing ('NA', or not available, in R) values by assuming a missing-at-random pattern of missingness (Enders & Bandalos, 2001; Brown, 2006; Allison, 2012; Sinco *et al.*, 2013). Path analysis was undertaken using the LAVAAN package in R (Rosseel, 2012). Relationships among traits and between traits and growth rate were all tested equally based off a null model (to facilitate analysis of individual traits, Fig. 1), which assumed that

Table 2 Results of linear regressions (correlation coefficient (*R*) and *P*-value (*P*)) for each plant trait against mean annual growth, maximum growth during the wet season (Jan–Mar) and minimum growth during the dry season (Jul–Sept) (Q1, Jan–Mar; Q2, April–Jun; Q3, Jul–Sep; Q4, Oct–Dec) for the control and drought plots.

	Control						Drought					
	Mean		Wet		Dry		Mean		Wet		Dry	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Tree light score	0.27	0.02	0.36	0.00	0.49	0.00	0.15	0.19	0.21	0.07	0.29	0.03
DBH	0.38	0.00	0.38	0.00	0.45	0.00	0.27	0.01	0.18	0.11	0.43	0.00
<i>Min g_s</i>	0.13	0.28	0.24	0.05	0.07	0.63	−0.03	0.79	0.11	0.36	0.10	0.45
<i>Max g_s</i>	0.07	0.56	0.05	0.66	0.13	0.35	0.07	0.58	0.03	0.84	0.26	0.06
<i>V_{cmax}</i>	0.24	0.04	0.09	0.45	0.26	0.05	0.21	0.08	0.08	0.51	0.47	0.00
<i>J_{max}</i>	0.32	0.01	0.17	0.16	0.31	0.02	0.38	0.00	0.29	0.02	0.46	0.00
<i>R_{leaf}</i>	0.02	0.87	0.04	0.72	0.17	0.21	0.20	0.08	0.22	0.05	0.08	0.57
<i>K_{s,max}</i>	0.13	0.33	0.12	0.35	0.07	0.64	0.07	0.61	0.15	0.23	0.15	0.31
PLC	0.05	0.73	0.11	0.39	0.10	0.47	0.04	0.75	0.15	0.23	0.16	0.29
<i>P</i> ₅₀	−0.26	0.09	0.04	0.82	0.14	0.43	−0.30	0.04	0.19	0.17	0.13	0.46
SM _{P50}	0.26	0.08	0.06	0.71	0.05	0.77	−0.37	0.01	0.36	0.01	0.25	0.14
ρ	0.21	0.09	0.15	0.25	0.29	0.05	−0.01	0.97	0.03	0.78	0.14	0.32
Ψ_{pd}	0.19	0.11	0.22	0.06	0.15	0.28	0.10	0.35	0.17	0.14	0.13	0.31
Ψ_{md}	0.15	0.21	0.27	0.02	0.13	0.35	0.19	0.08	0.32	0.00	0.24	0.06
LA : SA	0.08	0.56	0.02	0.86	0.06	0.72	0.09	0.51	0.10	0.45	0.11	0.48
<i>R_{stem}</i>	0.38	0.00	0.47	0.00	0.43	0.00	0.46	0.00	0.31	0.01	0.45	0.00
<i>leaf_n</i>	0.27	0.04	0.06	0.65	0.16	0.31	0.19	0.14	0.19	0.16	0.29	0.04
<i>leaf_P</i>	0.10	0.41	0.02	0.87	0.22	0.12	−0.13	0.28	0.12	0.29	0.04	0.76
LMA	0.04	0.72	0.09	0.44	0.25	0.07	0.05	0.66	0.13	0.30	0.06	0.66

Bold text and grey shaded cells indicate significant relationships at *P* < 0.05. Mean growth and the traits with lognormal distributions (variables in bold) were log-transformed (see the Materials and Methods section). See also Supporting Information Fig. S1 for graphical representations of mean growth relationships from this table.

