Rate of tree carbon accumulation increases continuously with tree size

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Forests are major components of the global carbon cycle, providing substantial feedback to atmospheric greenhouse gas concentrations¹. Our ability to understand and predict changes in the forest carbon cycle-particularly net primary productivity and carbon storageincreasingly relies on models that represent biological processes across several scales of biological organization, from tree leaves to forest stands^{2,3}. Yet, despite advances in our understanding of productivity at the scales of leaves and stands, no consensus exists about the nature of productivity at the scale of the individual tree⁴⁻⁷, in part because we lack a broad empirical assessment of whether rates of absolute tree mass growth (and thus carbon accumulation) decrease, remain constant, or increase as trees increase in size and age. Here we present a global analysis of 403 tropical and temperate tree species, showing that for most species mass growth rate increases continuously with tree size. Thus, large, old trees do not act simply as senescent carbon reservoirs but actively fix large amounts of carbon compared to smaller trees; at the extreme, a single big tree can add the same amount of carbon to the forest within a year as is contained in an entire mid-sized tree. The apparent paradoxes of individual tree growth increasing with tree size despite declining leaf-level⁸⁻¹⁰ and stand-level¹⁰ productivity can be explained, respectively, by increases in a tree's total leaf area that outpace declines in productivity per unit of leaf area and, among other factors, age-related reductions in population density. Our results resolve conflicting assumptions about the nature of tree growth, inform efforts to undertand and model forest carbon dynamics, and have additional implications for theories of resource allocation¹¹ and plant senescence¹².

A widely held assumption is that after an initial period of increasing growth, the mass growth rate of individual trees declines with increasing tree size^{4,5,13–16}. Although the results of a few single-species studies have been consistent with this assumption¹⁵, the bulk of evidence cited in support of declining growth is not based on measurements of individual tree mass growth. Instead, much of the cited evidence documents either the well-known age-related decline in net primary productivity (hereafter 'productivity') of even-aged forest stands¹⁰ (in which the trees are all of a similar age) or size-related declines in the rate of mass gain per

unit leaf area (or unit leaf mass)^{8–10}, with the implicit assumption that declines at these scales must also apply at the scale of the individual tree. Declining tree growth is also sometimes inferred from life-history theory to be a necessary corollary of increasing resource allocation to reproduction^{11,16}. On the other hand, metabolic scaling theory predicts that mass growth rate should increase continuously with tree size⁶, and this prediction has also received empirical support from a few site-specific studies^{6,7}. Thus, we are confronted with two conflicting generalizations about the fundamental nature of tree growth, but lack a global assessment that would allow us to distinguish clearly between them.

To fill this gap, we conducted a global analysis in which we directly estimated mass growth rates from repeated measurements of 673,046 trees belonging to 403 tropical, subtropical and temperate tree species, spanning every forested continent. Tree growth rate was modelled as a function of log(tree mass) using piecewise regression, where the independent variable was divided into one to four bins. Conjoined line segments were fitted across the bins (Fig. 1).

For all continents, aboveground tree mass growth rates (and, hence, rates of carbon gain) for most species increased continuously with tree mass (size) (Fig. 2). The rate of mass gain increased with tree mass in each model bin for 87% of species, and increased in the bin that included the largest trees for 97% of species; the majority of increases were statistically significant (Table 1, Extended Data Fig. 1 and Supplementary Table 1). Even when we restricted our analysis to species achieving the largest sizes (maximum trunk diameter >100 cm; 33% of species), 94% had increasing mass growth rates in the bin that included the largest trees. We found no clear taxonomic or geographic patterns among the 3% of species with declining growth rates in their largest trees, although the small number of these species (thirteen) hampers inference. Declining species included both angiosperms and gymnosperms in seven of the 76 families in our study; most of the seven families had only one or two declining species and no family was dominated by declining species (Supplementary Table 1).

When we log-transformed mass growth rate in addition to tree mass, the resulting model fits were generally linear, as predicted by metabolic scaling theory⁶ (Extended Data Fig. 2). Similar to the results of our main

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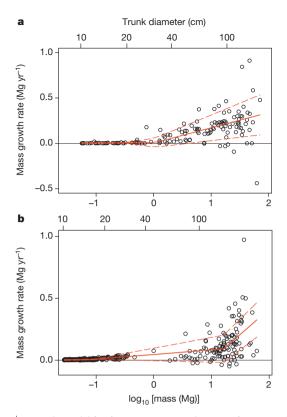


Figure 1 Example model fits for tree mass growth rates. The species shown are the angiosperm species (*Lecomtedoxa klaineana*, Cameroon, 142 trees) (**a**) and gymnosperm species (*Picea sitchensis*, USA, 409 trees) (**b**) in our data set that had the most massive trees (defined as those with the greatest cumulative aboveground dry mass in their five most massive trees). Each point represents a single tree; the solid red lines represent best fits selected by our model; and the dashed red lines indicate one standard deviation around the predicted values.

analysis using untransformed growth, of the 381 log-transformed species analysed (see Methods), the log-transformed growth rate increased in the bin containing the largest trees for 96% of species.

In absolute terms, trees 100 cm in trunk diameter typically add from 10 kg to 200 kg of aboveground dry mass each year (depending on species), averaging 103 kg per year. This is nearly three times the rate for trees of the same species at 50 cm in diameter, and is the mass equivalent to adding an entirely new tree of 10–20 cm in diameter to the forest each year. Our findings further indicate that the extraordinary growth recently reported in an intensive study of large *Eucalyptus regnans* and *Sequoia sempervirens*⁷, which included some of the world's most massive individual trees, is not a phenomenon limited to a few unusual species. Rather, rapid growth in giant trees is the global norm, and can exceed 600 kg per year in the largest individuals (Fig. 3).

