LETTERS

A general integrative model for scaling plant growth, carbon flux, and functional trait spectra

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Linking functional traits to plant growth is critical for scaling attributes of organisms to the dynamics of ecosystems[1,2] and for understanding how selection shapes integrated botanical phenotypes[3]. However, a general mechanistic theory showing how traits specifically influence carbon and biomass flux within and across plants is needed. Building on foundational work on relative growth rate[4–6], recent work on functional trait spectra[7–9], and metabolic scaling theory[10,11], here we derive a generalized trait-based model of plant growth. In agreement with a wide variety of empirical data, our model uniquely predicts how key functional traits interact to regulate variation in relative growth rate, the allometric growth normalizations for both angiosperms and gymnosperms, and the quantitative form of several functional trait spectra relationships. The model also provides a general quantitative framework to incorporate additional leaf-level trait scaling relationships[7,8] and hence to unite functional trait spectra with theories of relative growth rate, and metabolic scaling. We apply the model to calculate carbon use efficiency. This often ignored trait, which may influence variation in relative growth rate, appears to vary directionally across geographic gradients. Together, our results show how both quantitative plant traits and the geometry of vascular transport networks can be merged into a common scaling theory. Our model provides a framework for predicting not only how traits covary within an integrated allometric phenotype but also how trait variation mechanistically influences plant growth and carbon flux within and across diverse ecosystems.

Plant functional traits are measurable morphological and physiological attributes that significantly affect whole-plant performance and thus, presumably, the main components of fitness: survival, growth and reproduction[12]. Much plant ecology and evolutionary biology aims to identify critical functional traits and to quantify their variation and covariation[13]. Such work has identified functional trait spectra (FTS)[5,7,8,14], which are correlations that describe how several functional traits—including leaf measures[8], patterns of whole-plant allocation[15], and attributes of stem hydraulics[16,17]—interrelate with each other. It is presumed that FTS[13] provide a basis for linking the ways in which organisms influence large-scale patterns in ecosystem function[1,2] and for understanding how so many species can coexist in communities[12,13]. However, theory deriving the origin of FTS and for linking FTS with whole-plant fitness, growth and ecosystem function is still unclear[2,18] (but see refs 4 and 19). Here, we argue that FTS must be interpreted within the context of integrated allometric phenotypes[18]. That is, variability and covariation of traits must be linked to whole-plant performance, such as growth.

Work on relative growth rate (RGR) and metabolic scaling theory (MST) has assumed that many trait correlations are ultimately governed by the isometric scaling[4,5,20,21] of whole-plant net biomass growth rate, dM/dt, and total plant photosynthetic (leaf) biomass, M_L (see also ref. 7). Specifically, as given by MST:

$$\frac{dM}{dt} = \dot{M} = \beta_A M_L \quad (1)$$

where β_A is an allometric constant and is the net biomass produced per unit leaf mass (see Supplementary Information). There are several key leaf traits influencing the net production of carbon and biomass. For example, variation in RGR (measured as the rate of total biomass produced per mass of plant, $g\,g^{-1}\,t^{-1}$) has traditionally[4,5,21] been linked to three key traits: (1) the leaf net carbon assimilation rate (NAR, measured in grams of C assimilated per cm^2 of leaf per unit time t: $g\,C\,cm^{-2}\,t^{-1}$); (2) the specific leaf area (the leaf area per unit leaf mass a_L/m_L, measured in $cm^2\,g^{-1}$); and (3) the leaf weight ratio (the ratio of total leaf mass to total plant mass, M_L/M). Therefore, dividing equation (1) by total mass M is equivalent to the classical decomposition[4] (for example, $RGR = NAR \times a_L/m_L \times M_L/M$) where $\beta_A = NAR \times a_L/m_L$. However, below we show that this decomposition of RGR lacks the critical traits influencing growth and the allometric dependency of leaf mass M_L.

