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RESEARCH ARTICLE

Functional traits are more strongly correlated with biomass than diameter growth

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Abstract

1. The functional basis of tree growth is often evaluated based on trunk diameter even though diameter is only one dimension of growth that may not be an integrative measure of resource allocation.
2. We tested the hypothesis that growth—functional trait relationships are stronger when key sources of variation in tree growth are also accounted for, namely tree height and DBH, as well as size-related variation in wood density and seed production using data from 3881 trees of 24 species in a subtropical forest using ordinary least square regression and standard major axis regression.
3. Wood density varied with tree size for 14 of 24 species, generally increasing with size. For 18 of 24 species, the correlations of leaf mass per area and an index of photosynthetic investment (PI) with biomass growth was stronger than with diameter growth rate. Juveniles did not show stronger relationships than adults but biomass growth adding up with seed production showed stronger relationships with PI than biomass growth alone for three of eight species.
4. *Synthesis*. Thus, our study helps resolve a paradox of trait-based ecology, that is, weak growth—trait relationships, as stronger relationships emerged when accounting for more sources of intraspecific, among-tree variation in resource allocation.

KEYWORDS
allocation, Dinghushan Nature Reserve, leaf biomass, leaf mass per area, reproduction, specific leaf area, wood density

1 | INTRODUCTION

Tree growth is an important process that makes possible many ecosystem functions of forests, such as carbon sequestration through tree biomass accumulation. Functional traits, which are measurable phenotypic characters that are relevant for individual-level performance, are thought to mediate a tree's ability to acquire resources from the environment and reflect how trees allocate those resources for growth, survival and reproduction (Garnier et al., 2004). As such, the relationships between trait variation and these vital rates are expected to be strong (McGill et al., 2006). However, strong relationships are often not found, regardless of whether analyses were conducted at the individual or species level (Poorter et al., 2008; Wright et al., 2010; Paine et al., 2015; but see Visser et al., 2016; Yang et al., 2018).

One possible explanation for weak relationships between tree growth and functional traits is that the way functional trait variation is incorporated into analyses of growth—trait relationships does not capture their functional linkage with vital rates and how this linkage changes as trees age (summarized by Yang et al., 2018). For example, leaf mass per area (LMA) is a trait related to the leaf-level investment to photosynthetic tissue, and is often correlated with other traits related to photosynthesis, such as foliar nitrogen and chlorophyll concentrations (Reich et al., 1999; Wright et al., 2004). LMA is therefore expected to correlate strongly with tree growth rate (Lambers & Poorter, 1992), but weak correlations have usually been found (Paine et al., 2015; Poorter et al., 2008; Wright et al., 2010). Weak correlations may arise because LMA is also related to other functions besides photosynthesis, including defence of leaves, leaf lifespan and drought tolerance, that often intervene in the growth process and are also related to survival (Fine et al., 2006; Herms & Mattson, 1992). For example, even though lower LMA is usually associated with greater leaf-level photosynthetic capacity, which can promote faster growth, higher LMA may ultimately enable faster growth than lower LMA in some environments because the cost of higher herbivory on lower LMA leaves is greater than the lost opportunity cost of not making more photosynthetically efficient leaves. These functions affect variation of LMA and could act to decouple its relationship with growth (Onoda et al., 2017). There is also dramatic continuous variation in LMA as trees grow (Bin et al., 2022; Sendall & Reich, 2013), which might act to decouple trait—growth relationships estimated using species-level trait data that do not account for the continuous size-dependent trait variation. Moreover, tree growth is a function of whole-plant photosynthesis, and LMA is only one of several determinants of photosynthetic capacity (Enquist et al., 2007; Givnish, 1988). For example, greater photosynthetic capacity can also be achieved by increasing crown size or changing leaf display to increase light interception (Ackerly, 1996; Enquist et al., 2007; King et al., 2005; Poorter et al., 2008). In support of this, an estimate of the investment in leaf display that accounted for crown size and LMA correlated strongly with diameter growth rate of four tree species in a tropical forest (Yang et al., 2018).

Weak relationships of tree growth with functional traits may also owe to how tree growth itself is measured. Although Enquist et al. (2007) found biomass growth is predictable using a generalized trait-based model, growth in trunk diameter and the diameter-derived basal area have been standard measures in studies seeking to understand the functional basis of tree growth (King et al., 2005; Poorter et al., 2008; Wright et al., 2010; Visser et al., 2016; Yang et al., 2018; but see Enquist et al., 2007; Stephenson et al., 2014). Diameter, however, is only one dimension of above-ground tree growth. Other dimensions of growth, such as height and above-ground biomass growth, have less commonly been used, in part because these measurements are more time-consuming to make regularly, compared to trunk diameter (Larjavaara & Muller-Landau, 2013). Tree diameter growth also does not account for the fact that wood density can change with tree size (Larjavaara, 2010), which alters the amount of photosynthetic products required for growth of woody stems as the tree ages. Wood density is a key functional trait related to tree structural support, hydraulic conductance, exploitation of light and pathogen resistance (Chave et al., 2009; King et al., 2006; Larjavaara & Muller-Landau, 2010; Russo et al., 2010). Small trees face the needs to increase light interception and to avoid risks of pathogen infection and being damaged by falling debris (Larjavaara & Muller-Landau, 2010; Thomas, 1996a), whereas the need to withstand strong wind is greater for large trees (King et al., 2009; Putz et al., 1983; Thomas, 1996a). As trees grow, there may be a shift from lighter wood allowing faster height growth to denser wood providing greater structural support (Wiemann & Williamson, 1989). For trees of similar sizes in a managed forest, reduced wood density has also been found in those exposed to higher light environments, when thinned for management (Cao et al., 2008), suggesting that wood density can vary with changing environmental conditions that are encountered as trees grow (Bin et al., 2022). Accounting for continuous size-dependent changes in functional traits and for the key components of variation in above-ground growth of woody tissues, namely wood density, trunk diameter and tree height, at the individual level may produce stronger growth—trait relationships than using diameter-based estimates of tree growth or species-level trait variation.

In addition to growth, photosynthetic products are also allocated to survival, as well as reproduction for adults, causing allocation-based demographic trade-offs (Kohyama, 1993; Russo et al., 2021; Wright et al., 2005). Allocation to survival is challenging to measure, compared with allocation to growth and reproduction. Allocation to growth versus reproduction differs among species (Wheelwright & Logan, 2004), and among years for the same individual (Ichie et al., 2013; Kelly & Sork, 2002). However, by definition, juveniles do not face growth—reproduction trade-offs. For them, growth should therefore be more closely related to the amount of photosynthetic products, since juveniles only allocate to functions promoting growth or survival, likely reducing the possible sources of variation affecting the relationship between functional trait expression and growth rates, as allocation to reproduction is not occurring. Therefore, for juveniles, trait—growth relationships may be stronger than for adults. Conversely, for adults, estimates of allocation to growth plus reproduction should correlate more strongly with trait variation than either should individually. Additionally, growth rates and reproduction are both related to species' maximum size, with taller species growing faster but reproducing at larger sizes whereas shorter species show the reverse demographic characteristics (Aiba & Kohyama, 1996; King, 1990; Kohyama, 1993; Thomas, 1996a, 1996b). Thus, the allocation of resources to growth and reproduction among tree species may be associated with their maximum size in a way that smaller statured species (e.g. understorey trees, shrubs) allocate more to reproduction relative to size than larger statured species (Kohyama et al., 2003).