Our data set included many natural and unmanaged forests in which the growth of smaller trees was probably reduced by asymmetric competition with larger trees. To explore the effects of competition, we calculated mass growth rates for 41 North American and European species that had published equations for diameter growth rate in the absence of competition. We found that, even in the absence of competition, 85% of the species had mass growth rates that increased continuously with tree size (Extended Data Fig. 3), with growth curves closely resembling those in Fig. 2. Thus, our finding of increasing growth not only has broad generality across species, continents and forest biomes (tropical, subtropical and temperate), it appears to hold regardless of competitive environment.

Importantly, our finding of continuously increasing growth is compatible with the two classes of observations most often cited as evidence of declining, rather than increasing, individual tree growth: with increasing tree size and age, productivity usually declines at the scales of both tree organs (leaves) and tree populations (even-aged forest stands).

First, although growth efficiency (tree mass growth per unit leaf area or leaf mass) often declines with increasing tree size⁸⁻¹⁰, empirical observations and metabolic scaling theory both indicate that, on average, total tree leaf mass increases as the square of trunk diameter^{17,18}. A typical tree that experiences a tenfold increase in diameter will therefore undergo a roughly 100-fold increase in total leaf mass and a 50–100-fold

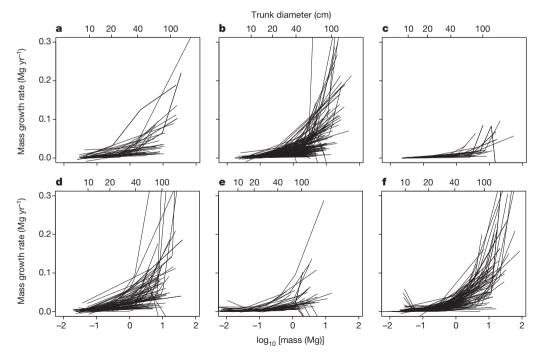


Figure 2 Aboveground mass growth rates for the 403 tree species, by continent. a, Africa (Cameroon, Democratic Republic of the Congo); b, Asia (China, Malaysia, Taiwan, Thailand); c, Australasia (New Zealand); d, Central and South America (Argentina, Colombia, Panama); e, Europe (Spain); and

f, North America (USA). Numbers of trees, numbers of species and percentages with increasing growth are given in Table 1. Trunk diameters are approximate values for reference, based on the average diameters of trees of a given mass.

Table 1 | Sample sizes and tree growth trends by continent

Continent	Number of trees	Number of species	Percentage of species with increasing mass growth rate in the largest trees (percentage significant at $P \le 0.05$)
Africa	15,366	37	100.0 (86.5)
Asia	43,690	136	96.3 (89.0)
Australasia	45,418	22	95.5 (95.5)
Central and South America	18,530	77	97.4 (92.2)
Europe	439,889	42	90.5 (78.6)
North America	110,153	89	98.9 (94.4)
Total	673,046	403	96.8 (89.8)

The largest trees are those in the last bin fitted by the model. Countries are listed in the legend for Fig. 2.

increase in total leaf area (depending on size-related increases in leaf mass per unit leaf area^{19,20}). Parallel changes in growth efficiency can range from a modest increase (such as in stands where small trees are suppressed by large trees)²¹ to as much as a tenfold decline²², with most changes falling in between^{8,9,19,22}. At one extreme, the net effect of a low (50-fold) increase in leaf area combined with a large (tenfold) decline in growth efficiency would still yield a fivefold increase in individual tree mass growth rate; the opposite extreme would yield roughly a 100-fold increase. Our calculated 52-fold greater average mass growth rate of trees 100 cm in diameter compared to those 10 cm in diameter falls within this range. Thus, although growth efficiency often declines with increasing tree size, increases in a tree's total leaf area are sufficient to overcome this decline and cause whole-tree carbon accumulation rate to increase.

Second, our findings are similarly compatible with the well-known age-related decline in productivity at the scale of even-aged forest stands. Although a review of mechanisms is beyond the scope of this paper^{10,23}, several factors (including the interplay of changing growth efficiency and tree dominance hierarchies²⁴) can contribute to declining productivity at the stand scale. We highlight the fact that increasing individual tree growth rate does not automatically result in increasing stand productivity because tree mortality can drive orders-of-magnitude reductions in population density^{25,26}. That is, even though the large trees in older, even-aged stands may be growing more rapidly, such stands have fewer trees. Tree population dynamics, especially mortality, can thus be a significant contributor to declining productivity at the scale of the forest stand²³.

For a large majority of species, our findings support metabolic scaling theory's qualitative prediction of continuously increasing growth

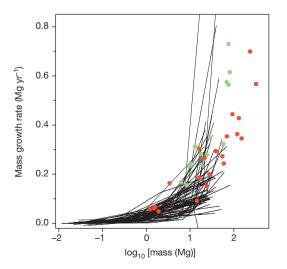


Figure 3 Aboveground mass growth rates of species in our data set compared with *E. regnans* and *S. sempervirens*. For clarity, only the 58 species in our data set having at least one tree exceeding 20 Mg are shown (lines). Data for *E. regnans* (green dots, 15 trees) and *S. sempervirens* (red dots, 21 trees) are from an intensive study that included some of the most massive individual trees on Earth⁷. Both axes are expanded relative to those of Fig. 2.

at the scale of individual trees⁶, with several implications. For example, life-history theory often assumes that tradeoffs between plant growth and reproduction are substantial¹¹. Contrary to some expectations^{11,16}, our results indicate that for most tree species size-related changes in reproductive allocation are insufficient to drive long-term declines in growth rates⁶. Additionally, declining growth is sometimes considered to be a defining feature of plant senescence¹². Our findings are thus relevant to understanding the nature and prevalence of senescence in the life history of perennial plants²⁷.

Finally, our results are relevant to understanding and predicting forest feedbacks to the terrestrial carbon cycle and global climate system¹⁻³. These feedbacks will be influenced by the effects of climatic, land-use and other environmental changes on the size-specific growth rates and size structure of tree populations—effects that are already being observed in forests^{28,29}. The rapid growth of large trees indicates that, relative to their numbers, they could play a disproportionately important role in these feedbacks³⁰. For example, in our western USA old-growth forest plots, trees >100 cm in diameter comprised 6% of trees, yet contributed 33% of the annual forest mass growth. Mechanistic models of the forest carbon cycle will depend on accurate representation of productivity across several scales of biological organization, including calibration and validation against continuously increasing carbon accumulation rates at the scale of individual trees.