Building on this model, using MST, we derive a trait-explicit scaling model of allometric plant growth (see Supplementary Information). The net biomass assimilation rate can be rewritten as $NAR = c\dot{A}_L/\omega$, where $\dot{A}_L$ (grams of C per cm^2 per unit time) is the leaf area specific photosynthetic rate, c is the net proportion of fixed carbon converted into biomass[22] (the carbon use efficiency, which is dimensionless), and ω is the fraction of whole-plant mass that is carbon (see Supplementary Information). Recent studies support an approximately linear relationship between NAR and $\dot{A}_L$ (see Supplementary Information), suggesting that c/ω does not covary systematically with leaf level photosynthetic rate. Using this expression[4,5,21] for NAR, the equation for whole-plant growth becomes:

$$\dot{M} = \beta_A M_L = NAR \times a_L/m_L \times M_L = \left(\frac{c}{\omega}\dot{A}_L\right)\left(\frac{a_L}{m_L}\right)M_L \quad (2)$$

where a_L is individual leaf area and m_L is individual leaf mass. All of the plant traits listed in equation (2) can vary intra- and interspecifically, so it is important to note that only when in the absence of parameter covariation should these values be estimated as independent averages only (see Supplementary Information). However, covariance terms in the expectation of β_A can be included by measuring multiple traits for each individual or species simultaneously.

Next we expand equation (2) by incorporating the importance of whole-plant size and allometric biomass allocation into the equation for growth rate: equation (2). MST and empirical data show that M_L scales with whole-plant mass as: $M_L = \beta_L M^{\theta}$. According to MST, the

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Table 1 | Predicted normalization constants for several prominent scaling relationships

Plant growth quantity	Predicted functional equation from traits	Predicted normalization value	Observed normalization value
Allometric normalization for whole-plant growth rate per unit allometric mass	$\beta_G \approx \left(\frac{a_L}{m_L}\right)\left(\frac{c}{\omega}\dot{A}_L t_s^{max}\right)\beta_L$	Angiosperm $\beta_G = 2.43\ g^{1/4}\ yr^{-1}$; 95% CI = 0.44–11.92 Gymnosperm $\beta_G = 1.35\ g^{1/4}\ yr^{-1}$; 95% CI = 0.41–4.42	Angiosperm $\beta_G = 4.44\ g^{1/4}\ yr^{-1}$; 95% CI = 1.77–11.09 Gymnosperm $\beta_G = 1.36\ g^{1/4}\ yr^{-1}$; 95% CI = 0.80–2.40
Allometric normalization for whole-plant growth rate per unit leaf mass	$\beta_A \approx \left(\frac{a_L}{m_L}\right)\left(\frac{c}{\omega}\dot{A}_L t_s^{max}\right)$	Angiosperm $\beta_A = 5.53\ g\ yr^{-1}$; 95% CI = 0.74–29.27 Gymnosperm $\beta_A = 1.53\ g\ yr^{-1}$; 95% CI = 0.35–6.37	Angiosperm $\beta_A = 2.57\ g\ yr^{-1}$; 95% CI = 1.52–4.37 Gymnosperm $\beta_A = 1.07\ g\ yr^{-1}$; 95% CI = 0.71–1.63
Normalization for inverse scaling of leaf and growth time (carbon use efficiency, c)	$c \approx \frac{\omega \dot{M}_A}{\left(\frac{a_L}{m_L}\right)\dot{A}_L t_s^{max}\beta_L M^{\theta}}$	$c = 0.427$; 95% CI = 0.377–0.477	$c = 0.44$; 95% CI = 0.41–0.47
FTS normalization for the relationship between a_L/m_L and allometric leaf mass fraction, β_L	$\tau \approx \frac{\omega \dot{M}_A}{c\dot{A}_L t_s^{max} M^{\theta}}$	All taxa average = $0.0035\ cm^2\ g^{-3/4}$; 95% CI = 0.003–0.005	RMA regression = $0.004\ cm^2\ g^{-3/4}$; 95% CI = 0.003–0.006

For the first two rows, plant mass M is normalized to $M = 1$ g. Three out of four predicted scaling constants fell within the 95% confidence intervals of empirical scaling constant estimates. The other prediction—the value of β_A for angiosperms—was quite close to the observed value, falling within a factor of two of the observed value. The last two rows show the predicted values of c and τ, the prefactor (see Supplementary Information) for the trait-scaling relationship between a_L/m_L and the allometric leaf mass fraction: $a_L/m_L = \tau(\beta_L)^{-1}$. As described in the Supplementary Information, all of the growth quantities and statistics reported here are calculated from compilations of global trait, biomass and growth data.

