ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

The sensitivity of wood production to seasonal and interannual variations in climate in a lowland Amazonian rainforest

Lucy Rowland · Y. Malhi · J. E. Silva-Espejo ·
F. Farfán-Amézquita · K. Halladay · C. E. Doughty ·
P. Meir · O. L. Phillips

Abstract Understanding climatic controls on tropical forest productivity is key to developing more reliable models for predicting how tropical biomes may respond to climate change. Currently there is no consensus on which factors control seasonal changes in tropical forest tree growth. This study reports the first comprehensive plot-level description of the seasonality of growth in a Peruvian tropical forest. We test whether seasonal and interannual variations in climate are correlated with changes in biomass increment, and whether such relationships differ among trees with different functional traits. We found that biomass increments, measured every 3 months on the two plots, were reduced by between 40 and 55 % in the peak dry season (July–September) relative to peak wet season (January–March). The seasonal patterns of biomass accumulation are significantly ($p < 0.01$) associated with seasonal patterns of rainfall and soil water content; however, this may reflect a synchrony of seasonal cycles rather than direct physiological controls on tree growth rates. The strength of the growth seasonality response among trees is significantly correlated to functional traits: consistent with a hypothesised trade-off between maximum potential growth rate and hydraulic safety, tall and fast-growing trees with broad stems had the most strongly seasonal biomass accumulation, suggesting that they are more productive in the wet season, but more vulnerable to water limitation in the dry season.

Keywords Tropical tree growth · Temperature sensitivity · Soil water availability · Functional traits · Amazon rainforest · Seasonality

L. Rowland (✉) · P. Meir
School of Geosciences, The University of Edinburgh,
Edinburgh, UK
e-mail: lucy.rowland@ed.ac.uk

Y. Malhi · K. Halladay · C. E. Doughty
School of Geography and the Environment,
The University of Oxford, Oxford, UK

J. E. Silva-Espejo · F. Farfán-Amézquita
Universidad San Antonio Abad, Cusco, Peru

P. Meir
Australian National University, Canberra, ACT 0200, Australia

O. L. Phillips
School of Geography, The University of Leeds, Leeds, UK

Introduction

Tropical rainforests have the highest gross primary productivity in the world (Beer et al. 2010), yet the patterns and controls on this productivity remain quite poorly understood. Studying seasonal changes in tropical forest function has become increasingly important in the context of developing vegetation models which simulate the correct ecological responses (Kim et al. 2012). Similarly, understanding seasonal changes in forest function is necessary to interpret the seasonal changes in productivity measured using eddy covariance data (Carswell et al. 2002; Hutyra et al. 2007; Bonal et al. 2008; Iida et al. 2012). Temporal studies of the seasonal variation of stem biomass increment may therefore be particularly valuable to understanding the climate sensitivity and possible shifts in the productivity of these ecosystems.

Several studies have demonstrated that seasonal and interannual tropical stem growth rates respond positively to water supply (Baker et al. 2003a; Brienen and Zuidema 2005; Clark et al. 2010; da Costa et al. 2010; Chaturvedi

et al. 2011; Wagner et al. 2012). However, others have found that nighttime air temperatures are more strongly related to tropical tree growth rates than available water (Clark et al. 2003; Feeley et al. 2007). Currently no study has sampled the whole tree community over a sufficiently long period to capture multiple dry seasons of different intensity. The only long-term study (5 years or more) of seasonal stem growth in tropical trees has been made in Costa Rica (Clark and Clark 1994; Clark et al. 2010), in a forest with a wet and relatively aseasonal climate. Knowledge of the seasonal patterns of stem growth in the western half of Amazonia is limited to dendrochronology studies on a limited selection of species (Brienen and Zuidema 2005). This limitation creates a huge gap in understanding the rhythm of the world's largest tropical forest, especially given the documented strong differences in forest floristics, structure, and function across Amazonia (Baker et al. 2004; ter Steege et al. 2006; Quesada et al. 2012). Moreover, most of the ~7 million km^2 of remaining humid forests in the Neotropics are seasonal, much of this on soils derived from Andean sediments (Hoorn et al. 2010), yet the current generation of dynamic global vegetation models are unable to simulate with sufficient accuracy the growth and mortality of these forests (Delbart et al. 2010).

Tree functional traits and growth strategies are important to consider when modelling the response of tree biomass increment to seasonal variations in climate (Poorter et al. 2010; Fyllas et al. 2012). Trait selection is often associated with a growth-mortality trade-off (Poorter et al. 2010; Wright et al. 2010; Fan et al. 2012). Investment in high wood density allows trees to create durable structures and to withstand environmental stress (Chave et al. 2009; Poorter et al. 2010; Wright et al. 2010; Iida et al. 2012). There is a strong functional trade-off between early successional species—low wood density, short-lived, shade-intolerant trees which invest in rapid growth to prevent mortality from shading—and late successional (climax) species, which tend to be shade tolerant, slower growing trees and which allocate resources to reducing mortality risks, whilst limiting investment in growth (Richards 1996; Baker et al. 2003b; Muller-Landau 2004).

This trade-off between fast-growing low wood density trees and slow-growing, high wood density trees has been associated with hydraulic architecture (Hacke et al. 2006; Sperry et al. 2008; Poorter et al. 2010). In tropical species wood density is negatively, and tree height and tree diameter positively related to vessel diameter and hydraulic conductivity (Bucci et al. 2004; McCulloh et al. 2010; Zach et al. 2010; McCulloh et al. 2011, 2012). The small, densely packed vessels of high wood density trees make them resistant to drought-induced embolism, but less efficient at transporting and storing water in the stem (Hacke et al. 2006; Pratt et al. 2007; Meinzer et al. 2009;

McCulloh et al. 2012). In contrast, low wood density species, which require greater hydraulic efficiency to support rapid growth, tend to have fewer, larger vessels. These trees sacrifice hydraulic safety and are at greater risk of embolism, yet they have a greater capacitance to buffer themselves against diurnal changes in xylem tension (Hacke et al. 2006; Pratt et al. 2007; Meinzer et al. 2009; Fan et al. 2012; McCulloh et al. 2012). However, wood density may reflect variation in wall thickness, lumen size as well as vessel packing density and therefore wood density may not always clearly correlate with hydraulic properties. For example, Meinzer et al. (2008) found no significant relationship between wood densities and stem conductivity in tropical trees in Panama, and a study of tropical savannah trees has suggested that leaf traits provide a better indicator than stem traits to adaptation to drought stress (Hao et al. 2008).