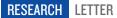
METHODS SUMMARY

We estimated aboveground dry mass growth rates from consecutive diameter measurements of tree trunks-typically measured every five to ten years-from longterm monitoring plots. Analyses were restricted to trees with trunk diameter \geq 10 cm, and to species having \geq 40 trees in total and \geq 15 trees with trunk diameter \geq 30 cm. Maximum trunk diameters ranged from 38 cm to 270 cm among species, averaging 92 cm. We converted each diameter measurement (plus an accompanying height measurement for 16% of species) to aboveground dry mass, M, using published allometric equations. We estimated tree growth rate as $G = \Delta M / \Delta t$ and modelled G as a function of log(M) for each species using piecewise regression. The independent variable log(M) was divided into bins and a separate line segment was fitted to G versus log(M) in each bin so that the line segments met at the bin divisions. Bin divisions were not assigned a priori, but were fitted by the model separately for each species. We fitted models with 1, 2, 3 and 4 bins, and selected the model receiving the most support by Akaike's Information Criterion for each species. Our approach thus makes no assumptions about the shape of the relationship between G and log(M), and can accommodate increasing, decreasing or hump-shaped relationships. Parameters were fitted with a Gibbs sampler based on Metropolis updates, producing credible intervals for model parameters and growth rates at any diameter; uninformative priors were used for all parameters. We tested extensively for bias, and found no evidence that our results were influenced by model fits failing to detect a final growth decline in the largest trees, possible biases introduced by the 47% of species for which we combined data from several plots, or possible biases introduced by allometric equations (Extended Data Figs 4 and 5).

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

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 Pan, Y. et al. A large and persistent carbon sink in the world's forests. Science 333, 988–993 (2011).



- Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y. & Moorcroft, P. R. 2. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. J. Geophys. Res. 114, G01002 (2009).
- Caspersen, J. P., Vanderwel, M. C., Cole, W. G. & Purves, D. W. How stand 3 productivity results from size- and competition-dependent growth and mortality. . PLoS ONE **6,** e28660 (2011).
- 4. Kutsch, W. L. et al. in Old-Growth Forests: Function, Fate and Value (eds Wirth, C., Gleixner, G. & Heimann, M.) 57-79 (Springer, 2009).
- Meinzer, F. C., Lachenbruch, B. & Dawson, T. E. (eds) Size- and Age-Related Changes 5 in Tree Structure and Function (Springer, 2011).
- Enquist, B. J., West, G. B., Charnov, E. L. & Brown, J. H. Allometric scaling of 6 production and life-history variation in vascular plants. Nature 401, 907-911 (1999)
- 7 Sillett, S. C. et al. Increasing wood production through old age in tall trees. For. Ecol. Manage. 259, 976-994 (2010).
- 8. Mencuccini, M. et al. Size-mediated ageing reduces vigour in trees. Ecol. Lett. 8, 1183-1190 (2005).
- 9. Drake, J. E., Raetz, L. M., Davis, S. C. & DeLucia, E. H. Hydraulic limitation not declining nitrogen availability causes the age-related photosynthetic decline in loblolly pine (Pinus taeda L.). Plant Cell Environ. 33, 1756-1766 (2010).
- 10 Ryan, M. G., Binkley, D. & Fownes, J. H. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27, 213-262 (1997).
- Thomas, S. C. in Size- and Age-Related Changes in Tree Structure and Function 11.
- (eds Meinzer, F. C., Lachenbruch, B. & Dawson, T. E.) 33-64 (Springer, 2011). Thomas, H. Senescence, ageing and death of the whole plant. New Phytol. 197, 12.
- 696-711 (2013).
- Carey, E. V., Sala, A., Keane, R. & Callaway, R. M. Are old forests underestimated as global carbon sinks? *Glob. Change Biol.* 7, 339–344 (2001).
 Phillips, N. G., Buckley, T. N. & Tissue, D. T. Capacity of old trees to respond to environmental change. *J. Integr. Plant Biol.* 50, 1355–1364 (2008).
- 15 Piper, F. I. & Fajardo, Ā. No evidence of carbon limitation with tree age and height in Nothofagus pumilio under Mediterranean and temperate climate conditions. Ann. Bot. **108,** 907–917 (2011).
- Weiner, J. & Thomas, S. C. The nature of tree growth and the "age-related decline in 16. forest productivity". Oikos 94, 374-376 (2001).
- 17. Jenkins, J. C., Chojnacky, D. C., Heath, L. S. & Birdsey, R. A. Comprehensive Database of Diameter-based Biomass Regressions for North American Tree Species General Technical Report NE-319, http://www.nrs.fs.fed.us/pubs/6725 (USDA Forest Service, Northeastern Research Station, 2004).
- 18. Niklas, K. J. & Enquist, B. J. Canonical rules for plant organ biomass partitioning and annual allocation. Am. J. Bot. 89, 812-819 (2002).
- 19. Thomas, S. C. Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. Tree Physiol. 30, 555-573 (2010).
- Steppe, K., Niinemets, Ü. & Teskey, R. O. in Size- and Age-Related Changes in Tree 20 Structure and Function (eds Meinzer, F. C., Lachenbruch, B. & Dawson, T. E.) 235–253 (Springer, 2011).
- 21. Gilmore, D. W. & Seymour, R. S. Alternative measures of stem growth efficiency applied to Abies balsamea from four canopy positions in central Maine, USA. For. Ecol. Manage. **84,** 209–218 (1996).
- Kaufmann, M. R. & Ryan, M. G. Physiographic, stand, and environmental effects on 22 individual tree growth and growth efficiency in subalpine forests. Tree Physiol. 2, 47–59 (1986).
- 23. Coomes, D. A., Holdaway, R. J., Kobe, R. K., Lines, E. R. & Allen, R. B. A general integrative framework for modelling woody biomass production and carbon sequestration rates in forests. J. Ecol. 100, 42–64 (2012).
- Binkley, D. A hypothesis about the interaction of tree dominance and stand 24. production through stand development. For. Ecol. Manage. 190, 265-271 (2004).