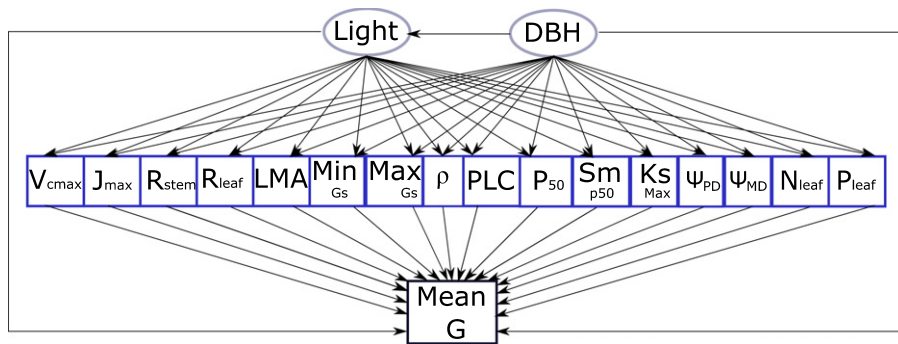


Fig. 1 The initial path model which was minimised to most effectively predict relative, log-transformed mean growth rates (Mean G, black box) from a suite of 15 traits (see the Materials and Methods section and Supporting Information Methods S1), in addition to tree diameter at breast height (DBH) and tree light score (Light) and correlations among traits. Black solid arrows show direct correlations tested. For the model starting point it was assumed that DBH and Light could influence all traits, all traits could influence the growth variable and all traits could influence each other – that is, no initial assumptions were made about whether direct relationships were positive or negative.

all traits could be controlling growth. Traits were either considered to have direct correlations, with one variable directly influencing another, or to co-vary together. Tree-level light environment and DBH, and plot-level drought condition (control or drought plot) were also assumed to be able to influence each trait, as well as each growth rate variable directly. Once the null-path model was structured and run, sequential relationships between variables, as well as individual variables, were removed when they no longer significantly contributed to or connected to the model. Following the criteria described in a study by Brown (2006), relationships between variables were sequentially removed if their P -value was nonsignificant ($P < 0.05$ based on z tests and changes in Akaike information criterion (AIC) values), and variables were removed if this decreased the Robust Maximum Likelihood statistic (RMLS), increasing the model χ^2 P -value (i.e. the likelihood that no significant difference between the model and the data structure was found). We note that, unlike many other statistical models, the aim is to increase the P -value and decrease the RMLS, in order to minimise the statistical difference between the model and the data structure (Brown, 2006). The modification indices function (*modindices*) in the LAVAAN package was also used to check whether any relationships between variables that were not included in the final hypothesised model could be used to improve the fit between the model and the data.

To test the role of phylogeny in controlling trait relationships, and specifically to test for an effect of the phylogenetic distance between genera on the trait relationships with tree growth, we performed phylogenetic generalised least squared regression (PGLS) using the CAPER package in R (Orme, 2013). Phylogenetic distance data for each of our genera was provided by Neves *et al.* (2020). We also performed mixed-effect model analyses, using the LME4 package (Bates *et al.*, 2015), on all our significant path analysis relationships to test the following: whether a model which included genus or species nested within genus as a random effect on the intercept had a lower AIC than one without it, and whether large differences between the marginal (without genus as a random variable) and conditional (with genus as a random variable) R^2 were found (LMERTEST package, Kuznetsova *et al.*, 2017).