value of θ is itself an important functional trait that reflects the geometry of the branching architecture. Its value (see Supplementary Information) ultimately controls the scaling of the number of leaves[10,23]. For seedlings and stems with few to no branchings, $\theta \approx 1$. However, for most plants larger than seedlings, MST and empirical data show $\theta \approx 3/4$ (ref. 23). Also, based on elaborations of MST[11] (Supplementary Information) we can show that the term β_L is governed by additional functional traits and plant size. Specifically, $\beta_L = M_L M^{-\theta} = M_L(\rho V)^{-\theta} = \phi_L \rho^{-\theta}$, where V is the total volume of the branching network or plant body and ρ is the whole-plant tissue density. The allometric constant $\phi_L \equiv M_L/V^{\theta}$ measures the mass of leaves per allometric volume of the plant body. Therefore, substituting for the M_L term in equation (2) yields an expanded trait-based growth law:

$$\dot{M} = \left(\frac{c}{\omega}\dot{A}_L\right)\left(\frac{a_L}{m_L}\right)\beta_L M^{\theta} = \left(\frac{c}{\omega}\dot{A}_L\right)\left(\frac{a_L}{m_L}\right)\left(\phi_L \rho^{-\theta}\right)M^{\theta} \quad (3)$$

Taking equation (3) and dividing both sides by the total mass M restores an explicit and expanded trait-based equation for RGR ($\dot{M}/M$):

$$\frac{\dot{M}}{M} = \left(\frac{c}{\omega}\dot{A}_L\right)\left(\frac{a_L}{m_L}\right)\left(\phi_L \rho^{-\theta}\right)M^{\theta-1} \quad (4)$$

As supported by empirical data[22], equation (4) predicts that the RGR should decrease as a function of plant size as $M^{\theta-1}$, whenever θ is less than 1.0 (refs 11, 24).

Building from the RGR literature, equations (2) to (4) effectively merge MST and FTS into a general growth law governed by key functional traits and the geometry of vascular transport networks. Furthermore, equations (3) to (4) provide a novel derivation of the MST normalization for allometric growth:

$$\beta_G \equiv \beta_L \beta_A = \left(\frac{c}{\omega}\dot{A}_L\right)\left(\frac{a_L}{m_L}\right)\left(\frac{M_L}{M^{\theta}}\right) = \left(\frac{c}{\omega}\dot{A}_L\right)\left(\frac{a_L}{m_L}\right)\phi_L \rho^{-\theta} \quad (5)$$