- 25. Pretzsch, H. & Biber, P. A re-evaluation of Reineke's rule and stand density index. For. Sci. 51, 304-320 (2005).
- 26. Kashian, D. M., Turner, M. G., Romme, W. H. & Lorimer, C. G. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology 86, 643-654 (2005).
- 27. Munné-Bosch, S. Do perennials really senesce? Trends Plant Sci. 13, 216-220 (2008)
- 28 Jump, A. S., Hunt, J. M. & Peñuelas, J. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Glob. Change Biol. 12, 2163-2174 (2006)
- Lindenmayer, D. B., Laurance, W. F. & Franklin, J. F. Global decline in large old trees. 29. Science 338, 1305–1306 (2012).
- 30. Enquist, B. J., West, G. B. & Brown, J. H. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. Proc. Natl Acad. Sci. USA 106, 7046-7051 (2009).

Supplementary Information is available in the online version of the paper.

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Author Contributions N.L.S. and A.J.D. conceived the study with feedback from R.C. and D.A.C., N.L.S., A.J.D., R.C. and S.E.R. wrote the manuscript. R.C. devised the main analytical approach and wrote the computer code. N.L.S., A.J.D., R.C., S.E.R., P.J.B., N.G.B., D.A.C., E.R.L., W.K.M. and N.R. performed analyses. N.L.S., A.J.D., R.C., S.E.R., P.J.B., D.A.C., E.R.L., W.K.M., E.Á., C.B., S.B., G.C., S.J.D., ÅD., C.N.E., O.F., J.F.F., H.R.G., Z.H., M.E.H., S.P.H., D.K., Y.L., J.-R.M., A.M., L.R.M., R.J.P., N.P., S.-H.S., I-F.S., S.T., D.T., P.J.v.M., X.W., S.K.W. and M.A.Z. supplied data and sources of allometric equations appropriate to their data.

Author Information Fitted model parameters for each species have been deposited in USGS's ScienceBase at http://dx.doi.org/10.5066/F7JS9NFM. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to N.L.S. (nstephenson@usgs.gov).

METHODS

Data. We required that forest monitoring plots provided unbiased samples of all living trees within the plot boundaries, and that the trees had undergone two trunk diameter measurements separated by at least one year. Some plots sampled minimally disturbed old (all-aged) forest, whereas others, particularly those associated with national inventories, sampled forest stands regardless of past management history. Plots are described in the references cited in Supplementary Table 1.

Our raw data were consecutive measurements of trunk diameter, *D*, with most measurements taken 5 to 10 years apart (range, 1–29 years). *D* was measured at a standard height on the trunk (usually 1.3–1.4 m above ground level), consistent across measurements for a tree. Allometric equations for 16% of species required, in addition to consecutive measurements of *D*, consecutive measurements of tree height.

We excluded trees exhibiting extreme diameter growth, defined as trunks where D increased by $\geq 40 \text{ mm yr}^{-1}$ or that shrank by $\geq 12s$, where s is the standard deviation of the D measurement error, s = 0.9036 + 0.006214D (refs 31, 32); outliers of these magnitudes were almost certainly due to error. By being so liberal in allowing negative growth anomalies, we erred on the side of reducing our ability to detect increases in tree mass growth rate. Using other exclusion values yielded similar results, as did a second approach to handling error in which we reanalysed a subset of our models using a Bayesian method that estimates growth rates after accounting for error, based on independent plot-specific data quantifying measurement error³³.

To standardize minimum *D* among data sets, we analysed only trees with $D \ge 10$ cm at the first census. To ensure adequate samples of trees spanning a broad range of sizes, we restricted analyses to species having both ≥ 40 trees in total and also ≥ 15 trees with $D \ge 30$ cm at the first census. This left us with 673,046 trees belonging to 403 tropical and temperate species in 76 families, spanning twelve countries and all forested continents (Supplementary Table 1). Maximum trunk diameters ranged from 38 cm to 270 cm among species, and averaged 92 cm.

Estimating tree mass. To estimate each tree's aboveground dry mass, M, we used published allometric equations relating M to D (or for 16% of species, relating M to D and tree height). Some equations were species-specific and others were specific to higher taxonomic levels or forest types, described in the references in Supplementary Table 1. The single tropical moist forest equation of ref. 34 was applied to most tropical species, whereas most temperate species had unique species-specific equations. Most allometric equations are broadly similar, relating $\log(M)$ to $\log(D)$ linearly, or nearly linearly—a familiar relationship in allometric scaling of both animals and plants³⁵. Equations can show a variety of differences in detail, however, with some adding $\log(D)$ squared and cubed terms. All equations make use of the wood density of individual species, but when wood density was not available for a given species we used mean wood density for a genus or family³⁶.

Using a single, average allometry for most tropical species, and mean wood density for a genus or family for several species, limits the accuracy of our estimates of *M*. However, because we treat each species separately, it makes no difference whether our absolute *M* estimates are more accurate in some species than in others, only that they are consistent within a species and therefore accurately reveal whether mass growth rates increase or decrease with tree size.

For two regions—Spain and the western USA—allometric equations estimated mass only for a tree's main stem rather than all aboveground parts, including branches and leaves. But because leaf and stem masses are positively correlated and their growth rates are expected to scale isometrically both within and among species^{18,37,38}, results from these two regions should not alter our qualitative conclusions. Confirming this, the percentage of species with increasing stem mass growth rate in the last bin for Spain and the western USA (93.4% of 61 species) was similar to that from the remainder of regions (97.4% of 342 species) (P = 0.12, Fisher's exact test).