Results

Mean growth rates were 18% greater on the drought plot relative to the control. This was driven by a significant increase in the growth rate during mid wet season (Jan–Mar), rather than in growth rates in any other quarter of the year (Fig. 2). Results from bivariate linear correlations between our 17 traits with log-transformed mean annual growth reveal that the strongest correlation with log-transformed mean annual growth was with R_{stem} (Fig. 3, Table 2), while V_{max} and J_{max} also showed significant ($P < 0.05$) relationships in the control forest, with R values of 0.32 and 0.38 respectively (Table 2; Fig. S2). We note that converting these correlations to mixed effects models with light score as a random factor did not significantly improve these correlations ($P = 0.09$ –

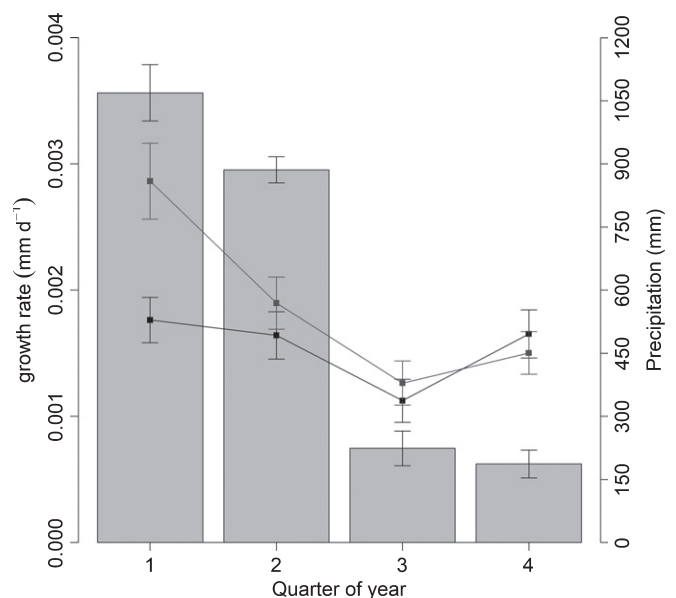


Fig. 2 Shifts in the average growth across the four quarters of the year (1 = Jan–Mar, 2 = Apr–Jun, 3 = Jul–Sep, 4 = Oct–Dec) on the control (black line) and drought (grey line) plots, and the total rainfall over these same periods averaged over 2010–2016. Error bars indicate the standard error of the mean.

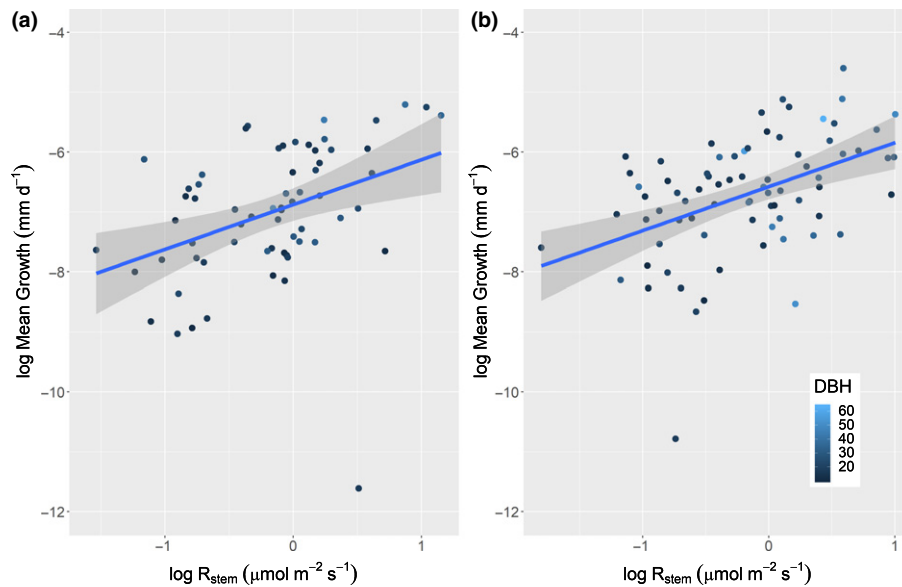


Fig. 3 Linear relationships between log mean growth rate and log stem respiration rate (R_{stem}) on the control (a) and drought (b) plots. The coloured shading on the dots indicates the diameter at breast height of the trees (DBH, cm). The line indicates the significant linear regression line and the grey shaded area represents the 95% confidence interval.