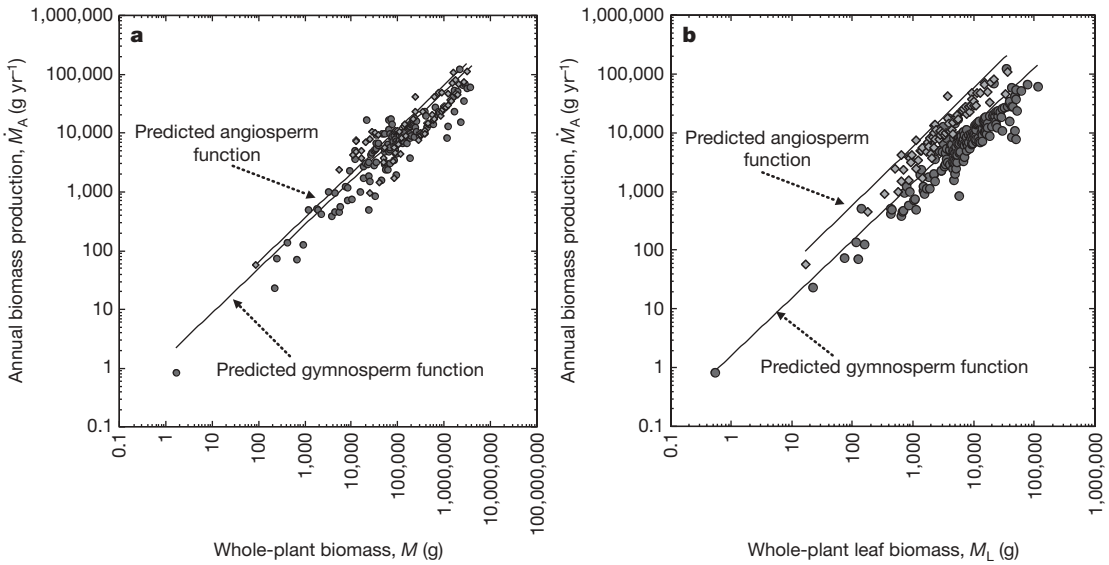

Figure 1 | Using plant traits to predict allometric growth for gymnosperms and angiosperms. a, Allometric scaling of M (roots, stems, and leaves) versus $\dot{M}_A$. **b**, Allometric scaling of M_L versus $\dot{M}_A$. Angiosperms, circles; gymnosperms, diamonds. The predicted allometric scaling functions are $\dot{M}_A = \beta_G M^{\theta}$ and $\dot{M}_A = \beta_A M_L^{1.0}$ respectively. The values of β_A and β_G were calculated for each taxon, based on resampling global values of taxon specific mean trait values as specified by equations (2) and (3) (see Supplementary Information and Table 1). Further, as discussed by MST, for trees larger than seedlings, we used the value of $\theta = 3/4$.

Table 2 | Predicted scaling exponents governing leaf trait and whole-plant allocation patterns

Functional trait scaling relationship	Predicted scaling function	Predicted exponent	Observed
a_L/m_L as a function of β_L	$\frac{a_L}{m_L}=\tau(\beta_L)^{-1}$	−1.0	−1.16; RMA 95% CI = −0.71 to −1.6 (this study; Fig. 3a)
$[(\omega\dot{M}_A)/(\beta_L M^\theta)]$ as a function of $\frac{a_L}{m_L}\dot{A}_L t_S$	$[(\omega\dot{M}_A)/(\beta_L M^\theta)]=c\left(\frac{a_L}{m_L}\dot{A}_L t_S\right)^{1.0}$	1.0	0.90; RMA 95% CI = 0.74 to 1.07 (this study; Fig. 3b)
β_L as a function of ρ	$\beta_L=\phi_L(\rho)^{-\theta}$	For terminal branches and small plants $\theta\approx-1.0$	$\theta\approx-1.22$; RMA 95% CI = −0.97 to −1.49 (Supplementary Fig. 1)
$\dot{A}_L$ as a function of ρ	$\dot{A}_L=\frac{\dot{M}\omega}{M_L c}\times\frac{m_L}{a_L}(\rho)^0$	0	0 (Supplementary Fig. 3)
a_L/m_L as a function of ρ	$\frac{a_L}{m_L}=\frac{\dot{M}\omega}{M_L c\dot{A}_L}(\rho)^0$	0	0 (data compilation from ref. 9; see also Supplementary Fig. 4)
ρ as a function of the leaf area ratio $\frac{a_L^{total}}{\phi_L M^\theta}$	$\rho=\frac{cV^\theta M_c}{\omega m_L\dot{M}t}\left(\frac{a_L^{total}}{\phi_L M^\theta}\right)^{-1/\theta}$	$-1/\theta$	Negative correlation (reported in ref. 64 in Supplementary Information)

See Supplementary Information for a detailed derivation of these and several other FTS relationships. For all of the trait correlations of *y* versus *x*, the *x*-variable trait is denoted within parentheses. Each of these trait correlations are expected to be general across all plants only if the traits in the prefactor (the traits not identified as the *x*-variable trait) do not covary with the *x*-variable trait (see section XII of the Supplementary Information). For each of these trait functional relationships: (1) both whole-plant and leaf level traits will govern the exact relationship; and (2) the geometry of the plant branching network, reflected in θ, influences each of these relationships. For each of these trait correlations, the observed empirical data generally support these predictions. The value of M_c is the mass of carbon assimilated by photosynthesis and a_L^{total} is the total leaf area of the plant (see Supplementary Information).

Thus, the value of β_G can now be predicted by measuring several key functional traits (a_L/m_L, $\dot{A}_L$, c, ω, ϕ_L, ρ and θ or M_L/M^θ, instead of $\phi_L\rho$) and, if necessary, their covariances. Additional knowledge of M would then allow us to predict growth rate.