Modelling mass growth rate. We sought a modelling approach that made no assumptions about the shape of the relationship between aboveground dry mass growth rate, *G*, and aboveground dry mass, *M*, and that could accommodate monotonically increasing, monotonically decreasing, or hump-shaped relationships. We therefore chose to model *G* as a function of $\log(M)$ using piecewise linear regression. The range of the *x* axis, $X = \log(M)$, is divided into a series of bins, and within each bin *G* is fitted as a function of *X* by linear regression. The position of the bins is adaptive: it is fitted along with the regression terms. Regression lines are required to meet at the boundary between bins. For a single model-fitting run the number of bins, *B*, is fixed. For example, if B = 2, there are four parameters to be fitted for a single species: the location of the boundary between bins, S_2 ; and an intercept term. Those four parameters completely define the model. In general, there are 2*B* parameters for *B* bins.

Growth rates, while approximately normally distributed, were heteroskedastic, with the variance increasing with mass (Fig. 1), so an additional model was needed for the standard deviation of G, σ_G , as a function of $\log(M)$. The increase of σ_G

with log(M) was clearly not linear, so we used a three-parameter model:

$$\sigma_G = k$$
 (for log(M) < d)
 $\sigma_G = a + b \log(M)$ (for log(M) $\ge d$)

where the intercept *a* is determined by the values of *k*, *d* and *b*. Thus σ_G was constant for smaller values of log(*M*) (below the cutoff *d*), then increased linearly for larger log(*M*) (Fig. 1). The parameters *k*, *d* and *b* were estimated along with the parameters of the growth model.

Parameters of both the growth and standard deviation models were estimated in a Bayesian framework using the likelihood of observing growth rates given model predictions and the estimated standard deviation of the Gaussian error function. A Markov chain Monte Carlo chain of parameter estimates was created using a Gibbs sampler with a Metropolis update^{39,40} written in the programming language R (ref. 41) (a tutorial and the computer code are available through http://ctfs.arnarb. harvard.edu/Public/CTFSRPackage/files/tutorials/growthfitAnalysis). The sampler works by updating each of the parameters in sequence, holding other parameters fixed while the relevant likelihood function is used to locate the target parameter's next value. The step size used in the updates was adjusted adaptively through the runs, allowing more rapid convergence⁴⁰. The final Markov chain Monte Carlo chain describes the posterior distribution for each model parameter, the error, and was then used to estimate the posterior distribution of growth rates as estimated from the model. Priors on model parameters were uniform over an unlimited range, whereas the parameters describing the standard deviation were restricted to >0. Bin boundaries, X_i , were constrained as follows: (1) boundaries could only fall within the range of *X*, (2) each bin contained at least five trees, and (3) no bin spanned less than 10% of the range of X. The last two restrictions prevented the bins from collapsing to very narrow ranges of X in which the fitted slope might take absurd extremes.

We chose piecewise regression over other alternatives for modelling G as a function of M for two main reasons. First, the linear regression slopes within each bin provide precise statistical tests of whether G increases or decreases with X, based on credible intervals of the slope parameters. Second, with adaptive bin positions, the function is completely flexible in allowing changes in slope at any point in the X range, with no influence of any one bin on the others. In contrast, in parametric models where a single function defines the relationship across all X, the shape of the curve at low X can (and indeed must) influence the shape at high X, hindering statistical inference about changes in tree growth at large size.

We used $\log(M)$ as our predictor because within a species M has a highly non-Gaussian distribution, with many small trees and only a few very large trees, including some large outliers. In contrast, we did not log-transform our dependent variable G so that we could retain values of $G \le 0$ that are often recorded in very slowly growing trees, for which diameter change over a short measurement interval can be on a par with diameter measurement error.

For each species, models with 1, 2, 3 and 4 bins were fitted. Of these four models, the model receiving the greatest weight of evidence by Akaike Information Criterion (AIC) was selected. AIC is defined as the log-likelihood of the best-fitting model, penalized by twice the number of parameters. Given that adding one more bin to a model meant two more parameters, the model with an extra bin had to improve the log-likelihood by 4 to be considered a better model⁴².

Assessing model fits. To determine whether our approach might have failed to reveal a final growth decline within the few largest trees of the various species, we calculated mass growth rate residuals for the single most massive individual tree of each species. For 52% of the 403 species, growth of the most massive tree was underestimated by our model fits (for example, Fig. 1a); for 48% it was overestimated (for example, Fig. 1b). These proportions were indistinguishable from 50% (P = 0.55, binomial test), as would be expected for unbiased model fits. Furthermore, the mean residual (observed minus predicted) mass growth rate of these most massive trees, $+0.006 \text{ Mg yr}^{-1}$, was statistically indistinguishable from zero (P = 0.29, two-tailed *t*-test). We conclude that our model fits accurately represent growth trends up through, and including, the most massive trees.

Effects of combined data. To achieve sample sizes adequate for analysis, for some species we combined data from several different forest plots, potentially introducing a source of bias: if the largest trees of a species disproportionately occur on productive sites, the increase in mass growth rate with tree size could be exaggerated. This might occur because trees on less-productive sites—presumably the sites having the slowest-growing trees within any given size class—could be underrepresented in the largest size classes. We assessed this possibility in two ways.

First, our conclusions remained unchanged when we compared results for the 53% of species that came uniquely from single large plots with those of the 47% of species whose data were combined across several plots. Proportions of species with increasing mass growth rates in the last bin were indistinguishable between the two groups (97.6% and 95.8%, respectively; P = 0.40, Fisher's exact test). Additionally,

the shapes and magnitudes of the growth curves for Africa and Asia, where data for each species came uniquely from single large plots, were similar to those of Australasia, Europe and North America, where data for each species were combined across several plots (Table 1, Fig. 2 and Extended Data Fig. 2). (Data from Central and South America were from both single and combined plots, depending on species.)