0.99). Furthermore, in the control forest tree light score and DBH also maintained significant relationships with mean annual growth, with R values of 0.27 and 0.38, respectively. By contrast, for the drought forest we find that alongside the correlations found for J_{max} ($R=0.38$) and R_{stem} ($R=0.46$), there is a strong significant negative relationship between mean annual growth and SM_{P50} , which is absent in the control forest (Fig. 4; Table 2). We also find a weaker but still significant negative correlation with P_{50} , represented as positive values (Table 2). Interestingly, for the drought trees, relative to the control, a significant

relationship between mean annual growth and DBH is maintained, but the R^2 value is reduced to 0.27, whilst the relationship with tree light score is lost (Table 2). A full correlation matrix of all traits is shown in Table S2.

The correlates with growth rate were more stable between the dry and wet seasons for the control plot than they were for the drought plot. For the control plot, three of the five variables that correlated with mean annual growth also correlated with both mean wet and dry season growth (R_{stem} , tree light score and DBH; Table 2; Fig. S2) and these three traits were the strongest

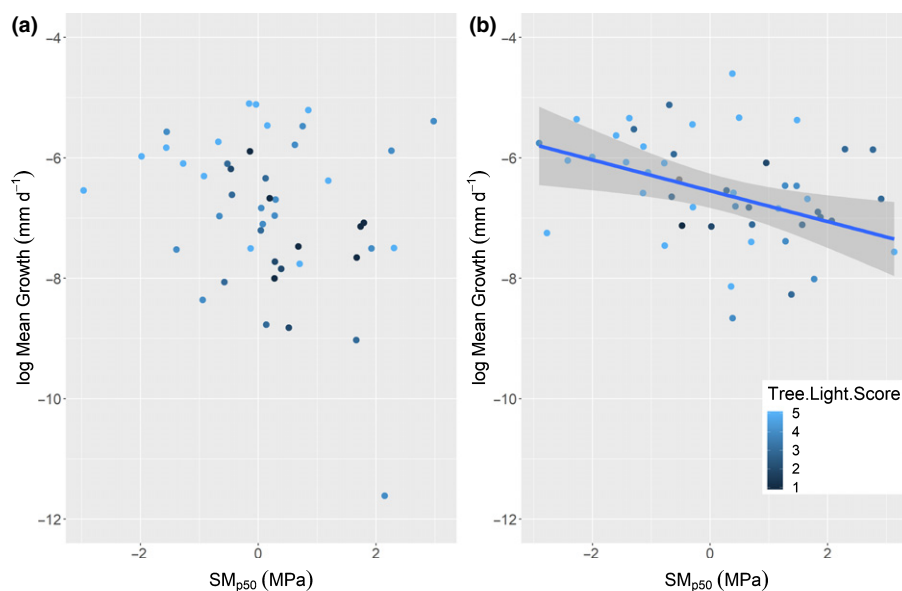


Fig. 4 Linear relationships between log mean growth rate and the hydraulic safety margin (SM_{P50}) on the control (a) and drought (b) plot. The coloured shading on the dots indicates the tree light score of the trees. The line indicates the significant linear regression line and the grey shaded area represents the 95% confidence interval.