Here we analyse quarterly growth data from more than 5 years from research plots in western Amazonia, the longest such time series [covering all trees ≥10 cm diameter at breast height (DBH) in a plot] from any seasonal tropical forest. Specifically we report patterns of tree biomass increment from October 2005 to January 2011, in two 1-ha permanent forest plots situated on contrasting soils in southern Peru. The aim of this study was to explore how tropical tree growth is affected by seasonal changes in water availability. We test the following hypotheses:

- Seasonal variation in woody biomass increment in this forest is correlated with seasonal variations in water availability.
- Interannual variability in seasonal patterns of rainfall and soil water content (SWC) is related to the rate of woody biomass accumulation.
- Trees with greater growth rates, diameter and height, and lower wood density have greater seasonal variability in woody biomass accumulation than trees with high wood density.

Materials and methods

Site

The study was conducted on two long-term 1-ha plots located ~3 km apart at the Tambopata Biological Reserve, in Madre de Dios region, Peru. The two plots [TAM05 (12°49′49.04″S, 69°16′13.92″W) and TAM06 (12°49′49.04″S, 69°16′13.92″W)] are permanent sample plots of the RAINFOR network and were established in 1983 and monitored according to frequently used protocols (http://www.geog.leeds.ac.uk/projects/rainfor/). Together the plots span a large range of the edaphic variation in

Table 1 Summary of plot, climate, soils and leaf data for Tambopata plots

	TAM05	TAM06
Biomass[a] 2011 (Mg ha^{-1})	262.3	298.2
Stem count	563	699
Rainfall[b] (mm year^{-1})	2,417	2,417
MAT[b] (°C)	25.2	25.2
Soil type	Haplic Cambisol (Alumic, Hyperdystric, Clayic)	Haplic Alisol (Hyperdystric, Siltic)
Soil sand[c] (%)	39.76	2.43
Soil clay[c] (%)	43.53	45.66
Soil silt[c] (%)	16.71	51.91
Soil N[c] (%)	0.16	0.17

[a] Plot-level biomass values are calculated from 2011 census data downloaded from forestplots.net (Lopez-Gonzalez et al. 2011) using biomass equations from Feldpausch et al. (2011) and wood density from the global wood density database (Chave et al. 2009; Zanne et al. 2009)

[b] Mean annual rainfall and mean annual temperature (*MAT*) are average values from 1960 to 1998 used in Malhi et al. (2004)

[c] Soil data are from Quesada et al. (2010)

south-west Amazonia (Quesada et al. 2010). All trees ≥10 cm diameter (at 1.3 m or above the buttress) were tagged and identified to species level. Our site has a mean precipitation (2,417 mm year^{-1}; Malhi et al. 2004) close to the annual average for the Amazon basin (2,138 mm year^{-1}; Galbraith et al. 2010) and a dry season length (4–5 months; Malhi et al., in press) also close to the average for a majority of the Amazon (Good et al. 2011). A summary of a basic plot, climate and soil data is shown in Table 1.

TAM05 is situated on poorly drained relatively infertile Haplic Cambisol soil (Alumic, Hyperdystric, Clayic). In contrast TAM06 is situated on a more fertile Haplic Alisol (Hyperdystric, Siltic) near the La Torre river. The plots have different environment and vegetation; TAM05 is located on an old Pleistocene terrace with lower fertility, whereas TAM06 is located on a Holocene alluvial terrace with relatively high fertility (Anderson et al. 2009). Average wood density was higher for TAM05 (0.61 ± 0.01 g cm^{-3}) than TAM06 (0.49 ± 0.01 g cm^{-3}, where ± indicates SEM). In TAM05 only 3.7 % (18) of trees were arborescent palms trees; in contrast on TAM06 30.1 % (118) of stems were palms. As palms have low wood density and generally do not have large diameter stems they accounted for proportionally less biomass −1.5 % of the total biomass for TAM05, and 11.6 % for TAM06. These edaphic and structural differences could have significant effects on the seasonal patterns in biomass accumulation and so data for the two plots were analysed separately. A detailed description

of the soils, climate and carbon cycle of these plots is given in Malhi et al. (in press).

Meteorological data

Solar radiation, air temperature, relative humidity and precipitation time series were collected from an automatic weather station (AWS) in a clearing near TAM06 (12.84°S, 69.29°W). The original data have been recorded at 30-min resolution since March 2005. These data were quality controlled to remove errors and unrealistic outliers, and then averaged into monthly values. Monthly mean values were discarded if >10 % of the 30-min data for a month were missing; these monthly means were then gap filled as follows: solar radiation was gap filled using mean monthly values from the same months in the other years. Mean daily temperature, which includes daytime and nighttime values, was gap filled using daily values from a nearby SENAMHI (Peruvian Meteorological Service) station at Puerto Maldonado (12.58°S, 69.20°W). Where data were available from the field site and from SENHAMHI, values from the SENAMHI station were regressed against daily values from the field-site AWS to adjust for the differences between the stations. The adjusted values from SENAMHI were used to gap fill the temperature data. Remaining gaps in temperature data were filled with the average of months from other years or, for nighttime data, by subtracting the mean nighttime and daytime temperature difference for months in other years from the mean daytime average.

Relative humidity data were rarely available from the AWS and so the more complete time series from the SENAMHI station was used. The precipitation time series was gap filled using values from the SENAMHI station at 0700 and 1900 hours (local time) which were aggregated to produce monthly estimates. If fewer than 90 % of the maximum possible daily values were available, the month was considered to be missing. Where these data were missing, monthly values from the relevant pixel of the Tropical Rainfall Measuring Mission 3B43 product were used.

The forest water deficit (FWD) is a simplified measure of the water stress in tropical forests and was calculated using the methodology described by Aragão et al. (2007). It is calculated as the difference between rainfall and estimated evapotranspiration, and is cumulated over a single year assuming evapotranspiration from a forest canopy in the Amazon is 100 mm per month, as has been found to be approximately correct from studies using empirical measurements (Fisher et al. 2009). Methodology for SWC (0–30 cm depth) data collection is reported elsewhere (Malhi et al., in press). Finally, monthly meteorological, FWD and SWC data were averaged to quarterly means to match the period of dendrometer increments.