In this study, we investigated the hypothesis that, for functional traits related to whole-tree photosynthetic carbon production, there will be stronger growth—trait relationships when continuous size-dependent variation in these traits, multiple components of above-ground woody growth and seed production are accounted for. To test this hypothesis, we evaluated four predictions: (P1) wood density increases with tree size within species; (P2) compared with diameter growth, biomass growth accounting for individual-level variation in wood density and tree height has stronger relationships with LMA and an index of photosynthetic investment (PI), and these trait—growth relationships vary with species' maximum height; (P3) juveniles have stronger trait—growth relationships than adults, considering both diameter growth and biomass growth with respect to LMA and PI; and (P4) allocation to reproduction plus biomass growth should relate more strongly with LMA and PI than either growth rate or seed production does alone. We evaluated these predictions using an individual-level data set of wood density, leaf mass per area, crown size, trunk diameter at breast height (DBH), tree height and seed production for a total of 3881 stems of 24 woody species in a 1.44-ha canopy crane plot in a subtropical forest in China (Bin et al., 2024). Specifically, the individual-level data we incorporated into the growth—trait models were (1) measurements of traits related to photosynthetic carbon production (LMA, crown size) to estimate PI for each tree; (2) tree height, diameter and individual-level variation in wood density; (3) estimates of seed production for each tree.

2 | METHODS

2.1 | Study site

Our study was conducted in Dinghushan (DHS) Nature Reserve (112°30′39″–112°33′41″E, 23°09′21″–23°11′30″N), Guangdong province, China. This region is characterized by a south-subtropical monsoon climate, with a mean annual temperature of 20.9°C and mean annual precipitation of 1929 mm. The climax vegetation in this reserve is subtropical monsoon evergreen broadleaved forest (Ye et al., 2008). We did not need permission for fieldwork. Two forest plots in this reserve, a 120 × 120 m plot and a 400 × 500 m (20-ha) plot, are relevant to this study. In 2013, a 60-m tower crane with a rotating 60-m long jib was erected in DHS, and the 120 × 120 m plot was established, with the tower crane at its centre (hereafter, crane plot). The 20-ha plot was established in 2005 (Ye et al., 2008). The distance between these two plots is about 900 m. The 20-ha plot is located at higher elevation than the crane plot (20-ha plot: 230–470 m; crane plot: 50–100 m). In both plots, all individuals of woody species with DBH ≥1.0 cm were tagged and identified to species, and DBH and location within the plot were measured to the nearest 0.1 cm and 0.1 m, respectively (Bin et al., 2022; Ye et al., 2008).

2.2 | Measurement of tree height and seed production

In 2017, the crane plot was recensused, and the height and crown radii in the south—north (L_{sn}) and east—west (L_{ew}) directions of all living stems in the plot were also measured (Appendix S1). Crown area was approximated using an ellipsoid, calculated as $\pi \times (L_{sn}/2) \times (L_{ew}/2)$ (m^2).

In the 20-ha plot, seeds have been collected twice a month since November 2008 from 149 seed traps (0.5 m^2 in area), arranged along the trails in the plot. Seed mass data were obtained by weighing ≥30 mature seeds dried at 70°C for 72 h or collected from literature. Species-specific fecundity and seed dispersal models have been fitted for 13 species using seed rain data from 2009 to 2018 (Bin et al., 2019). Eight of these species were also present in the crane plot. For these eight species, we used the species-specific fecundity parameters and reproductive size thresholds (to define adult trees based on the minimum DBH at which seed production has been observed to occur) from Bin et al. (2019), along with tree diameter to predict the number of seeds produced annually by each adult tree in the crane plot, which, together with seed mass, was used to estimate average annual seed production (g) of each adult tree in the crane plot. Allocation to reproduction entails allocation to the production of reproductive tissues, including seeds, flowers and fruits. Here, we considered only seed production, which is likely to be correlated with total reproduction allocation (Huxman et al., 1999), as data for other aspects of reproduction were not available.

2.3 | Individual-level LMA and wood density

During the second census, we took leaf and wood samples for measuring individual-level LMA and wood density (see Appendix S1 for more details; Cornelissen et al., 2003). For each individual, we randomly sampled six leaves collected in the field, removed their petioles, scanned the leave blades (CanoScan LiDE 700F) and obtained the areas of leaf blades (cm^2; ImageJ version 1.43u; National Institutes of Health, Bethesda, MD). The leaf blades were dried in an oven at 70°C for 72 h and weighed for dry mass (g). We calculated LMA ($g{\cdot}cm^{-2}$) by dividing the leaf dry mass by the leaf area. The mean values for LMA of each tree were used in the following analyses.

Similar to previous studies (He & Deane, 2016; Swenson & Enquist, 2008), twigs of about 1 cm in diameter were sampled from healthy branches from 2095 stems in December, 2017 and from another 1937 stems in December, 2019. After stripping off the bark, the twig samples were cut into several 6-cm long sections, and wood density was measured on five of these sections for each individual. We first measured the fresh volumes (cm^3) of these samples with the water displacement method. The wood samples were then dried at 70°C for 96 h and weighed (g). Wood density was calculated by dividing the dry weight of a wood sample by its fresh volume ($g{\cdot}cm^{-3}$), and samples from a tree were averaged to obtain the individual-level wood density.

2.4 | Statistical analyses

In statistical analyses, we first focused on species with at least 30 individuals for testing the relationships of wood density with size (P1) and then included species with at least 10 individuals for the remaining tests for P2 to P4, resulting in the following numbers of species included in the analyses for each prediction: P1, 24 species; P2, 23 species; P3, 11 species; and P4, 8 species. To reduce skewness, all variables were log-transformed prior to analysis. All statistical analyses were conducted using R 3.4.2 (R Core Team, 2017).

2.4.1 | P1—Wood density in relation to size

To evaluate P1, we fit models of wood density as a function of tree size (DBH or tree height) for each species, using ordinary least squares regression following previous studies on size dependence of traits (Bin et al., 2022). The model with smaller AIC was selected as the better model. As some wood samples were taken in 2019, which was not a plot census year, we estimated diameter and height in 2019 for these stems based on species-specific diameter growth functions and height—diameter allometric functions (Bin et al., 2022). The results based on the estimated diameters and heights were similar to the results obtained assuming all wood samples were all taken in 2017 (Appendix S1). Therefore, for simplicity, we only report the latter results here.

2.4.2 | P2—Biomass growth versus diameter growth in relation to LMA and PI

To evaluate P2, we fit standardized major axis (SMA) regression models of diameter and biomass growth rates as functions of traits related to photosynthesis (Warton et al., 2012). Following Chave et al. (2005), biomass was calculated as,

$$B = fw\pi(D/2)^2H \tag{1}$$

where B (g) is biomass of a tree, w, D and h are wood density (g·cm^{-3}; individual-level value but assumed to be constant between censuses), tree diameter (cm) and height (cm), respectively; f is the form factor, which depends on tree taper. We used a form factor of 0.6, which has been shown to apply to broadleaved trees (Cannell, 1984; Chave et al., 2005), as all tree species in our study are evergreen broadleaved trees. We did not consider crown biomass (Zuleta et al., 2023) because estimating changes in crown volume as part of the regular census of all trees is very challenging and trunk biomass accounts for most of total tree above-ground biomass (Peichl & Arain, 2007). This does not present a major problem as we aimed to study the individual-level relationship of tree growth with traits, not to quantify forest biomass, and we have explicitly accounted for changes in trunk (tree height growth as well as diameter growth) of every tree in the estimation of biomass, which makes up the majority of above-ground biomass. Biomass growth (G_b) was calculated as,

$$G_b = \left(B_2 - B_1\right) / t, \tag{2}$$

where B_1 and B_2 are the biomass at the first and second censuses, and $t = 4$ is the time interval in years between the two censuses. Tree heights were not measured during the first census. To calculate B_1 and B_2, we therefore used heights estimated from species-specific height-DBH allometric models fit with DBH and tree height measured during the second census (Bin et al., 2022; Appendix S2). To avoid any rare cases of negative height growth, we did not use the predicted height in the first and the observed height in the second census. We evaluated whether our results were robust to error in biomass measurement using a simulation study (Appendix S3). Diameter growth (G_d) was calculated as

$$G_d = \left(D_2 - D_1\right) / t, \tag{3}$$

where notations were the same as in Equations (1) and (2). Using the individual-level LMA and crown area, we estimated PI as Yang et al. (2018).

$$\text{LMA} \times \text{crown area} \tag{4}$$

We did not use allometric equations to estimate leaf biomass from DBH because this would have created dependence between the response and predictor variables, which we avoided by estimating PI from data that are independent of biomass and DBH.