We assessed our model in four ways. First, using equations (2) to (4) for both angiosperms and gymnosperms, we calculated the respective values of β_G and β_A by compiling global trait data sets in addition to the growing-season length, t_S^{max} (see Supplementary Information). Because growth data were on an annual basis (whole-plant biomass production $\dot{M}_A$ in units of g yr^{-1}), we approximated equation (3) by converting to an annual timescale by multiplying $\dot{A}_L$ by t_S^{max} (see Table 1 and the Supplementary Information). Confidence intervals were generated by resampling the trait distributions 100,000 times. Figure 1 and Tables 1 and 2 show that our predictions successfully approximate, with no free parameters, empirical scaling of plant growth. As supported by data, our model predicts that gymnosperms should have a higher value of β_A than angiosperms but, interestingly, both taxa have similar values of β_G due to opposing mean trait differences in a_L/m_L and $\dot{A}_L$ (Tables 1 and 2 and Fig. 1).

Second, as specified by equation (3), we assembled a smaller data set that consisted of species-specific mean trait values and individual data for plant biomass and growth. Then we used the trait data to predict the individual annual growth rates $\dot{M}_A$. Plotting the predicted $\dot{M}_A$ versus the observed $\dot{M}_A$ provides support for the model (Fig. 2).

Third, as a quantitative test, we rearranged the growth law to predict the geometric mean of a difficult-to-measure plant trait: carbon use efficiency, *c*. We calculated *c* in two ways. Rearranging equation (3) reveals that a plot of the inverse of whole-plant growth time versus the inverse of leaf physiological time (both expressed per unit leaf mass in units of t^{-1})—$[(\omega\dot{M}_A)/(\beta_L M^\theta)]$ versus $[(a_L/m_L)(\dot{A}_L t_S^{max})]$—will yield a straight line with a slope of 1.0 and an intercept the value of which is the average carbon use efficiency *c*. Empirical data generally support this prediction (Fig. 3a). The intercept of this fitted regression is the estimated value of *c* (reduced major axis regression, RMA intercept = 0.40, 95% confidence interval, CI = 0.33–0.49), which overlaps with empirical[22,25] measures of *c*. Interestingly, Fig. 3 also shows large residual variation, indicating that *c* varies between and possibly within taxa. Next, solving for *c* in equation (3), we used functional traits to calculate whole-plant *c* for several individuals. In close agreement with data[22] the value of *c* across individuals averaged 0.427 and ranged from ~0.2 to ~0.7 (see Table 1 and the Supplementary Information).

Interestingly, variation in our calculated value of *c* is positively correlated with elevation and latitude (see Supplementary Fig. 1), and negatively related to t_S^{max} ($r^2=0.119$, d.f. = 75, $F=10.17$, $P=0.002$). However, multiple regression indicates that both t_S^{max} and latitude explain 85% of variation in *c* ($r^2=0.726$, d.f. = 67, Akaike information criterion, AIC = −303.17). These findings are similar to those of recent studies indicating that lowland tropical forests are less carbon efficient[26] than forests having cold, short growing seasons[25,27]. Further, such variation in *c* is consistent with the hypothesis that variation in growth and tissue nutrient content across temperature gradients is adaptive[27,28], as well as that in more tropical/warm environments increased rates of herbivory and/or carbon loss to symbionts and enemies[29] may come at a cost to growth. Together, these results highlight a potential use of our model: estimating a hard-to-measure plant trait (*c*), that has profound implications for ecosystem carbon budgets, with data on growth and a handful of plant traits.

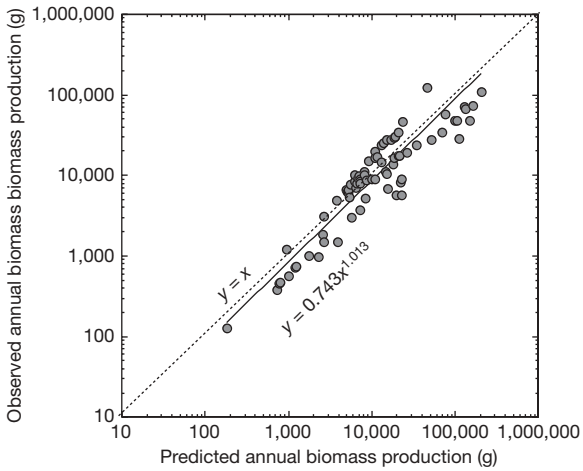

Figure 2 | Using plant traits to predict individual growth rates. For each individual, we used *M* (roots, stems, leaves) and the calculated t_S^{max} (see Supplementary Information) to calculate the predicted annual biomass production, $\dot{M}_A$. We note that the fitted RMA intercept and slope are indistinguishable from 1.0 (fitted RMA intercept = 0.743, 95% CI = 0.322–1.71; slope = 1.01, 95% CI = 0.923–1.10, $R^2=0.855$, $n=79$, $P<0.001$), indicating that predicting annual growth from trait data provides a reasonable approximation of annual growth (see Supplementary Information). The dashed line is the unity line, where the predicted values equal the observed values. Use of Ordinary Least Squares Regression does not change our results.