Dendrometer measurements

Since 2005, both plots have had continuous and intensive monitoring of their carbon cycle, according to the Global Ecosystems Monitoring (GEM) protocol (gem.tropicalforests.ox.ac.uk). Here we focus only on the dendrometer data from April 2005 to January 2011. Dendrometers were installed and measured at 1.3 m height on all trees $\geq$10 cm DBH, unless the stem of the tree was buttressed, in which case the dendrometer was installed above the buttresses. Immediately prior to the installation of the dendrometers the diameter of all trees was measured using a diameter tape. From April 2005 stem increments were measured from the dendrometers every 3 months at the start of January, April, July and October. During the first 3–6 months after installation stem increments can be underestimated as dendrometers go through an adjustment period (Keeland and Sharitz 1993; da Silva et al. 2002). Therefore the first two increment periods (6 months; April–June 2005 and July–September 2005) were excluded from our analysis. From October 2005 to January 2011, we conducted 23 quarterly censuses of the dendrometers.

Diameter changes measured by dendrometers were converted to biomass estimates using a tropical moist forest biomass allometric equation, which uses tree height, tree diameter and wood density (Chave et al. 2005). Tree height was measured using a laser range-finder for all trees $\geq$10 cm, on both plots, once in 2005. However, to account for the effect of changes in height over time in our biomass calculations tree height was calculated from stem diameter each quarter, for each stem, using a western Amazon region-specific allometric model (Feldpausch et al. 2011). Wood density was estimated based on the Global Wood Density Database (Zanne et al. 2009). To distinguish growth patterns from patterns of tree mortality and recruitment, only trees which were alive and at least 10 cm diameter from April 2005 to January 2011 were included in our growth calculations. In our analysis we use data from 895 trees (474 from TAM05 and 421 from TAM06); palm trees and lianas were excluded from our analysis.

Correcting errors

Unusually large positive or negative changes in growth increment are characteristic of errors which occurred during dendrometer measurement. Removing such errors is important to eliminate bias in plot-level biomass increments, which would occur if there is a large overestimation (positive error) or underestimation (negative error) in growth increment from a dendrometer. For each tree, identified errors were corrected by replacing them with the mean increment from the same quarterly period in the other available years. In total 394 increments were corrected,

<1.5 % of the measured tree increment data points used in this study. Errors were identified as follows:

To detect errors associated with over-estimates from dendrometer bands, increment data were plotted if the maximum increment was greater than 0.1 cm and the difference between the maximum and the mean increment was >3 SDs. Plotted increment data were then visually assessed to confirm that the detected error was real and not a result of a repeated growth pattern. If the increment was identified as an error, it was corrected. This screening process was repeated three times to catch repeat errors in the data and to re-check previously uncorrected data.

To detect errors associated with underestimates from dendrometer band increments the same screening process as above was performed; however, trees' increment data were plotted if the minimum increment was <−0.1 cm and the difference between the minimum and mean increment >3 SDs from the mean negative increment for a specified tree. As the above plotted increment data were then visually assessed and the minimum increment was identified as an error, it was corrected. As above, this screening process was repeated three times to catch repeat errors in the data and to re-check previously uncorrected data.

Following the removal of these errors from the data, a factor to compensate for water-induced changes in stem diameter was subtracted from all measurements. During dry periods, when relative humidity is lower, desiccation of tree bark and changes in tree water storage in tropical trees can cause significant reductions in diameter that are unrelated to dry biomass (Baker et al. 2003b; Stahl et al. 2010). To account for gain and reduction of incremental growth associated with changes in stem water retention, bole shrinkage was estimated for each quarterly period from the mean negative growth pattern in trees which showed no overall growth (diameter growth <0 mm, $n = 192$). To account for the impact of shrinkage on our estimates, this shrinkage term was applied to all trees. If the degree of seasonal shrinkage is correlated with growth rates (see below), this correction would underestimate the correction required for faster growing trees.

Statistical analysis

All statistical analyses were carried out in the statistical package R (R 2.14.2, R-project software, http://www.r-project.org R 2.14.2) and all errors are reported as the SEM. Where propagation of errors was necessary this was done by quadrature (Aragão et al. 2009; Malhi et al. 2009). Single linear correlations were assessed between all meteorological and SWC data and mean quarterly biomass increment for each plot. A generalised linear model (GLM) was used to model mean quarterly biomass on each plot using all the meteorological variables available for the full period (i.e. excluding SWC), and a categorical variable

which described season. Forward and backward stepwise regression was then performed separately on the GLMs to assess which variables best described the seasonality of the biomass increment of dicots on each plot. A separate GLM for each plot was created to assess the effects of using the mean quarterly biomass for 2007–2011, the period during which SWC data were available. The goodness of fit of GLM using different combinations of variables was assessed using Akaike's information criteria (AIC).

To explore possible causal relationships further, we also examined interannual anomalies in the seasonal growth rates, to assess how deviations from a mean state of a variable impacted deviation from mean patterns of tree biomass increment. Anomalies were estimated for each of the five meteorological variables (FWD, precipitation, air temperature, short-wave radiation, relative humidity), the SWC from each plot, and for the total biomass increments for TAM05 and TAM06. We defined an anomaly as the value for each quarterly interval, minus the mean value for that period over all years (2005–2011).

To assess the seasonality of the relative biomass accumulation per tree we employed a normalised seasonality index (SI). The SI was created for each complete year of measurements (four measurements per year) for all trees. SI was calculated as

$$SI = \frac{BI_{dry} - BI_{wet}}{BI_{max}}$$

where BI_{dry} and BI_{wet} are the biomass increments in peak dry season (July–September), and peak wet season (January–March) of a given year, for a given tree and BI_{max} is the maximum seasonal growth rate recorded for that tree.

To assess how SI is related to functional traits, mean log wood density, tree height, diameter and average growth rate per family were regressed against mean SI per family in linear and multiple linear models. Multiple linear models were thinned using both forward and backward stepwise regression. This analysis was done at the family level to allow for adequate replication per group; at the family level 46.3 % of families had more than ten individuals and only 24.1 % had fewer than three individuals, whereas at species level only 7.3 % of species had more than ten individuals and 66.9 % had fewer than three individuals, at the genus level 19.3 % of genera had more than ten individuals and 42.1 % had fewer than three individuals.

Results

Stem and biomass distributions

For TAM05 and TAM06, respectively 67.1 and 65.3 % of stems were between 10 and 20 cm in diameter (Fig. 1a).

However, the greatest mean biomass increments per tree was produced by trees >50 cm diameter, which contained 42.3 and 51.3 % of the respective biomass on TAM05 and TAM06 (Fig. 1b–c). The mean biomass increment of individual trees (dicots) over our study period was significantly positively correlated with stem diameter ($r^2 = 0.38$, $p < 0.001$). The unequal distribution of stem counts across size classes and biomass increment per tree tend to cancel out when total plot-level biomass increment is computed, which was much more evenly distributed across stem size classes (Fig. 1d).