We fit a total of four SMA models with diameter growth and biomass growth as the response variables and the interaction of species with LMA or PI as the explanatory variable as implemented in the *sma* function. As species is a grouping factor, the models returned species-specific estimates of the intercept and the slope, the probably (the p-value) and R^2. R^2 was used to evaluate the proportion of variance in growth rate explained by LMA or PI. We used SMA rather than linear mixed-effect models with species as a random effect because we were interested in the species-specific responses and sought to avoid parameter shrinkage (Gelman et al., 2013), mixed-effect models are more suitable when the community-level response is of interest. We then tested the correlation between species' maximum height and the strength (R^2) and the magnitude (slope) of the trait—growth relationships using Pearson's correlation tests. For each model type across species, p-values were adjusted using Benjamini and Hochberg's (1995) method as implemented in the *p.adjust* function.

2.4.3 | P3—Growth of juveniles versus adults in relation to LMA and PI

To evaluate P3, we fit the same relationships as in P2, but using a subset of 11 species for which models could be fit for both juveniles and adults in order to compare their goodness of fit. We categorized trees into juveniles (DBH < the reproductive threshold) and adults (DBH ≥ the reproductive threshold) for each species based on previous observations of species-specific reproductive size thresholds, the minimum diameter for each species to reproduce (Bin et al., 2019). In order to include as many species as possible but ensure sufficient sample size, species with ≥10 juveniles and ≥10 adults were included in this analysis, following a previous study on reproductive allometry (Thomas, 1996b).

To account for the effect of difference in sample sizes for juvenile and adult trees, we used a rarefaction procedure to compare the goodness of fit of the relationships for juveniles versus adults. Using the stage with lower replication as the sample size (*n*), we took the same number (*n*) of random samples with replacement from the set of juvenile and adult trees (separately) to obtain random samples of the diameter growth, biomass growth, LMA and PI for each randomly sampled individual, and the SMA models were fitted each time. This procedure was repeated 1000 times, generating 1000 regression slopes and R^2 values. Their mean values and 95% confidence intervals were plotted for comparisons.

2.4.4 | P4—Allocation to reproduction and/or growth in relation to LMA and PI

To evaluate P4, we first estimated seed production using seed mass, tree diameter and fecundity parameter from a previous study (Bin et al., 2019) and then compared SMA models of biomass growth plus seed production together versus either alone as a function of LMA or PI. The fecundity parameter, *F*, ranged from an annual 10.30 to 151.52 seeds per cm^2 basal area (mean = 25.05, SD = 51.62) among the eight species.

Average annual seed production (*P*; *g*) for each adult of these eight species in the crane plot was calculated as,

$$P = F\,\pi(D/2)^2\,s \tag{5}$$

where *s* is the average seed weight, in unit of *g*. We calculated annual biomass allocation to growth plus seed production (*M*) as $M = G_b + P$. For juveniles, $P = 0$ and $M = G_b$. We then fit SMA models of *M*, G_b and *P* with the interaction between species and PI or LMA, respectively.

3 | RESULTS

3.1 | P1—Wood density in relation to size

Species mean wood density ranged from 0.242 to 0.678 g·cm^{-3} for the 24 species in our study. There were significant relationships of wood density with DBH for 12/24 (50%) and height for 13/24 (54.2%) species (Figure 1a,b), with a total of 14 (58.3%) species showing a significant relationship with either DBH or tree height (Figure 1d). Of these 14 species, DBH was the better predictor for nine of them; only *Castanopsis fissa* and *Castaonopsis chinensis* exhibited negative relationships of wood density with DBH and height (Figure 1a,b). Among the 24 species, the adjusted R^2 of the better model ranged from 0.021 to 0.377, with a mean of 0.129 (Figure 1c).

3.2 | P2—Biomass growth versus diameter growth in relation to LMA and PI

For most species, the R^2 for the relationship with biomass growth was larger than with diameter growth for both LMA (20/23 species, 87.0%) and PI (23/23 species, 100%), and the R^2 for the relationship with PI was larger than with LMA for both biomass growth (22/23 species, 95.7%) and diameter growth (16/23 species, 69.6%) (Table 1; Figure 2). Except for *Blastus cochinchinensis*, all other species showed positive biomass growth—PI relationships while 16/23 species showed positive diameter growth—PI relationships (Table 1). The number of species with positive biomass growth—LMA relationships (17/23, 73.9%) was similar to that with positive diameter growth—LMA relationships (16/23, 69.6%) (Table 1; Figure 2). Simulation analyses incorporating measurement error in biomass growth (Appendix S3) showed that for 18/23 (78.3%) species with LMA as the predictor and 22/23 (95.7%) species with PI as the predictor, the R^2 of models with simulated biomass growth was larger than the R^2 of models with diameter growth as the response variable (Table S2), indicating that our result was robust to small errors in biomass estimation.

Before adjustment of *p*-values for multiple comparisons, R^2 of the biomass growth—LMA, diameter growth—PI and biomass growth—PI and slope of the biomass growth—PI relationships were positively correlated with species maximum height, but none of these relationships remained statistically significant after adjustment (Table S3).

3.3 | P3—Growth of juveniles versus adults in relation to LMA and PI

There were no significant differences between the R^2 of all four relationships (diameter or above-ground biomass growth as a function of LMA or PI) for juveniles and adults (Figure 3). The confidence intervals largely overlapped for juveniles and adults of all species and all relationships (Figure 3). The regression slope did not differ between juveniles and adults, either (Figure 4). For both juveniles and adults, species exhibited either positive or nonsignificant relationships, regardless of the growth measure and the trait (Figure 4). When biomass growth was the response variable, more significant relationships were found for both juveniles and adults (7–9 species compared with 3–6 species) than when diameter growth was the response variable (Figure 4).