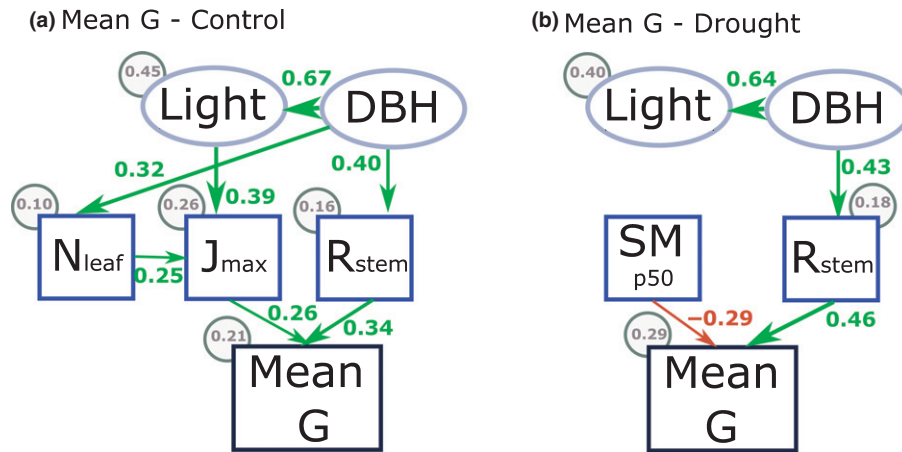


Fig. 5 Result of the path analysis performed for log-transformed mean growth rate (Mean G, black box) on the control (a) and drought (b) plots. Variables used in the path model to predict growth are shown in blue boxes, arrows represent positive (green) and negative (red) correlations (solid unidirectional arrows). Grey numbers inside the circles indicate the R^2 value for each variable within the path model, and numbers next to each arrow indicate the standardised parameter coefficient estimates for each connection. Only arrows significant at $P < 0.05$ are shown. Statistical fits for the model are shown in Table 2.

three correlations across both the wet and dry seasons. By contrast, only R_{stem} and J_{max} were found to be correlated with both mean wet season and mean dry season growth rates on the drought plot. The traits DBH, SM_{p50} , Ψ_{md} and R_{stem} had significant correlations with wet season growth rates (Table 2; Fig. S2), whereas dry season growth rates were only found to be correlated with tree light score, DBH, V_{camx} , J_{max} , R_{stem} and N_{leaf} for the drought plot trees. Furthermore, during the wet season, the season with the highest growth rates, the strongest correlations with growth rates on the drought plot were found for traits related to plant hydraulic properties (Table 2; Fig. S2). By contrast, during the dry season, traits related to photosynthetic capacity and plant respiration had the strongest correlations with growth on the drought plot.

Using a path model analysis to determine how the measured traits, alongside DBH and tree light score interact and combine to determine log-transformed mean growth rates, we find the minimum significant model for each of the plots to be considerably different. On the control plot, when the 17 traits are tested within a single model, we find that only J_{max} and R_{stem} are retained in the path model as directly influencing growth rate (Fig. 5a). Combined, J_{max} and R_{stem} control 21% of the variation in mean annual growth rates; however, 26% of the variation in J_{max} is controlled directly by tree light score and N_{leaf} , with an indirect effect of DBH on N_{leaf} (Fig. 5a). Additionally, DBH explained 16% of the variation in R_{stem} . In contrast to this finding, on the drought plot SM_{p50} and R_{stem} explain 29% of the variance in mean annual growth rates, with no direct or indirect effect of tree light score, but with 18% of the variation in R_{stem} being explained by DBH (Fig. 5b). For both of these path models we obtained a very good fit between the model and the data, with the robust maximum likelihood scores < 10 and the P -value, describing statistical differences between the model and the data, being 0.98 and 0.94 for the control and drought plots, respectively (Table 3). We tested whether the minimum significance model for the control plot (Fig. 5a)

provides the same predictive power for the drought plot (Fig. S3). A direct connection between J_{max} and mean annual growth could not be found when considered in addition to the relationship between R_{stem} and mean annual growth (Fig. S3). Furthermore, the model presented in Fig. S3 had a greater AIC and root mean square error and a much poorer fit to the data (RMLS = 22.83; $P = 0.63$; Table 3).