Second, for a subset of combined-data species we compared two sets of model fits: (1) using all available plots (that is, the analyses we present in the main text), and (2) using only plots that contained massive trees-those in the top 5% of mass for a species. To maximize our ability to detect differences, we limited these analyses to species with large numbers of trees found in a large number of plots, dispersed widely across a broad geographic region. We therefore analysed the twelve Spanish species that each had more than 10,000 individual trees (Supplementary Table 1), found in 34,580 plots distributed across Spain. Massive trees occurred in 6,588 (19%) of the 34,580 plots. We found no substantial differences between the two analyses. When all 34,580 plots were analysed, ten of the twelve species showed increasing growth in the last bin, and seven showed increasing growth across all bins; when only the 6,588 plots containing the most massive trees were analysed, the corresponding numbers were eleven and nine. Model fits for the two groups were nearly indistinguishable in shape and magnitude across the range of tree masses. We thus found no evidence that the potential for growth differences among plots influenced our conclusions.

Effects of possible allometric biases. For some species, the maximum trunk diameter D in our data sets exceeded the maximum used to calibrate the species' allometric equation. In such cases our estimates of M extrapolate beyond the fitted allometry and could therefore be subject to bias. For 336 of our 403 species we were able to determine D of the largest tree that had been used in calibrating the associated allometric equations. Of those 336 species, 74% (dominated by tropical species) had no trees in our data set with D exceeding that used in calibrating the allometric equations, with the remaining 26% (dominated by temperate species) having at least one tree with D exceeding that used in calibrating the allometric equations G in the last bin for the first group (98.0%) was indistinguishable from that of the second group (96.6%) (P = 0.44, Fisher's exact test). Thus, our finding of increasing G with tree size is not affected by the minority of species that have at least one tree exceeding the maximum value of D used to calibrate their associated allometric equations.

A bias that could inflate the rate at which *G* increases with tree size could arise if allometric equations systematically underestimate *M* for small trees or overestimate *M* for large trees⁴³. For a subset of our study species we obtained the raw data—consisting of measured values of *D* and *M* for individual trees—needed to calibrate allometric equations, allowing us to determine whether the particular form of those species' allometric equations was prone to bias, and if so, the potential consequences of that bias.

To assess the potential for allometric bias for the majority (58%) of species in our data set—those that used the empirical moist tropical forest equation of ref. 34—we reanalysed the data provided by ref. 34. The data were from 1,504 harvested trees representing 60 families and 184 genera, with *D* ranging from 5 cm to 156 cm; the associated allometric equation relates $\log(M)$ to a third-order polynomial of $\log(D)$. Because the regression of *M* on *D* was fitted on a $\log-\log$ scale, this and subsequent equations include a correction of exp[(RSE)²/2] for the error in back-transformation, where RSE is the residual standard error from the statistical model⁴⁴. Residuals of *M* for the equation revealed no evident biases (Extended Data Fig. 4a), suggesting that we should expect little (if any) systematic size-related biases in our estimates of *G* for the 58% of our species that used this equation.

Our simplest form of allometric equation—applied to 22% of our species—was log(M) = a + blog(D), where *a* and *b* are taxon-specific constants. For nine of our species that used equations of this form (all from the temperate western USA: *Abies amabilis, A. concolor, A. procera, Pinus lambertiana, Pinus ponderosa, Picea sitchensis, Pseudotsuga menziesii, Tsuga heterophylla* and *T. mertensiana*) we had values of both *D* and *M* for a total of 1,358 individual trees, allowing us to fit species-specific allometric equations of the form log(M) = a + blog(D) and then assess them for bias. Residual plots showed a tendency to overestimate *M* for the largest trees (Extended Data Fig. 4b), with the possible consequence of inflating estimates of *G* for the largest relative to the smallest trees of these species.

To determine whether this bias was likely to alter our qualitative conclusion that G increases with tree size, we created a new set of allometric relations between D and M—one for each of the nine species—using the same piecewise linear regression approach we used to model G as a function of M. However, because our goal was to eliminate bias rather than seek the most parsimonious model, we fixed the number of bins at four, with the locations of boundaries between the bins being fitted by the model. Our new allometry using piecewise regressions led to predictions of M with no apparent bias relative to D (Extended Data Fig. 4c). This new, unbiased allometry gave the same qualitative results as our original, simple allometry

regarding the relationship between G and M: for all nine species, G increased in the bin containing the largest trees, regardless of the allometry used (Extended Data Fig. 5). We conclude that any bias associated with the minority of our species that used the simple allometric equation form was unlikely to affect our broad conclusion that G increases with tree size in a majority of tree species.

As a final assessment, we compared our results to those of a recent study of E. regnans and S. sempervirens, in which M and G had been calculated from intensive measurements of aboveground portions of trees without the use of standard allometric equations7. Specifically, in two consecutive years 36 trees of different sizes and ages were climbed, trunk diameters were systematically measured at several heights, branch diameters and lengths were measured (with subsets of foliage and branches destructively sampled to determine mass relationships), wood densities were determined and ring widths from increment cores were used to supplement measured diameter growth increments. The authors used these measurements to calculate *M* for each of the trees in each of the two consecutive years, and *G* as the difference in M between the two years⁷. E. regnans and S. sempervirens are the world's tallest angiosperm and gymnosperm species, respectively, so the data set was dominated by exceptionally large trees; most had $M \ge 20$ Mg, and M of some individuals exceeded that of the most massive trees in our own data set (which lacked E. regnans and S. sempervirens). We therefore compared E. regnans and S. sempervirens to the 58 species in our data set that had at least one individual with $M \ge 20$ Mg. Sample sizes for *E. regnans* and *S. sempervirens*—15 and 21 trees, respectively—fell below our required \geq 40 trees for fitting piecewise linear regressions, so we simply plotted data points for individual E. regnans and S. sempervirens along with the piecewise regressions that we had already fitted for our 58 comparison species (Fig. 3).