3.4 | P4—Trait relationships accounting for allocation to seed production

For most species, LMA explained comparable amounts of variation in biomass growth and *M*, and usually explained far less variation in seed production (Table 2). An exception was *Blastus cochinchinensis*, an understorey species, for which LMA explained 13% more variation in *M* than biomass growth (Table 2). The amount of variation in biomass growth, seed production and *M* explained by PI varied widely, but was always higher than for LMA, except for *Ardisia quinquegona* (Table 2). PI exhibited significant relationships with seed production for five of eight species, whereas this was the case for only two of eight species for LMA (Figure 5b,e). For only three of eight species did PI explain substantially more

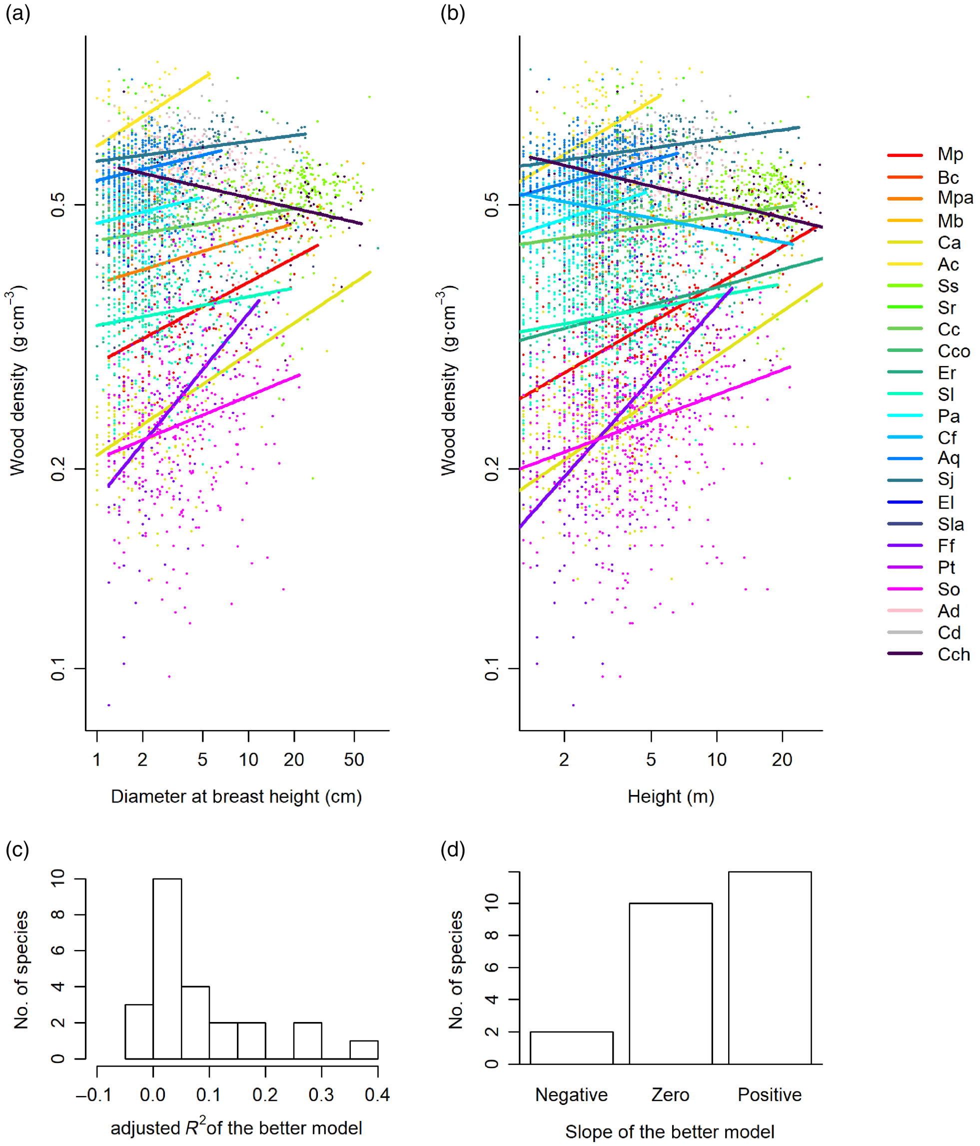

FIGURE 1 The individual-level relationship between wood density and tree size, (a) diameter at breast height and (b) tree height, for tree species in a subtropical forest in China. In panels (a) and (b), different colours denote different species, and regression lines are drawn only for species with significant relationships. Panels (c) and (d) show the distributions of the estimates of the adjusted R^2 and the slope for the best-fitting size model (either diameter or height) for each species. Species codes are as follows: Mp, *Mallotus paniculatus*; Bc, *Blastus cochinchinensis*; Mpa, *Microcos paniculata*; Mb, *Machilus breviflora*; Ca, *Canarium album*; Ac, *Aidia canthioides*; Ss, *Schima superba*; Sr, *Syzygium rehderianum*; Cc, *Cryptocarya chinensis*; Cco, *Cryptocarya concinna*; Er, *Engelhardtia roxburghiana*; Sl, *Sterculia lanceolata*; Pa, *Psychotria asiatica*; Cf, *Castanopsis fissa*; Aq, *Ardisia quinquegona*; Sj, *Syzygium jambos*; El, *Evodia lepta*; Sla, *Sarcosperma laurinum*; Ff, *Ficus fistulosa*; Pt, *Pygeum topengii*; So, *Schefflera octophylla*; Ad, *Aporosa dioica*; Cd, *Canthium dicoccum*; Cch, *Castanopsis chinensis*.

variation in *M* than in biomass growth or seed production alone (Table 2).

4 | DISCUSSION

Trunk diameter growth has long been used as a standard measure of tree growth in studies seeking to understand its functional basis (King et al., 2005; Poorter et al., 2008; Thomas, 1996a; Wright et al., 2010; Yang et al., 2018), even though it is only one of the above-ground dimensions of tree growth. In addition, woody growth also depends on the density of woody tissues and the amount of photosynthetic products allocated to them. If we are to understand whether traits related to photosynthesis can predict above-ground woody growth, it makes sense that measures of growth and functional trait metrics that integrate these components should be used. Our study of individual-level woody growth and functional trait variation supported these ideas. For over 75% of these species, growth—trait relationships were stronger for above-ground biomass than for diameter, and a measure of whole-tree photosynthetic capacity (PI) explained more variation in growth than did an organ-level leaf trait related to photosynthetic rates, LMA. There were also dramatic changes in wood density with tree size for over half

TABLE 1 Slope and R^2 estimates from standard major axis regressions between growth measures (diameter growth, G_d, and biomass growth, G_b) and individual-level leaf mass per area (LMA) and photosynthetic investment (PI) for tree species in a subtropical forest in China.

	G_d~LMA		G_b~LMA		G_d~PI		G_b~PI	
Species	**Slope**	R^2	**Slope**	R^2	**Slope**	R^2	**Slope**	R^2
Mp	2.621**	0.220	5.004**	0.393	0.509**	0.297	1.459***	0.698
Bc	−3.979*	0.408	−3.783	0.230	0.827	0.246	0.787	0.330
Mpa	4.675	0.051	7.131	0.065	0.988	0.019	1.506**	0.411
Mb	5.141***	0.320	9.189***	0.421	0.991***	0.411	1.816***	0.779
Ca	4.605***	0.359	10.106***	0.504	0.834***	0.447	1.873***	0.753
Ac	6.790	0.008	−11.035	0.020	1.253	0.108	1.762**	0.435
Ss	3.283***	0.099	5.355***	0.299	0.926***	0.091	1.504***	0.411
Sr	3.911	0.006	−8.783	0.000	0.607	0.091	1.363***	0.801
Cc	5.938***	0.393	12.905***	0.605	0.836***	0.433	1.864***	0.667
Cco	7.329**	0.077	10.885***	0.132	0.985***	0.156	1.493***	0.402
Er	5.476***	0.231	10.294***	0.340	0.706***	0.376	1.326***	0.584
Sl	3.566***	0.115	7.025***	0.314	0.684***	0.175	1.340***	0.565
Pa	4.896	0.009	5.964*	0.078	1.029	0.030	1.265***	0.188
Cf	6.761	0.071	11.029**	0.236	1.085***	0.382	1.770***	0.543
Aq	4.945**	0.061	6.145**	0.094	1.022	0.007	1.271**	0.093
Sj	7.817**	0.124	14.168***	0.186	0.791***	0.237	1.434***	0.608
Sla	−4.993	0.007	7.954	0.170	0.602	0.000	1.083***	0.550
Ff	5.072**	0.228	7.659***	0.349	1.160***	0.318	1.830***	0.637
Pt	1.363	0.078	2.914	0.015	0.847**	0.196	2.055**	0.381
So	3.628**	0.037	5.520***	0.060	0.854**	0.033	1.340***	0.415
Ad	5.709***	0.094	9.160***	0.108	0.844***	0.092	1.369***	0.506
Cd	3.938***	0.360	6.726***	0.473	0.916***	0.370	1.568***	0.541
Cch	2.912***	0.214	5.336***	0.326	0.894***	0.374	1.638***	0.670