Seasonal variations in meteorology

Mean monthly rainfall over the study period showed a consistent seasonal pattern, peaking in January at 375 ± 34 mm and falling to 28 ± 8 mm in August (Fig. 2a). Mean monthly temperature had no consistent seasonal pattern; the average mean monthly temperature was 24.6 ± 0.1 °C. Between 2007 and 2010 SWC (%) averaged 19.4 ± 1.3 % in TAM05 (the sandier site) and 32.6 ± 2.9 % in TAM06. The maximum difference in soil water was between the peak wet season (January–March) and the peak dry season (July–September) intervals (Fig. 2b); SWC varied by 45.1 ± 10.5 % in TAM05, and by 53.3 ± 14.6 % in TAM06.

Seasonal variations in biomass increment

Biomass increment was 39.0 ± 8.7 % and $55.7 \pm 9.8.3$ % lower, respectively, for TAM05 and TAM06 in the peak dry season quarter (July–September) than in the peak wet season (January–March; Fig. 2c). While the mean dry season biomass increment was similar between plots (Fig. 2c; 13.35 ± 0.72 kg C ha^{-1} day^{-1} on TAM05; 12.91 ± 1.04 kg C ha^{-1} day^{-1} TAM06; mean difference = 3.4 ± 9.0 %), during the peak wet season the stand-level biomass increment was 25.0 ± 9.7 % lower in TAM05 than in TAM06 (21.87 ± 2.26 kg C ha^{-1} day^{-1} on TAM05; $29.16. \pm 1.83$ kg C ha^{-1} day^{-1} TAM06). Strong seasonal patterns in the meteorological drivers, particularly precipitation and SWC, resulted in highly significant correlations between these variables and the quarterly biomass increment on the two plots (Fig. 3). The mean quarterly biomass increment of dicot trees in TAM06 was most strongly correlated with SWC and precipitation ($r^2 = 0.80$, $p < 0.001$, and $r^2 = 0.66$, $p < 0.001$, respectively; Fig. 3), while the mean quarterly dicot biomass increment in TAM05 was uncorrelated with SWC ($r^2 = 0.22$, $p = 0.09$), and more strongly correlated to precipitation ($r^2 = 0.44$, $p < 0.001$; Fig. 3) than other environmental variables. Mean dicot quarterly biomass increment was also significantly correlated with FWD
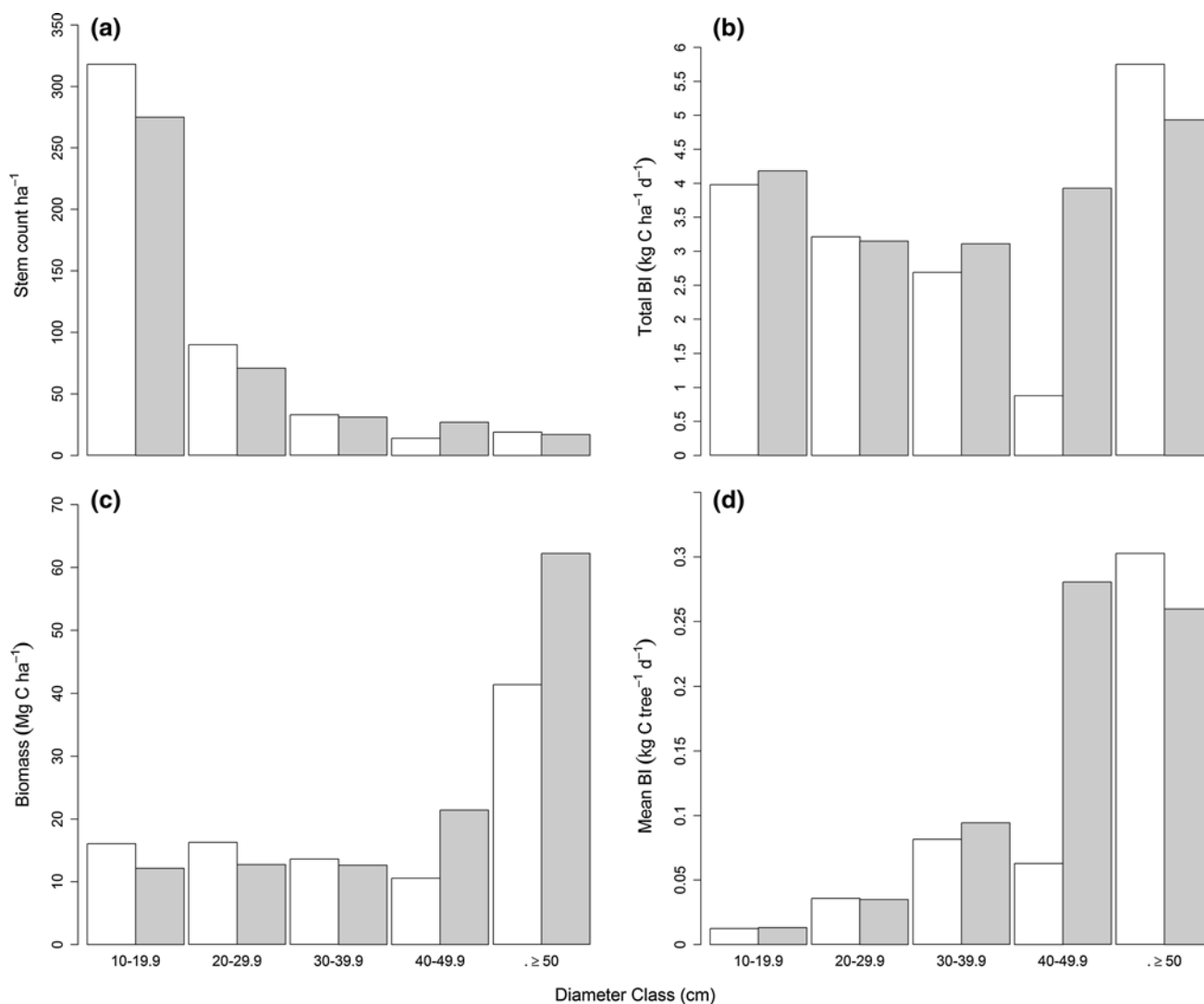
Fig. 1 **a** Stem counts (stems ha^{-1}), **b** total biomass increment (*BI*; kg C ha^{-1} day^{-1}), **c** total biomass (Mg C ha^{-1}), and **d** mean BI per tree (kg C tree^{-1} day^{-1}) for different wood diameter classes (*D*; cm) for TAM05 (*white bars*) and TAM06 (*grey bars*)