Fourth, we rearranged equations (3) to (4) to set one trait as a function of others to predict how traits trade off against one another and against growth rate (see Table 2 and Supplementary Information and Table 3 for a summary of key variables). Specifically, equations (3) to (4) (see also section XI of the Supplementary Information) allows us to predict, again with no free parameters, many interspecific trait correlations reported in the FTS literature including:

(1) that the specific leaf area, a_L/m_L, negatively covaries with the allometric leaf mass fraction β_L (see Fig. 4 in the Supplementary Information);

(2) that β_L scales inversely with plant tissue density with a slope of $-\theta$ (Supplementary Fig. 2);

(3); that many leaf traits including carbon flux $\dot{A}_L$ and a_L/m_L are usually independent of tissue density ρ (refs 15, 17 and Supplementary Figs 3 and 4);

(4) that ρ is negatively related to the allometric leaf area ratio (LAR, the quotient of total leaf area, $a_L^{total} = a_L N_L$, to total plant mass, where $LAR = a_L^{total}/\phi_L M^\theta$) and

(5) how these and other trait correlations (including the relationship between m_L and ρ) can also be influenced by additional trait covariation (Table 2 and Supplementary Fig. 4 and Supplementary Information).

As a result, our model provides a basis for understanding the mechanistic origin of several trait correlations and possibly trait covariation in general (see also ref. 30).

Thus, building on classic RGR studies, we have derived a general model for plant growth that integrates MST and includes many traits reported in the FTS literature. Further, the model provides a basis to understand numerous FTS trait correlations. As a result, our model shows that many of the observed correlations in the FTS literature are also influenced by additional traits detailed by MST, including plant size and the geometry of the vascular network branching architecture θ. Importantly, it also shows how allometric scaling normalizations (for example, β_L, β_A and β_G) that are not explicitly derived in MST uniquely originate in the key traits specified in FTS. In doing so, our model can then also explain the origins of vertical scatter in allometric relationships and how species differentiate from each other allometrically via differences in functional traits[12]. Furthermore, climatic or other site differences associated with functional trait variation can be linked to growth rate variation through the unified framework of our production model. Our model also indicates that studies assessing the generality of FTS must control for potential covariation in the traits listed in the scaling constants (see Supplementary Information) and that a few key plant traits (c, ϕ_L, θ and ω) have been overlooked in the FTS literature and may have important implications for plant communities and ecosystem functioning.

Our model can also be used as a point of departure for more detailed synthetic investigations (see Supplementary Information). For example, the explicit consideration of the allocation of metabolic production to reproduction and other plant organs will modify growth (see Supplementary Information). Also, the role of variation