Abbreviations: Ac, *Aidia canthioides*; Ad, *Aporosa dioica*; Aq, *Ardisia quinquegona*; Bc, *Blastus cochinchinensis*; Ca, *Canarium album*; Cc, *Cryptocarya chinensis*; Cch, *Castanopsis chinensis*; Cco, *Cryptocarya concinna*; Cd, *Canthium dicoccum*; Cf, *Castanopsis fissa*; Er, *Engelhardtia roxburghiana*; Ff, *Ficus fistulosa*; Mb, *Machilus breviflora*; Mp, *Mallotus paniculatus*; Mpa, *Microcos paniculata*; Pa, *Psychotria asiatica*; Pt, *Pygeum topengii*; Sj, *Syzygium jambos*; Sl, *Sterculia lanceolata*; Sla, *Sarcosperma laurinum*; So, *Schefflera octophylla*; Sr, *Syzygium rehderianum*; Ss, *Schima superba*.

*$p < 0.05$. **$p < 0.01$. ***$p < 0.001$.

of the species, with wood density increasing with size for most species, in some cases nearly doubling over the range of tree sizes in our study. This result implies that, for some species, there are considerable size-related increases in the amount of carbon investment required per unit of woody growth. Pools of photosynthetic carbon are allocated not only to growth but also to functions supporting survival and reproduction (Huang et al., 2020; Thomas, 1996b), and so whole-tree photosynthetic capacity should also be related to these vital rates. While we did not estimate allocation to survival, we did estimate individual-level reproductive allocation based on a model of seed production. Although biomass allocated to growth plus seed production had a stronger relationship with PI for only three of eight species than did biomass growth alone, PI was a better predictor than LMA of biomass growth, seed production and their sum in nearly all cases.

Our study offers new support to proposed explanations for the counterintuitive pattern that many studies have found of weak relationships between functional trait and diameter growth rate variation (Yang et al., 2018). Moreover, our study adds support of using functional trait, growth and fecundity measurements at the individual level, at which demographic processes and ecological functions operate (Zuidema & van der Sleen, 2022). Specifically, an estimate of whole-tree photosynthetic capacity that integrates organ-level and allometric traits, rather than organ-level traits alone, provided a better proxy for the individual's capacity to accumulate photosynthetic carbon, which is fundamental to growth. Using a growth measure that accounts for multiple dimensions of growth, especially tree height, and size-dependent variation in wood density, which dictates the biomass required to build volumes of woody tissues, is a better estimate of the carbon costs of growth. Accounting for multiple biomass allocation sinks should produce stronger relationships between vital rates and indices of an individual's capacity to accumulate photosynthetically fixed carbon. Our results imply that accounting for the whole-tree allocation patterns of individuals is needed to evaluate the functional basis of tree growth and carbon sequestration under global climate change.

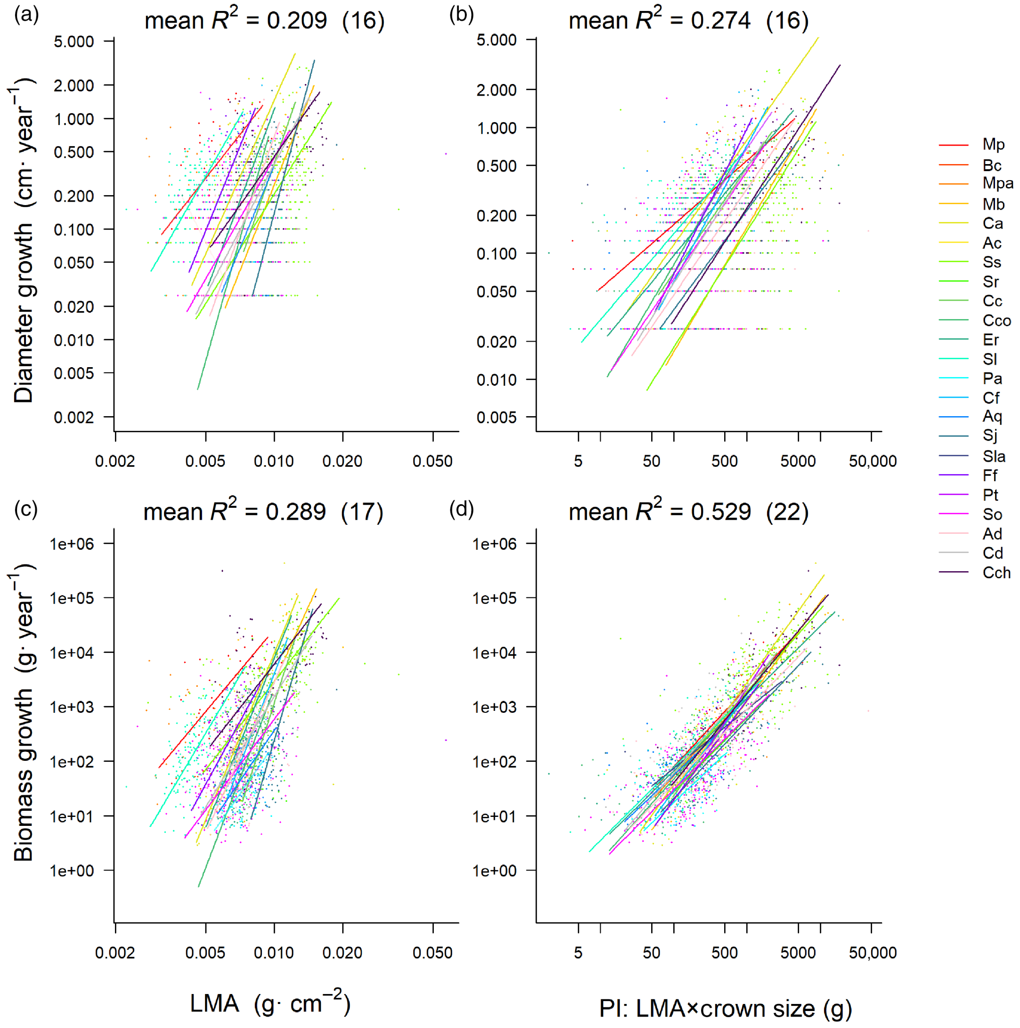

FIGURE 2 Variation in diameter (a, b) and biomass (c, d) growth in relation to leaf mass per area (LMA) and photosynthesis investment (PI) for tree species in a subtropical forest in China. Different colours denote different species, and standardized major axis regression lines are drawn only for species with significant relationships. Mean R^2 and the number of species (*n*; out of a total of 23 species) with a significant relationship are presented at the top of each panel. See the legend for Figure 1 for the species' binomials for each code.