($r^2 = 0.26$, $p = 0.02$ on TAM05; $r^2 = 0.34$, $p < 0.01$ on TAM06), and mean nighttime temperature on both plots ($r^2 = 0.20$, $p = 0.04$ on TAM05; $r^2 = 0.37$, $p < 0.01$ on TAM06), and for TAM06, also with mean daily temperature and relative humidity (Fig. 3). To model the mean quarterly biomass increment in each plot we performed forward and backward stepwise regression on two GLMs, which used all the meteorological variables available for the full period (i.e. excluding SWC), and a categorical variable which described season. Results showed that for both plots the models which best described patterns of biomass increment (lowest AIC), were those which only included the categorical variable which described season (TAM05, AIC = 142.62; TAM06, AIC = 140.69). For TAM05 a GLM using the seasonal categorical variable had lower AIC (100.40) than a model which included

both the categorical variable and SWC (AIC = 101.49). However, for TAM06 the GLM including both SWC and the seasonal categorical variable over the same period had a lower AIC (87.67) than using the seasonal categorical variable alone (AIC = 90.03).

We next consider growth rate anomalies. No significant correlations were found between biomass increment anomalies and meteorological anomalies on either plot (data not shown). This result supports the finding of the GLMs which suggest that, with the exception of SWC on TAM06, it is season rather than the variability of any meteorological variable between seasons of different years, which has the biggest influence on woody biomass increment. It is also noteworthy that interannual variations in growth do not correlate with interannual variation in any of the meteorological data.

Fig. 2 Monthly meteorological data. **a** Mean monthly precipitation (*PPT*, mm day^{-1}; *black bars*) and monthly mean short-wave radiation (*SWR*, W m^{-2}; *dashed grey line*). **b** Water deficit (*WD*, mm; *grey bars*) and volumetric soil water content (*SWC*) for TAM05 (*black dashed line*) and TAM06 (*%*; *grey dashed line*). **c** Mean quarterly biomass increment (Mg C ha^{-1} day^{-1}) for dicot trees on TAM05 (*solid black line*) and TAM06 (*dashed grey line*)
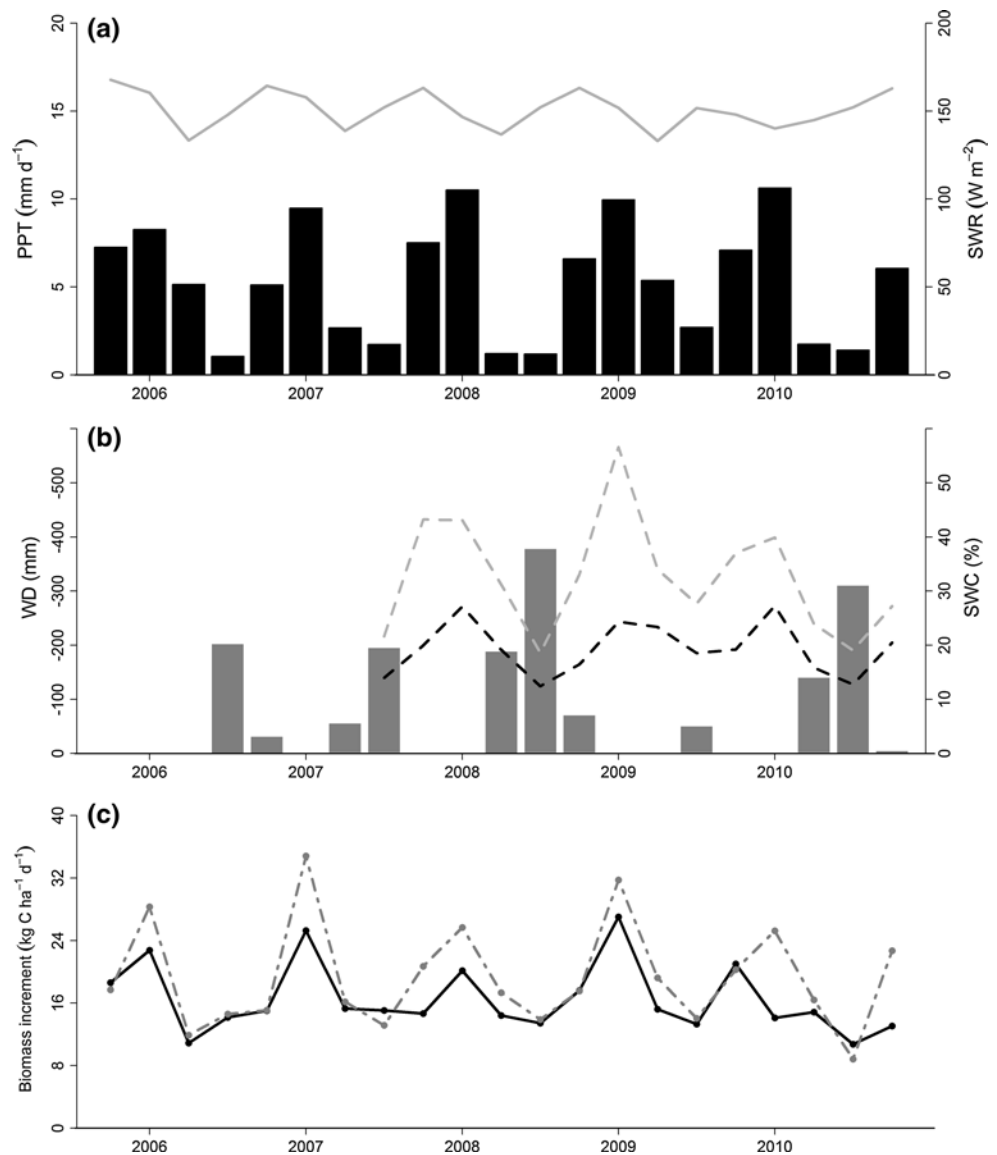

Seasonality Index and its relationship to tree structure and density

The mean SI of dicot tree growth was negative on both plots (TAM05 SI $= -0.05 \pm 0.02$, TAM06 SI $= -0.07 \pm 0.02$); as most trees grew less in the dry season. When trees were grouped into families, weak but significant correlations were found between the mean SI per family and mean log wood density ($r^2 = 0.09$, $p = 0.03$; Fig. 4a), mean log tree height ($r^2 = 0.16$, $p < 0.01$; Fig. 4b); and mean log tree diameter ($r^2 = 0.09$, $p = 0.03$; Fig. 4c). There was, however, a stronger significant correlation between mean log growth rate per family and mean SI ($r^2 = 0.24$, $p < 0.01$; Fig. 4d). When a multiple linear regression was performed between mean SI per family and mean log wood density (WD), mean log tree height (H), mean log diameter (D), and mean log biomass increment (BI) the combined

interaction of all of these terms significantly explained 53 % of the variance in SI [SI $=$ log(WD) $\times$ log(H) $\times$ log(D) $\times$ log(BI), $r^2 = 0.53$, $p < 0.01$]. A forward and backward stepwise regression on this multiple linear regression removed none of the variables in the above model. The number of trees in each family grouping on each plot is shown in Fig. 5.