As reported by ref. 7, *G* increased with *M* for both *E. regnans* and *S. sempervirens*, up to and including some of the most massive individual trees on the Earth (Fig. 3). Within the zone of overlapping *M* between the two data sets, *G* values for individual *E. regnans* and *S. sempervirens* trees fell almost entirely within the ranges of the piecewise regressions we had fitted for our 58 comparison species. We take these observations as a further indication that our results, produced using standard allometric equations, accurately reflect broad relationships between *M* and *G*.

Fitting log–log models. To model log(G) as a function of log(M), we used the binning approach that we used in our primary analysis of mass growth rate (described earlier). However, in log-transforming growth we dropped trees with $G \le 0$. Because negative growth rates become more extreme with increasing tree size, dropping them could introduce a bias towards increasing growth rates. Log-transformation additionally resulted in skewed growth rate residuals. Dropping trees with $G \le 0$ caused several species to fall below our threshold sample size, reducing the total number of species analysed to 381 (Extended Data Fig. 2).

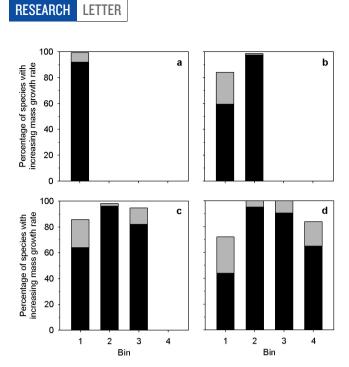
Growth in the absence of competition. We obtained published equations for 41 North American and European species, in 46 species-site combinations, relating species-specific tree diameter growth rates to trunk diameter D and to neighbourhood competition⁴⁵⁻⁴⁹. Setting neighbourhood competition to zero gave us equations describing estimated annual D growth as a function of D in the absence of competition. Starting at $D_0 = 10$ cm, we sequentially (1) calculated annual D growth for a tree of size D_t , (2) added this amount to D_t to determine D_{t+1} , (3) used an appropriate taxon-specific allometric equation to calculate the associated tree masses M_t and M_{t+1} , and (iv) calculated tree mass growth rate G_t of a tree of mass M_t in the absence of competition as $M_{t+1} - M_t$. For each of the five species that had separate growth analyses available from two different sites, we required that mass growth rate increased continuously with tree size at both sites for the species to be considered to have a continuously increasing mass growth rate. North American and European allometries were taken from refs 17 and 50, respectively, with preference given to allometric equations based on power functions of tree diameter, large numbers of sampled trees, and trees spanning a broad range of diameters. For the 47% of European species for which ref. 50 had no equations meeting our criteria, we used the best-matched (by species or genus) equations from ref. 17.

- Condit, R. *et al.* Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J. Trop. Ecol.* **20**, 51–72 (2004).
- Condit, R. et al. The importance of demographic niches to tree diversity. Science 313, 98–101 (2006).
- Rüger, N., Berger, U., Hubbell, S. P., Vieilledent, G. & Condit, R. Growth strategies of tropical tree species: disentangling light and size effects. *PLoS ONE* 6, e25330 (2011).
- Chave, J. et al. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145, 87–99 (2005).
- Sibly, R. M., Brown, J. H. & Kodric-Brown, A. (eds) Metabolic Ecology: A Scaling Approach (John Wiley & Sons, 2012).
- Zanne, A. E. et al. Data from: Towards a worldwide wood economics spectrum. In Dryad Digital Data Repository, http://dx.doi.org/10.5061/dryad.234 (2009).
- Enquist, B. J. & Niklas, K. J. Global allocation rules for patterns of biomass partitioning in seed plants. Science 295, 1517–1520 (2002).



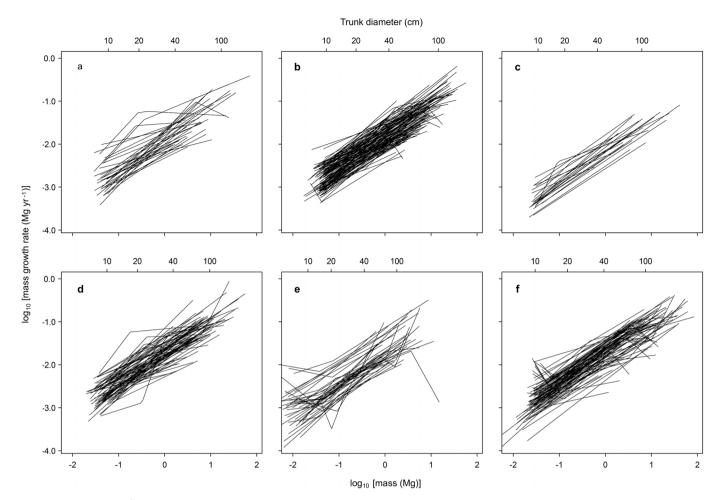
- 38. Niklas, K. J. Plant allometry: is there a grand unifying theory? Biol. Rev. 79, 871-889 (2004).
- 39. Metropolis, N., Rosenbluth, A. W., Rosenbluth, M. N., Teller, A. H. & Teller, E. Equation of state calculations by fast computing machines. J. Chem. Phys. 21, 1087-1092 (1953).
- 40 Rüger, N., Huth, A., Hubbell, S. P. & Condit, R. Determinants of mortality across a tropical lowland rainforest community. Oikos 120, 1047-1056 (2011).
- R Development Core Team. R: A Language and Environment for Statistical 41. Computing (R Foundation for Statistical Computing, 2009).
- 42. Hilborn, R. & Mangel, M. The Ecological Detective: Confronting Models with Data (Princeton Univ. Press, 1997).
- Chambers, J. Q., Dos Santos, J., Ribeiro, R. J. & Higuchi, N. Tree damage, allometric 43 relationships, and above-ground net primary production in central Amazon forest. For. Ecol. Manage. 152, 73–84 (2001).
- 44. Baskerville, G. L. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. 2, 49-53 (1972).