4.1 | Wood density in relation to size

While it is recognized that there is considerable between-species variation in wood density (Chave et al., 2009; Fajardo, 2018; Thomas, 1996a), within-species variation in relation to tree size has been far less documented, and we show that it can be considerable. Decreasing wood density with tree size has been observed for *Nothofagus pumilio*, a deciduous, broadleaved, light-demanding tree species (Fajardo, 2018) while the reversed trend was observed for *Melia azedarach*, a canopy tree species in western Thailand (Nock et al., 2009). In our study, we found size-related increases in wood density for all but two Fagaceae species, *Castanopsis fissa* and *Castanopsis chinensis*. Size-related changes in wood density might owe to factors related to biomechanical constraints on height—diameter allometries, durability and changes in access to light as a tree grows into higher forest strata (Cao et al., 2008; Larjavaara, 2010). Denser wood might be adaptive for shorter stems, as they are more vulnerable to physical damage from falling debris and herbivory by large mammals (Clark & Clark, 1991; Thomas, 1996a). Denser wood may be adaptive for taller stems that require more biomechanical support (King et al., 2006, 2009; Larjavaara & Muller-Landau, 2010). Taller stems are more vulnerable to toppling during strong winds (King et al., 2009; Putz et al., 1983; Wiemann & Williamson, 1989). This forest experiences East Asian monsoon winds, which may increase the adaptive value of the biomechanical support provided by increasing wood density with tree height (King et al., 2006, 2009; Larjavaara & Muller-Landau, 2010) and could explain the increase in wood density with tree size that we found for most species. Wood density is an important component of biomass (Chave et al., 2005, 2009). Studies of standing biomass and biomass growth on the whole, however, do not account for the considerable size-related increases in wood density we found in our study. Our results imply that as trees grow in size, they remain important for carbon storage and sequestration, because they continue to grow in stem volume and because their wood increases in density, meaning that a unit of growth sequesters more carbon.

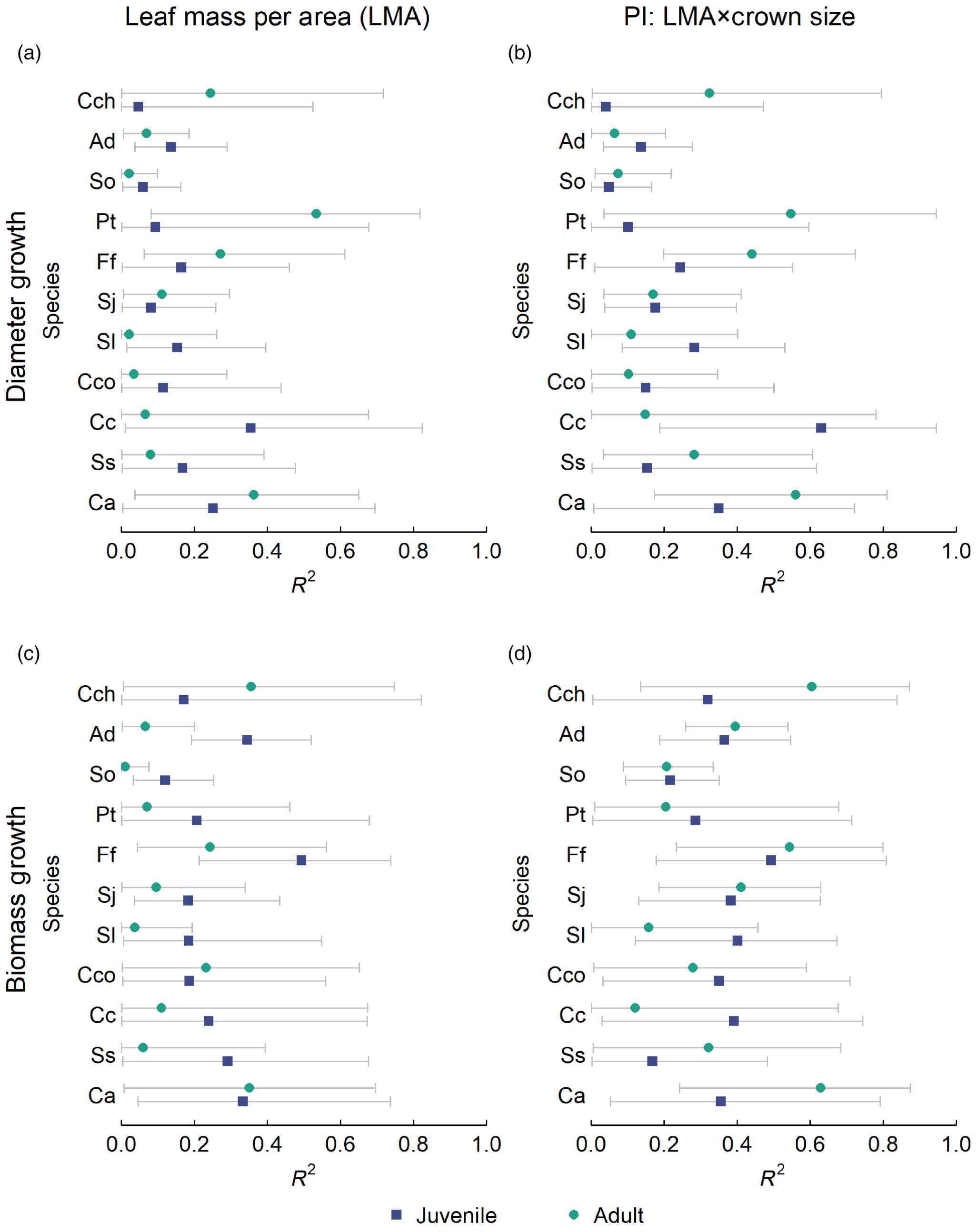

FIGURE 3 Comparisons of the R^2 for juveniles (green) versus adults (blue) for standardized major axis regression models of the relationships between growth (diameter, in panels a and b, or above-ground biomass growth, in panels c and d) and functional traits (leaf mass per area, LMA, in panels a and c, photosynthetic investment, PI, in panels b and d) for tree species in a subtropical forest in China. Horizontal segments show the estimates with 95% confidence intervals obtained for R^2. See the legend for Figure 1 for the species' binomials for each code.

4.2 | Tree growth in relation to functional trait variation

In studies of trait–growth relationships, diameter growth has been the most frequently used growth measure for saplings and adults (Iida et al., 2016; Poorter et al., 2008; Yang et al., 2018), though it is only one dimension of woody growth. However, much of trait-based ecology emphasizes whole-plant carbon balance and allocation trade-offs (Baltzer & Thomas, 2007; Hartmann et al., 2020; Kitajima & Myers, 2008; Sterck et al., 2013), and so it would stand to reason that growth measures that account for more sources of variation in carbon allocation should be used. Yet, surprisingly, in studies of trait–growth relationships in forests, biomass growth is rarely used, even though biomass is often the currency in studies of herbaceous plant growth (Fill et al., 2019; Hoover et al., 2014).

The principle underlying the expectation that growth and functional trait variation should be correlated is that functional traits determine the rate of acquisition of photosynthetically fixed