Discussion

Over a period of more than 5 years, diameter increments from all trees ≥ 10 cm diameter growing on two western Amazon plots reveal very strong seasonality (Fig. 2c). The reduced growth rate on both plots was positively correlated with dry season reductions in precipitation and SWC (Fig. 3a, g). The period with the greatest stem growth (mid
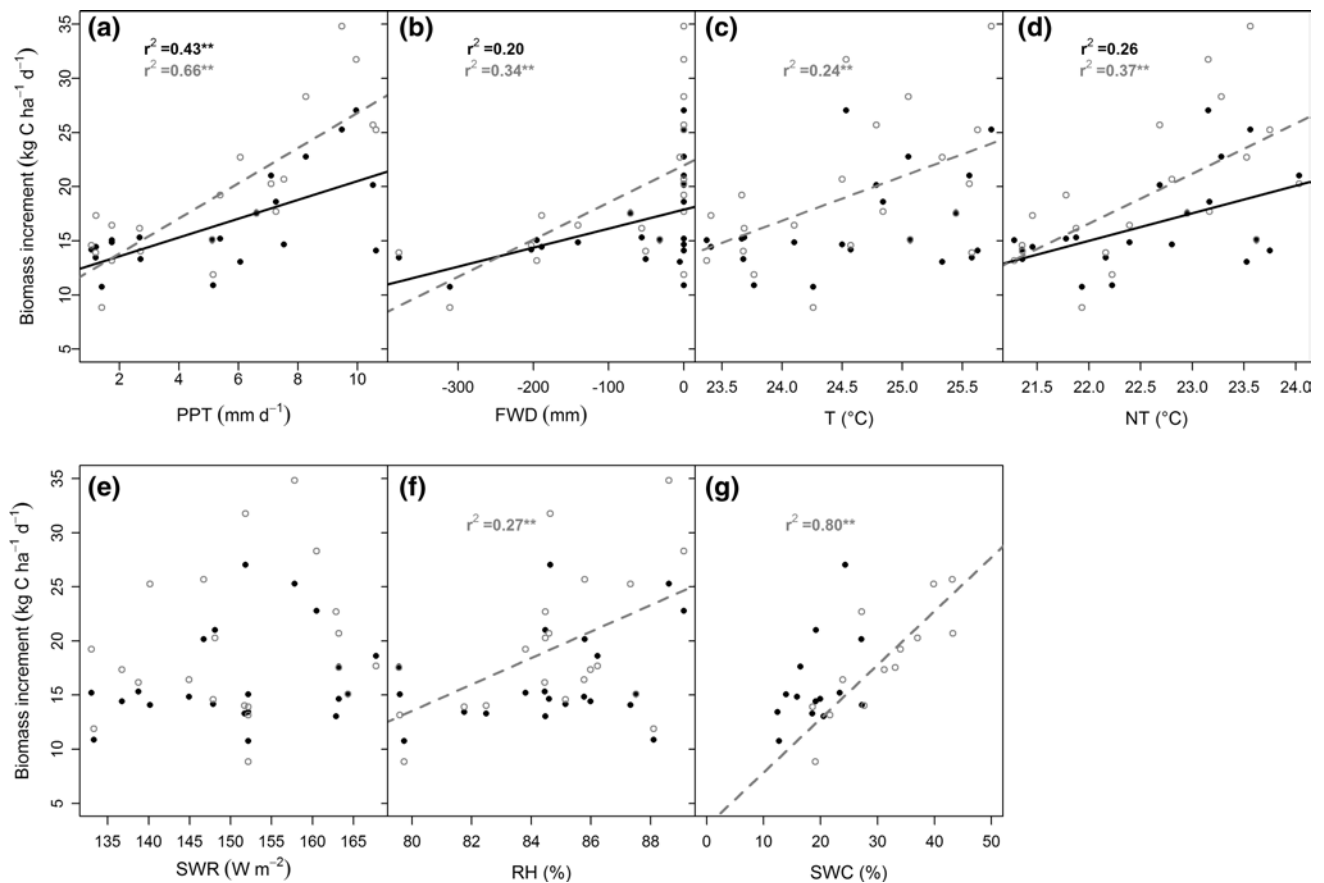
Fig. 3 a Correlation between the total biomass increment (Mg C ha^{-1} day^{-1}) per 3-month measurement period for TAM05 (*black filled circles*) and TAM06 (*grey open circles*) and the 3-month average of precipitation (PPT, mm day^{-1}), **b** forest water deficit (*FWD*, mm), **c** average air temperature (*T*, °C), **d** average nighttime temperature (*NT*, °C), **e** SWR (W m^{-2}), **f** relative humidity (*RH*, %), **g** SWC (%). Regression lines (*black* for TAM05 and *grey dotted* for TAM06) and r^2-values are shown if significant at <0.05. *******p* < 0.01. For other abbreviations, see Fig. 2

wet season) does not correspond to the period of greatest leaf production on both plots (the end of the dry season; Malhi et al., in press). Patterns of stem growth are therefore temporally coordinated with seasonal changes in precipitation, rather than seasonal patterns of leaf productivity.