Plant taxonomy was also found to be a poor predictor of mean growth rates. In a mixed effect model analysis, the inclusion of genus as a random effect on the intercept of models replicating the relationships of mean growth rates with traits in Fig. 5 did not significantly improve these models on either plot when the likelihood values were compared within an ANOVA analysis (P -values > 0.05 ; Table 4). Species nested within genus also provided no significant improvement to the model over using genus alone (data not shown). Phylogenetic least squared regression also demonstrated that the phylogenetic distance between genera was a poor predictor of mean growth rate. When the models for mean growth from the path analyses (Fig. 5) were entered into a phylogenetic generalised least squared regression, the lambda parameter remained equal to 0 (indicating all phylogenetic distances were adjusted to have no effect) and the kappa and delta parameters remained equal to 1, indicating no influence of phylogenetic distance on our growth models.

Discussion

We demonstrate that a shift in environmental conditions strongly influences the relationship between plant traits and growth rates within tropical trees, with a distinct shift from growth being controlled by traits relating to carbon production and use, to those related to embolism resistance following prolonged drought stress. We find that more complex traits that are likely to have stronger relationships with mechanistic plant functions are much better predictors of growth rates, with variables such as LMA and ρ being particularly poor at predicting growth rates.

Table 3 Results of the path analyses.

Variable predicted	Fig. 3		Fig. 4
	Control	Drought	Drought as control
Robust Maximum Likelihood score	8.60	4.09	22.83
P-value	0.98	0.94	0.63
Degrees of freedom	19	10	14
Root mean square error	0.00	0.00	0.09

The table gives the Maximum Likelihood statistic, the significance value for how different the model is from the data, the degrees of freedom in each path model and the root mean squared error of each model.

Table 4 Results from the mixed-effect models which were used to investigate the relationships between the mean growth rates, maximum wet season (Jan–Mar) growth rates, and minimum dry season (Jul–Sept) growth rates as functions of the relevant fixed effects from the path models.

Fig.	Dependent variable	Fixed effects	Random effects	Marginal R^2	Conditional R^2	P
5(a)	Control Mean G	J_{max} R_{stem}	Genus	0.20	0.20	0.99
5(b)	Drought Mean G	R_{stem} SM_{p50}	Genus	0.36	0.48	0.14

For each case, the model was run with and without genus as a random effect influencing the intercept of the model. The marginal R^2 (excluding the random effect of genus) and conditional R^2 (including the random effect of genus) values are shown alongside the P-values, indicating whether a model including genus as a random effect was significantly better than a model without it.

The power of plant traits to predict growth

Overall, we find that when combined, plant traits can predict between 20–30% of the variation in mean growth rate (Fig. 5). The plant traits that are effective for these predictions are, however, often those which are less commonly measured, including metrics relating to plant metabolism (photosynthesis and respiration) and to plant hydraulic status (Fig. 5, Table 2). These traits are more complex to measure than, for example, common traits like LMA or ρ . However, we demonstrate that these more complex traits are substantially more useful for predicting growth. Furthermore, many of these more complex traits are increasingly being incorporated into vegetation models (Christoffersen *et al.*, 2016; Xu *et al.*, 2016; Venturas *et al.*, 2018; Eller *et al.*, 2018b; Kennedy *et al.*, 2019), increasing the value of investing effort into building new trait databases which include structural, metabolic and hydraulic plant traits (Mencuccini *et al.*, 2019). This is of particular importance within tropical ecosystems, where the challenge of collecting such data is substantially greater than in lower diversity settings.

There has been considerable uncertainty concerning the ability of plant traits to explain demographic rates in forests (Falster *et al.*, 2018; J. Yang *et al.*, 2018), particularly within diverse tropical forests (Paine *et al.*, 2015; Liu *et al.*, 2016). We find that

traits commonly associated with the LES and WES such as leaf nutrient concentrations and LMA and ρ are not able to explain common metrics of plant growth (Table 2, Figs 5, S4). This may reflect these traits not being relevant outside of the LES (Moles, 2018) or only being relevant to growth at the initial stages of ontogeny (seedling to sapling), which were not studied here (Falster *et al.*, 2018). More surprisingly, we find no relationships between ρ and growth rate (Table 2; Fig. S4).