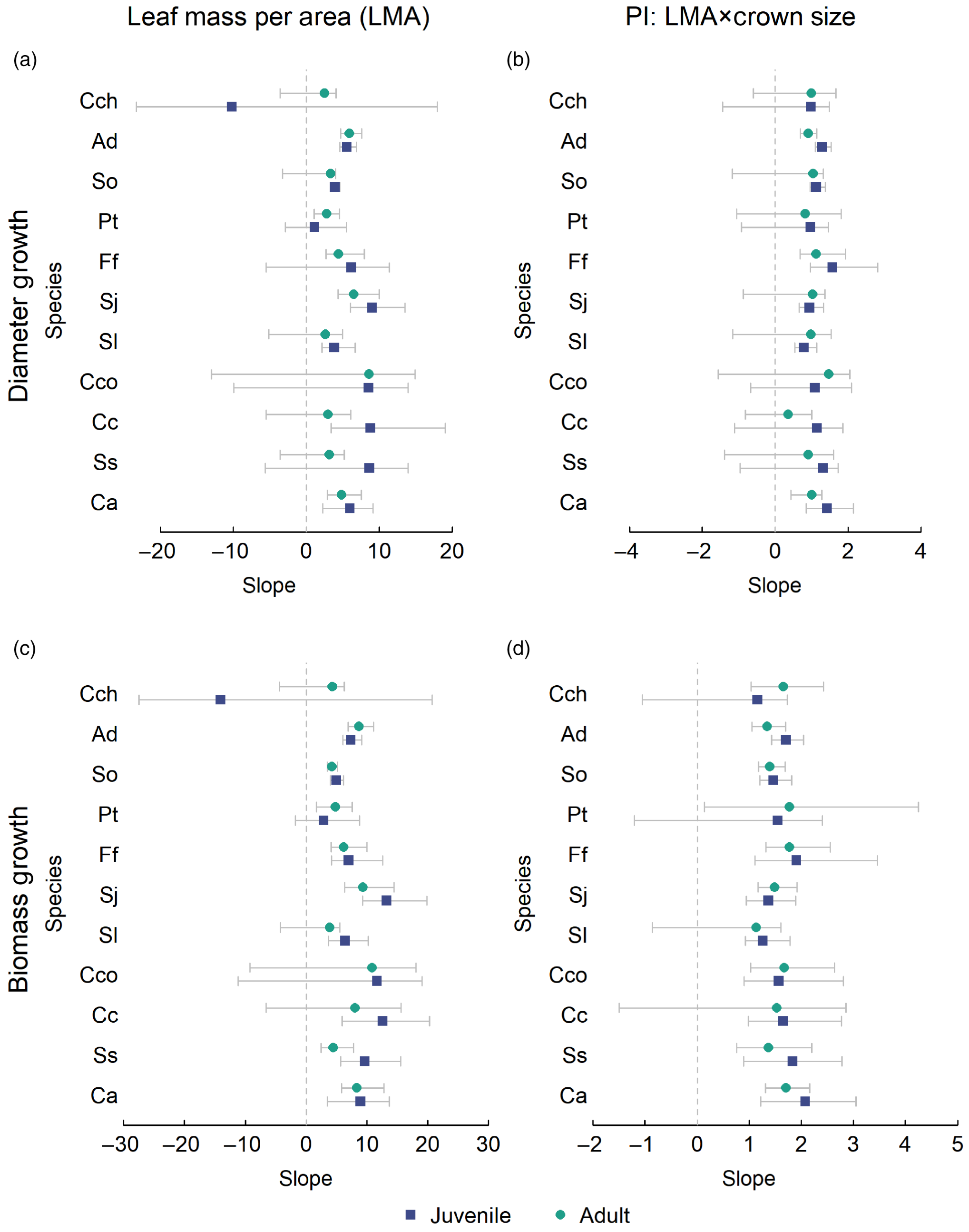

FIGURE 4 Comparisons of the standardized major axis regression slope estimates for juveniles (green) versus adults (blue) for models of the relationships between growth (diameter, in panels a and b or above-ground biomass growth, in panels c and d) and functional traits (leaf mass per area, LMA, in panels a and c, photosynthetic investment, PI, in panels b and d) for tree species in a subtropical forest in China. Horizontal segments show the estimates with 95% confidence intervals obtained for the slope. See the legend for Figure 1 for the species' binomials for each code.

carbon and other resources required for growth. Yet, counterintuitively, weak trait–growth relationships are found in many studies of woody species (Liu et al., 2016; Paine et al., 2015; Poorter et al., 2008; Umaña et al., 2018; Wright et al., 2010). Our findings suggest some explanations for these weak relationships. First, provided estimation equations are reasonably accurate, biomass growth should better correlate with trait variation, regardless of being measured directly or estimated by allometric functions, because biomass is also a measure of matter and has the same units as the masses of photosynthetically fixed carbon and other resources required for growth, grams. In principle, the growth–trait relationship would be similarly strong if stem diameter were linearly related to biomass. However, this is not the case, as biomass is the product of wood density and tree volume, and volume is a power function of diameter (Chave et al., 2005). Therefore, diameter growth has weak relationships with functional trait variation, at least in part due to the inconsistency in units of the variables being related. The allometric equations we used to predict

TABLE 2 The R^2 for standardized major axis regressions for the relationships of individual-level traits (LMA: leaf mass per area or PI: photosynthetic investment) with biomass growth (G_b), seed production (P) and biomass allocated to growth+seed production (M) in a subtropical forest in China.

	Leaf mass per area (LMA)			Photosynthetic investment (PI)		
Species	G_b	P	M	G_b	P	M
Mp	0.393***	0.127	0.330**	0.698***	0.497***	0.340**
Bc	0.230	0.063	0.364*	0.330	0.002	0.778***
Ac	0.020	0.116	0.018	0.435**	0.117	0.620***
Ss	0.299***	0.225***	0.216***	0.411***	0.506***	0.306***
Cc	0.605***	0.084	0.606***	0.667***	0.141	0.669***
Er	0.340***	0.534	0.340***	0.584***	0.934***	0.584***
Aq	0.094***	0.000	0.141***	0.093***	0.043*	0.204***
Cch	0.326***	0.292***	0.353***	0.670***	0.650***	0.640***

Abbreviations: Ac, *Aidia canthioides*; Aq, *Ardisia quinquegona*; Bc, *Blastus cochinchinensis*; Cc, *Cryptocarya chinensis*; Cch, *Castanopsis chinensis*; Er, *Engelhardtia roxburghiana*; Mp, *Mallotus paniculatus*; Ss, *Schima superba*.

*$p < 0.05$. **$p < 0.01$. ***$p < 0.001$.