Our study suggests that the strength of the positive effect of intra-annual variability in soil water availability on intra-annual variability in tree biomass increments could be related to functional adaptation to soil conditions. Consistent with other studies (Chaturvedi et al. 2011; Wagner et al. 2012), we found SWC is a very strong predictor of quarterly biomass increment for tropical trees, but only for TAM06 (Fig. 3a, g). However, we find stem biomass increment for TAM05 was significantly related to precipitation and FWD, but, in contrast to TAM06, had no relationship to SWC (Fig. 3). The average wood density of dicot trees, which in tropical trees has a positive relationship with vessel packing density and hydraulic safety (McCulloh et al. 2010; Zach et al. 2010; McCulloh et al. 2011, 2012), was slightly higher on TAM05 (0.62 ± 0.01 g cm^{-3}) than

TAM06 (0.58 ± 0.01 g cm^{-3}); TAM05 also had many more trees present in family groups with an average wood density >0.8 g cm^{-3}, which were not represented in TAM06 (Fig. 5). However, to accurately assess variations in wood density between the plots it is necessary to measure the wood density of each tree, rather than using wood density values from a database, as this would account for variations in wood density in response to environmental conditions. TAM05 had sandier soils and a lower annual mean SWC, we therefore speculate that more trees on this plot are adapted (or better adapted) to coping with reduced water availability than found at TAM06. This is supported by a low replication of species between TAM05 and TAM06; only 16.9 % of the 260 species analysed were found on both plots. This supports the findings of Engelbrecht et al. (2007), who suggest that drought sensitivity shapes species distributions in tropical forests.

However, as with growth seasonality in temperate forest ecosystems, it is possible that the seasonal patterns of growth are simply synchronised with the meteorological
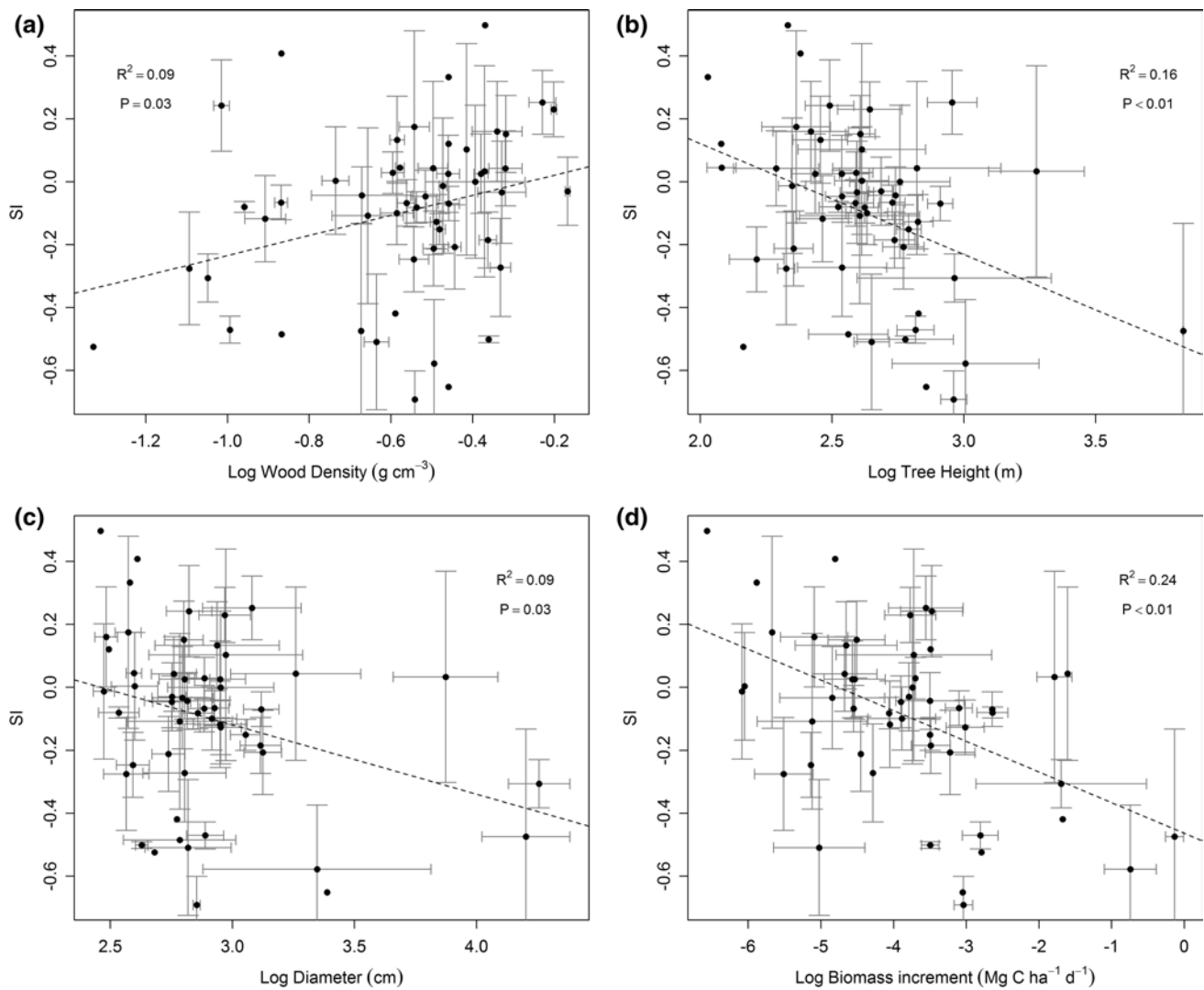
Fig. 4 Mean 2006–2010 seasonality index (*SI*) for dicots from both plots grouped by family and regressed against **a** mean log wood density (g cm^{-3}), **b** mean log tree height (m), **c** mean log wood diameter (m) and **d** mean log tree biomass increment (Mg C ha^{-1} day^{-1}). *Error bars* show SE. A negative SI indicates that trees grow less in peak dry season compared to peak wet season

seasonality, rather than being driven by it. We find that a categorical variable which described the quarterly seasons provided a better model of quarterly biomass increment than any single meteorological variable or a combination of these. Hence the correlations with seasonal factors may provide limited information about the longer-term response of forests to changes in environmental conditions. The analysis of anomalies across years, on the other hand, may provide evidence of some direct responses to environmental variability. Interestingly we failed to detect a relationship between the anomalies of quarterly biomass increment and the anomalies of any of the meteorological variables. This result suggests that year-to-year variations in precipitation, temperature, humidity, short wave radiation and SWC have little influence on year-to-year variations in growth,

over the 5-year period of this study. This supports dendrochronology studies in tropical forests which have found no relationship between annual ring width and annual climatic variables (Brienen and Zuidema 2005). Therefore we find little evidence in our analysis for the hypothesis that tropical forests experience reduced growth when temperatures are higher than average (Clark et al. 2003; Feeley et al. 2007); however, we acknowledge that our study only covers a period of 5 years and as such has relatively low sensitivity to interannual fluctuations.