It has been previously hypothesised that ρ constitutes a major control on growth rates (Chave *et al.*, 2009; Falster *et al.*, 2018; Phillips *et al.*, 2019) and on the growth–mortality trade-off in trees (Wright *et al.*, 2010; Ruger *et al.*, 2018). However, almost all the studies that demonstrate this in tropical forests use species averaged measures of wood density, which can generate fundamental problems with predicting trait–growth relationships (Y. Yang *et al.*, 2018), in part through ignoring the large within-species variation in wood density (Plourde *et al.*, 2015; Lehnebach *et al.*, 2019; Momo *et al.*, 2020). We argue that many of the trade-offs which may exist within the WES justifying a link between ρ and growth may break down at local scales when individual tree-by-tree data are used (e.g. Poorter *et al.*, 2018), as has also been shown to occur in relation to traits in the LES (Messier *et al.*, 2017; Anderegg *et al.*, 2018). This is likely related to the fact that regional analyses use species-averaged values and are only capable of evaluating potential trait relationships, whereas local analysis at the scale of individuals can evaluate realised trait relationships, accounting for the impact of environmental variability on individual performance (Poorter *et al.*, 2018). The most common species in mature tropical forests are arguably the most relevant to study to understand how these forests may respond to future environmental change. However, collectively these trees often span a relatively narrow wood density gradient. Our study taxa, which spanned many of the hyper-dominant species found across Amazonia (ter Steege *et al.*, 2013), had a mean and standard deviation for ρ of $0.66 \pm 0.10 \text{ g cm}^{-3}$ and $0.72 \pm 0.09 \text{ g cm}^{-3}$ when measured directly or derived from estimates in the global wood density database, respectively (Zanne *et al.*, 2009). Furthermore, close-to-zero correlations between growth rates and ρ on an individual basis may be being caused by both high intraspecific and within-tree variation in ρ (Table 2; Fig. S5; Plourde *et al.*, 2015; Lehnebach *et al.*, 2019; Momo *et al.*, 2020), alongside substantial variations in growth rates and their responses to environmental variables between trees of different sizes (Rowland *et al.*, 2015a). We note, however, that determining which measure of wood density to use to represent the whole-tree average is complex (Lehnebach *et al.*, 2019; Momo *et al.*, 2020) and such correlations may become more accurate at the stand scale if such an estimate could be accurately derived. In the absence of this, at local scales ρ may not always be a viable predictor of growth.

Within our study the majority of the variation in mean annual growth rates could not be explained by the variations in the traits we measured. This may be because other unmeasured factors, such as competition with other trees (Rozendaal *et al.*, 2020), play a significant role. It may also be related to other key limitations of our analysis, for example, the need to average growth over multiple years, during which some of our study trees may

have undergone a shift in light environment or trait values. This may be one of the drivers behind the reduced correlation between light scores and plant traits and growth in the drought plot path models. However, R_{stem} did explain a significant portion of its explained variance in growth (Fig 3; Table 2). A direct interpretation of the functional significance of growth– R_{stem} relationships is however, complex, given the uncertainty in what R_{stem} may be representing within the plant (Saveyn *et al.*, 2008; Teskey *et al.*, 2008; Aubrey & Teskey, 2009). A previous analysis has shown that a large amount of the R_{stem} flux in the trees on both plots remains uncorrelated with growth and is more likely to represent maintenance respiration, rather than growth respiration (Rowland *et al.*, 2018). This may be consistent with the greater correlations with R_{stem} in the drought (Table 2), relative to the control plot, where maintenance respiration rates are estimated to be significantly higher (Rowland *et al.*, 2018).