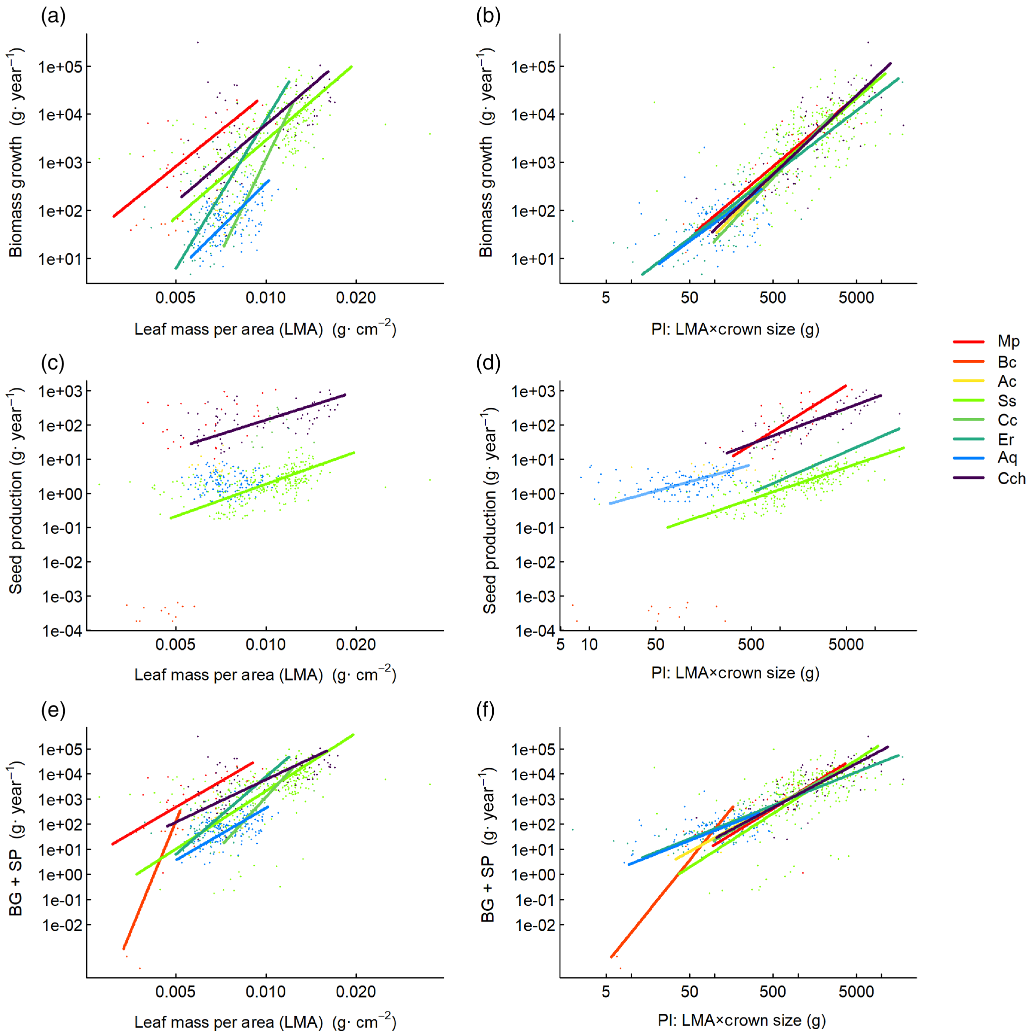

FIGURE 5 Variation in biomass growth (a, d), seed production (b, e) and biomass growth+seed production (c, f) as a function of leaf mass per area (LMA) (a-c) and photosynthetic investment (PI) (e-f) among tree species in a subtropical forest in China. See the legend for Figure 1 for the species' binomials for each code.

individual biomass were based on individual-level data on height, diameter and wood density, which gives a far better estimate of biomass compared to models using only diameter or species' mean estimates of wood density.

Second, weak trait—growth relationships (Liu et al., 2016; Paine et al., 2015; Poorter et al., 2008; Umaña et al., 2018; Wright et al., 2010) may owe in part to not accounting for the fact that for a tree to grow, photosynthetically fixed carbon must be allocated to the multiple dimensions comprising its growth. In support of this interpretation, for over 75% of species in our study, biomass growth had stronger relationships with LMA and PI than did diameter growth, indicating that accounting for the major dimensions of tree growth, such as diameter, height and size-related wood density variation can find stronger trait—growth relationships which might be confounded by unmeasured dimensions of growth if only one dimension of growth, for example, diameter, was considered.

There are other reasons for weak trait—growth relationships among woody species related to how functional trait variation is measured. Usually studies use only organ-level structural and biochemical traits, as these are more feasible to measure. However, due to phenotypic integration at the whole-plant level, multiple combinations of trait values can lead to the same growth rate (Marks & Lechowicz, 2006). Moreover, organ-level traits do not always reflect whole-plant functioning, especially for traits related to whole-plant photosynthetic carbon production, which are strongly influenced by tree architecture and leaf display (Givnish, 1988; Sterck et al., 2013; Yang et al., 2018). A previous study showed that an index of whole-plant photosynthetic capacity (PI: LMA multiplied by crown size) explained 30%–80% more variation in diameter growth rates of four species than did LMA alone, suggesting that not accounting for the sources of variation influencing carbon fixation was a cause for observing weak relationships (Yang et al., 2018). In our study, we also tested this relationship for 23 species using the same PI, but the average R^2 was only 0.289, considerably smaller than the proportion explained in this previous study. However, the mean R^2 increased to 0.529 when replacing diameter growth with biomass growth. Strong, positive relationships between whole-plant leaf biomass measures, similar to PI used here, and annual biomass production have also been found in managed forests (Enquist et al., 2007; Enquist & Niklas, 2002). It is important to note that our measure of biomass growth is only above-ground living trunk biomass, not accounting for woody growth of the crown and root system, litter production, nor of leaf mass, which together encompass plant production (Malhi, 2012). Likewise, our measure of whole-plant photosynthetic capacity does not account for differences in net rates of photosynthetic carbon fixation per unit investment in leaves (Enquist & Niklas, 2002). All of these additional factors can vary strongly among and within species and in relation to tree size and environmental resource availability (Enquist & Niklas, 2002). Nevertheless, the totality of our findings provides support for the idea that accounting for more of the sources of variation influencing both photosynthetic carbon fixation capacity and whole-plant carbon allocation during growth can improve the goodness of fit of trait—growth relationships among individuals.

4.3 | Accounting for allocation to reproduction

Juvenile, that is, non-reproductive, trees can differ from adults in many aspects, including allometries, strength of interspecific tradeoffs and trait—performance relationships (e.g. Poorter et al., 2008; Thomas, 1996a; Wright et al., 2010). However, many studies comparing juvenile versus adult trees use arbitrary size cut-offs that often are not accurate for tree species of different growth forms and maximum sizes. This can confound trait—growth relationships if the juvenile and adult categories contain a mix of trees that are and are not allocating carbon to reproduction. More recently, size thresholds distinguishing juvenile and adult trees have been estimated based on the diameter at first reproduction (Bin et al., 2019; Minor & Kobe, 2019; Visser et al., 2016), which can improve the fit of trait—growth relationships. For example, traits, tree size accounting for size at first reproduction and their interaction accounted for 26% of the individual-level basal area growth among Panamanian tree species (Visser et al., 2016).

Using species-specific reproductive thresholds and estimates of seed production based on seed traps, we estimated allocation to reproduction. In some cases, accounting for allocation to seed production dramatically improved the goodness of fit for models using PI as a predictor, but this was not true for all species. Indeed, sometimes explained variation was comparable or higher for seed production or biomass alone than for growth and seed production together. Thus, not accounting for the allocation to reproduction of adults and mixing reproductive and non-reproductive individuals may sometimes contribute to previously observed weak trait—growth relationships. However, allocation to non-seed reproductive structures can be substantial (Huxman et al., 1999), which might explain why our prediction was not always supported and points to the need for improved data on reproductive allocation.

5 | CONCLUSIONS

A paradox of the trait-based ecology framework for plants has been that trait—growth relationships, though expected to be strong, are often found to be weak among woody species, particularly for organ-level traits. Some resolutions have been proposed (Enquist et al., 2007; Yang et al., 2018), and here, we provided novel support for them with individual-level data from 24 species. Our study also suggests the hypothesis that differences among trees in resource allocation are an equally strong or stronger driver of demographic rate variation than is organ-level trait variation. It is important to acknowledge that measurements of functional traits and tree growth are time-consuming and costly, particularly to achieve the levels of replication at the individual level required for strong inference across multiple species. Trait-based ecology is a maturing field, and we suggest that greater consideration of the mechanistic links between traits and growth, as done in modelling studies (Koven et al., 2020; Russo et al., 2022; Sterck et al., 2011), can help establish more a solid foundation of trait-based ecology.

AUTHOR CONTRIBUTIONS

Yue Bin, Sabrina E. Russo and Juyu Lian designed the study. Jiantan Zhang and Yanpeng Li measured the functional traits. Yue Bin, Honglin Cao, Wanhui Ye and Juyu Lian conducted the fieldwork for data collection. Yue Bin and Sabrina E. Russo designed the data analysis approach, and Yue Bin analysed the data. All authors contributed substantially to the interpretation of the results. Yue Bin wrote the first draft. Yue Bin and Sabrina E. Russo revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All archived data are freely available at https://doi.org/10.57760/sciencedb.15838 (Bin et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supplementary Methods.

Appendix S2. Species-specific allometric relationship of tree height as a function of diameter at breast height (DBH).

Appendix S3. Supplementary analysis for testing the robustness of relationship of growth with traits to the estimate of biomass growth.

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