Difference in biomass increment between the dry and wet season is related to wood density, stem diameter, height and mean biomass increment (Fig. 4). We show a significant positive relationship between mean SI per family group with mean logged wood density and significant
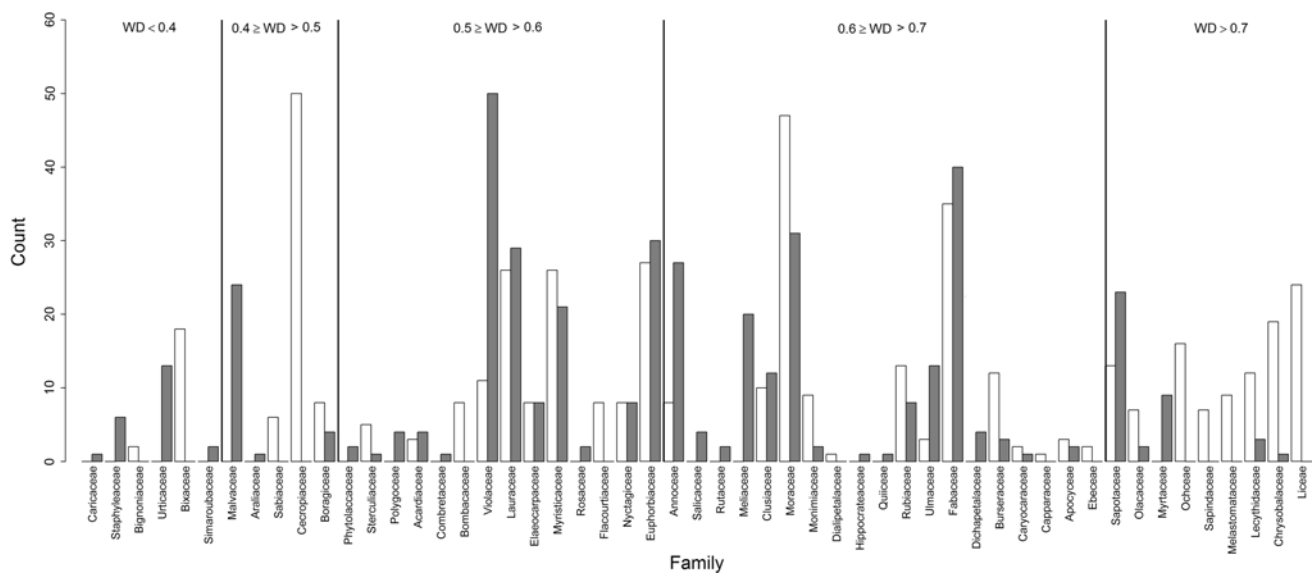
Fig. 5 Histogram of the number of trees in each family grouping on TAM05 (*white bars*) and TAM06 (*grey bars*). Families are ordered by wood density (*WD*, g cm^{-3}) from lowest to highest. *Vertical black lines* separate different categories of WD

negative relationships between mean SI per family and logged height and stem diameter and growth rate (Fig. 4). A multiple linear regression demonstrated that 54 % of the variability in average SI per family could be explained by the interaction of logged wood density, tree height, tree diameter and tree growth rates. These family-level results are in line with predictions from the theory of growth-mortality trade-offs. Fast-growing, low wood density trees tend to grow taller to avoid shading (King et al. 2005; Keeling and Phillips 2007), and have higher rates of photosynthesis and water demand. These trees therefore prioritise increased hydraulic conductivity through having larger vessels, but at the potential cost of being more prone to drought-induced embolism (Hacke et al. 2006; Pratt et al. 2007; Meinzer et al. 2009; McCulloh et al. 2012).

Taller, broader trees have a tendency to have larger diameter xylem vessels and lower vessel packing density (Hacke et al. 2006; Sperry et al. 2008; Zach et al. 2010; McCulloh et al. 2011; Fan et al. 2012). Taller trees in particular are at greater risk to cavitation because of their longer hydraulic path lengths (Poorter et al. 2010; Zach et al. 2010). Low wood density is also associated with lower vessel packing density and wider vessels in tropical trees (McCulloh et al. 2010; Zach et al. 2010; McCulloh et al. 2011). Therefore low, relative to high wood density trees have lower stomatal conductance during periods of drought to avoid embolism, and this restricts maximum photosynthetic capacity, and therefore growth rates (McCulloh et al. 2012). Our data were consistent with this interpretation as taller, faster-growing, lower wood density trees had greater growth rates in the wet relative to the dry season; this produced the

observed more negative SI (Fig. 4). Our findings are also consistent with observational and experimental drought studies in the Amazonia and elsewhere in the tropics, which report that taller trees with lower wood density tend to experience an elevated risk of mortality from restricted water availability (Nepstad et al. 2007; da Costa et al. 2010; Phillips et al. 2010).

The interaction of wood density, tree height and diameter, and average growth rate explained 54 % of the variance in the seasonal growth patterns of trees. The other 46 % of the variance remained unexplained by measured variables. Significant differences in growth rates between tropical forest species have previously been found in multiple studies (Clark and Clark 1992, 2001; Baker et al. 2003b; Dunisch et al. 2003; Baraloto et al. 2006; Chaturvedi et al. 2011; Newbery et al. 2011). It is therefore possible that species-specific growth adaptations in tropical trees may generate substantial variation in the observed relationships with functional attributes, such as wood density, diameter, height, and growth rate, and seasonality growth. The response of tropical trees to drier conditions has also been related to tree capacitance (McCulloh et al. 2011), leaf traits (Hao et al. 2008) and stomatal behaviour (ansiohydric versus isohydric; McDowell and Sevanto 2010). These factors may also explain some of the unexplained variance in the SI index between family groups.

In summary, at a site in the western Amazon we found that stand-level biomass accumulation decreased by ~40–55 % in the peak dry season relative to the peak wet season. The seasonal patterns of biomass accumulation were strongly associated with seasonal patterns of rainfall and

water supply, but such seasonal variation may reflect timing and synchrony of seasonal cycles rather than direct physiological controls on tree growth rates. Furthermore, we demonstrated significant differences between tree functional properties and the degree of seasonality of tree growth. This study is consistent with the notion that important growth-hydraulic limitation trade-offs exist among trees. We find fast-growing, low wood density, tall, and broad-stemmed trees experience greater reductions in dry season increment relative to wet season increment, suggesting that, although they have the capability for greater growth in wet season conditions, they are potentially at greater risk of hydraulic stress and consequent reduced growth as soil water availability drops. This group of trees are therefore more seasonal in their growth characteristics than slower growing, higher wood density trees. Our results suggest that the functional composition of tropical forests is an important determinant of annual patterns of biomass accumulation and that we might anticipate functionally driven shifts in species composition in response to changes in temperature and water.

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