Shifting controls on growth with climate change

We observe major changes between the traits which control mean annual growth and wet season to dry season growth rates in the control trees relative to the drought trees (Figs 3, S2; Table 2). Amongst the control trees, a consistent relationship with tree light conditions suggests growth in this forest may be strongly light-limited. Mean growth rates and particularly wet season growth rates were, however, elevated amongst our drought stressed trees. It is possible this is driven by prior drought-induced mortality of large trees driving both increasing light availability (Rowland *et al.*, 2015a; Fig. 2) and increasing availability of water during the wet season through reducing belowground competition. These elevated growth rates in the drought plot showed consistent and significant relationships with plant hydraulic traits (Table 2; Fig. 3), relationships which were absent from the control trees. Critically, the plant traits that are important in controlling growth, P_{50} and SM_{P50} are key metrics of plant resistance to embolism and exposure to hydraulic risk. These results suggest that growth rates are lower in trees with a greater resistance to embolism and greater hydraulic safety margins, consistent with the hypothesis that the greater hydraulic risks sustained by some tropical tree species can allow greater growth rates during prolonged drought stress at the cost of increased losses of conductivity (e.g. Eller *et al.*, 2018a). The emergence of a dominant hydraulic trade-off axis on the drought plot compared to a carbon production-allocation axis on the control plot may suggest a shift in which species may successfully compete in the long-term under conditions characterised by greater hydraulic stress and greater light availability.

Our data also support a strong shift in the seasonal controls on growth rates from the dry to wet season in the drought stressed trees, which is absent from the control trees. Within the dry season, growth rates were more strongly related to maximum photosynthetic capacities, DBH and plant respiration, whereas in the wet season plant hydraulic traits, stem and leaf respiration rates, tree size and light condition all had significant correlations with growth rates (Table 2). This suggests that drought not only shifts the controls on mean growth rates relative to the control plot, it

also drives considerable changes in what limits dry season and wet season growth rates. We note that due to the number of tests performed (114, Table 2) it is possible that some of our significant trait correlations are false positives.

The role of taxonomy in explaining growth

Our results indicate no strong link between taxonomy and growth. Instead, they suggest that DBH and/or tree light availability were better direct or indirect predictors of growth, particularly within the control plot (Table 2; Fig. 3). On the drought plot however, there was no influence of light availability on growth in the path model or in the bivariate correlations; it was found to be correlated only with wet season growth rates. This may reflect either the overall increase in light availability though the canopy, as a consequence of prior drought-induced mortality, or the relevance of traits that vary more with tree size than light in the growth of the drought stressed trees.

In summary, we demonstrate that the traits which control growth rates within a common group of tree species change when trees are exposed to a long-term (decadal) change in climate. Principally, we demonstrate a shift from growth being controlled by traits solely related to carbon cycling (assimilation and respiration) in well-watered trees to traits relating to a tree's capacity to take hydraulic risks under drought conditions. Critically, we find that commonly measured traits such as leaf mass per area (LMA) and woody tissue density (ρ) cannot predict growth rates in a tropical forest. However, we note that despite demonstrating the significant shift to an embolism-resistance to growth trade-off under drought conditions, our study highlights the fact that considerable uncertainty still remains concerning how plant function controls growth and across what time-scales this can change.





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Author contributions

LR collected and compiled the data alongside PRLB, ALG, IC, PBC, LVF, SSV, AARO, JASJ and ACLdC. LR designed the study with MM, ACLsC, PM, TD and RO. LR and MM performed the statistical analysis and wrote the paper; all other authors substantially contributed to revisions.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 The data used for this document.

Fig. S1 Linear relationships for all trait values with mean (a), wet season (b) and dry season (c) growth for the control and the droughted trees.

Fig. S2 Hydraulic vulnerability curves for sample trees.

Fig. S3 Path analysis model evaluating the application of the best-fit model from the control plot to the TFE data.

Fig. S4 Relationships between leaf mass per area and wood density with mean annual growth rates for the control and droughted trees.

Fig. S5 Box plots of wood density and mean growth rate separated by plot and genus.

Methods S1 Additional methods information.

Table S1 Matrix of all trait correlation coefficients with significance values.

Table S2 Genus, species and diameter of trees sampled in the study.

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