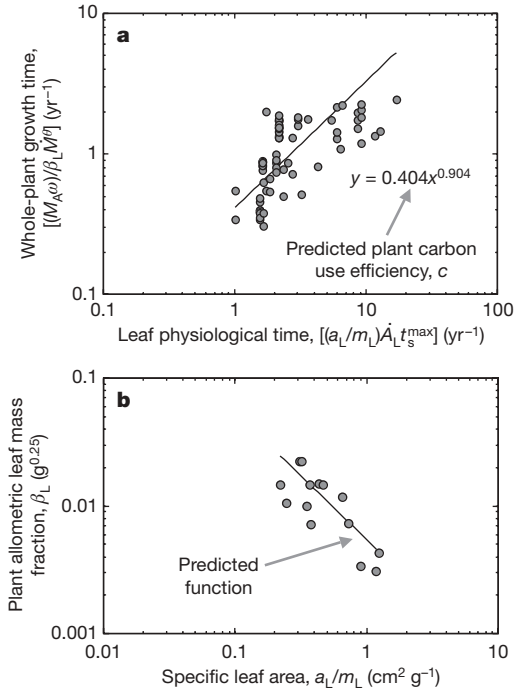

Figure 3 | Using plant traits and growth rate to predict carbon use efficiency and FTS. a, Plot of the relationship between the inverse of whole-plant growth time versus the inverse of leaf physiological time. According to our model, the best fit to the data should yield a straight line with a slope of 1.0 and an intercept the value of which is the carbon use efficiency, c (see Tables 1 and 2 and Supplementary Information). The fitted intercept, 0.40, is indistinguishable from values of c reported in the literature[22,25] (see Tables 1 and 2). We note that the large degree of residual variation indicates substantial variation in c across individuals. Indeed, much of the variation observed appears to be driven by environmental gradients (see Supplementary Fig. 1). **b**, Interspecific relationship between the leaf trait a_L/m_L and a whole-plant trait, the allometric leaf mass fraction, β_L. Our model predicts $a_L/m_L = \tau(\beta_L)^{-1}$, where $\tau \equiv \omega\dot{M}_A/c\dot{A}_L t_S^{max} M^\theta$ (measured in units of cm^2 g$^{-3/4}$). Thus, plotting a_L/m_L versus β_L should yield a slope of –1. The model provides a testable prediction for the origin of the scaling normalization, τ. For these individuals we obtained values for the traits that govern τ. Using these traits, we predict an average value of $\tau = 0.0035$ (95% CI = −0.005 to 0.003). The predicted line, $a_L/m_L = 0.0035(\beta_L)^{-1}$, closely matches the fitted regression (see Table 1) indicating, using no free fitted parameters, that our model accurately predicts this functional relationship.

Table 3 | Definitions of key variables

Symbol	Description	Units
M	Whole-plant mass (mass of the plant's branching network including the roots, stems, and leaf petioles)	g
β_A	Allometric normalization, the net whole-plant biomass produced per unit leaf mass, $\beta_A = NAR \times a_L/m_L = \dot{M}/M_L = (c\dot{A}_L/\omega)(a_L/m_L)$	g t^{-1} g^{-1}
β_L	Allometric normalization, the size-weighted leaf mass fraction, where $\beta_L = M_L/M^\theta$	g$^{(1-\theta)}$
β_G	Allometric normalization for growth, where $\beta_G = \beta_L\beta_A$	g$^{(1-\theta)}$
M_L	Whole-plant leaf mass	g
$\dot{A}_L$	Area-specific carbon assimilation rate of a leaf	g C cm^{-2} t^{-1}
$\dot{m}_L$	Rate of biomass production per leaf, $\dot{m}_L = \left(\frac{c}{\omega}\dot{A}_L\right)a_L$	g t^{-1}
a_L	Area of a leaf (for example, the lamina area of a leaf)	cm^2
m_L	Mass of a leaf	g
N_L	Number of leaves per plant, $N_L = M_L/m_L$	Dimensionless
ω	Carbon fraction of plant	Dimensionless
c	Carbon use efficiency	Dimensionless
ρ	Whole plant tissue density, $\rho = M/V$	g m^{-3}
$\dot{M}$	Whole-plant biomass production rate, $\dot{M} = dM/dt = (M_L/m_L)\dot{m}_L$	g t^{-1}
$\dot{M}_A$	Whole-plant annual biomass production	g yr^{-1}
ϕ_L	Leaf mass per allometrically weighted plant volume, $\phi_L = M_L/V^\theta$	g m$^{-3\theta}$
t_S^{max}	Growing season length	t
θ	Composite trait calculated by the ratios of branch radii and lengths (see Supplementary Information)	Dimensionless

See also Supplementary Information for a more detailed derivation and listing.

in tissue nutrient stoichiometry (nitrogen and phosphorus), temperature and light can be incorporated via influences on $\dot{A}_L$ and c (see Supplementary Information)[7,8,28].

The development of a general quantitative theory to understand how selection can shape integrated plant phenotypes and to make more accurate predictions for the role of plants in the cycling of water, nutrients and carbon within ecosystems is central to comparative botany, physiology, and ecosystem studies. Linking RGR, MST and FTS promises to provide a general framework for explaining how the ecological and evolutionary forces that influence botanical form, function and diversity then ramify to influence the fluxes and pools of matter and energy within and across ecosystems.

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