- 45. Canham, C. D. et al. Neighborhood analyses of canopy tree competition along
- environmental gradients in New England forests. *Ecol. Appl.* **16**, 540–554 (2006). 46. Coates, K. D., Canham, C. D. & LePage, P. T. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. 97, 118–130 (2009).
- 47. Pretzsch, H. & Biber, P. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Can. J. For. Res. 40, 370–384 (2010).
- 48. Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P. & Zavala, M. A. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Glob. Change Biol. 17, 2400-2414 (2011).
- Das, A. The effect of size and competition on tree growth rate in old-growth 49. coniferous forests. Can. J. For. Res. 42, 1983–1995 (2012).
 Zianis, D., Muukkonen, P., Makipaa, R. & Mencuccini, M. Biomass and stem volume
- equations for tree species in Europe. Silva Fennica Monogr. 4, 1-63 (2005).



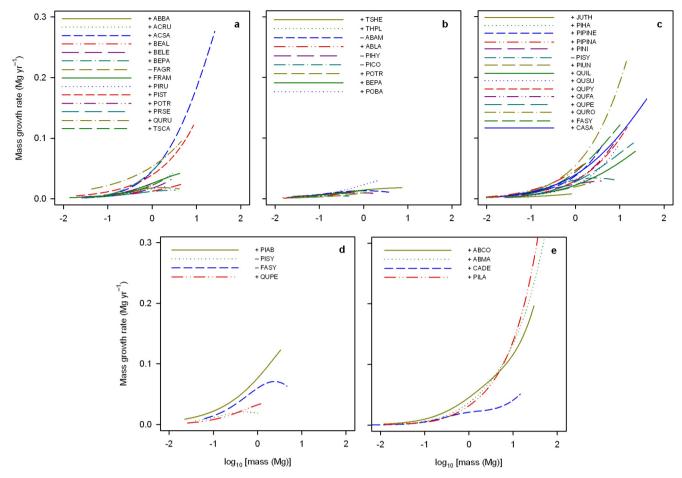
Extended Data Figure 1 | **Summary of model fits for tree mass growth rates.** Bars show the percentage of species with mass growth rates that increase with tree mass for each bin; black shading indicates percentage significant at $P \leq 0.05$. Tree masses increase with bin number. **a**, Species fitted with one bin (165 species); **b**, Species fitted with two bins (139 species); **c**, Species fitted with three bins (56 species); and **d**, Species fitted with four bins (43 species).

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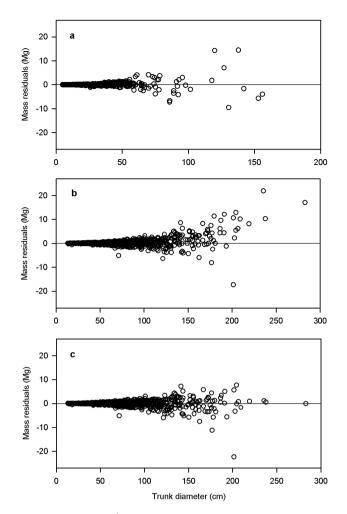
Extended Data Figure 2 | Log-log model fits of mass growth rates for 381 tree species, by continent. Trees with growth rates ≤ 0 were dropped from the analysis, reducing the number of species meeting our threshold sample size for analysis. **a**, Africa (33 species); **b**, Asia (123 species); **c**, Australasia

(22 species); **d**, Central and South America (73 species); **e**, Europe (41 species); and **f**, North America (89 species). Trunk diameters are approximate values for reference, based on the average diameters of trees of a given mass.

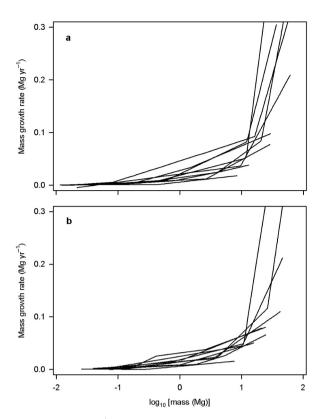


Extended Data Figure 3 | Aboveground mass growth rates for 41 tree species in the absence of competition. The '+' or '-' symbol preceding each species code indicates, respectively, species with mass growth rates that increased continuously with tree size or species with mass growth rates that declined in the largest trees. Sources of the diameter growth equations used to calculate mass growth were: a, ref. 45; b, ref. 46; c, ref. 48; d, ref. 47; and e, ref. 49. ABAM, Abies amabilis; ABBA, Abies balsamea; ABCO, Abies concolor; ABLA, Abies lasiocarpa; ABMA, Abies magnifica; ACRU, Acer rubrum; ACSA, Acer saccharum; BEAL, Betula alleghaniensis; BELE, Betula lenta; BEPA, Betula papyrifera; CADE, Calocedrus decurrens; CASA, Castanea sativa; FAGR, Fagus grandifolia; FASY, Fagus sylvatica; FRAM, Fraxinus americana; JUTH,

Juniperus thurifera; PIAB, Picea abies; PICO, Pinus contorta; PIHA, Pinus halepensis; PIHY, Picea hybrid (a complex of Picea glauca, P. sitchensis and P. engelmannii); PILA, Pinus lambertiana; PINI, Pinus nigra; PIPINA, Pinus pinaster; PIPINE, Pinus pinea; PIRU, Picea rubens; PIST, Pinus strobus; PISY, Pinus sylvestris; PIUN, Pinus uncinata; POBA, Populus balsamifera ssp. trichocarpa; POTR, Populus tremuloides; PRSE, Prunus serotina; QUFA, Quercus faginea; QUIL, Quercus ilex; QUPE, Quercus petraea; QUPY, Quercus pyrenaica; QURO, Quercus robar; QURU, Quercus rubra; QUSU, Quercus suber; THPL, Thuja plicata; TSCA, Tsuga canadensis; and TSHE, Tsuga heterophylla.



Extended Data Figure 4 | **Residuals of predicted minus observed tree mass. a**, The allometric equation for moist tropical forests³⁴—used for the majority of tree species—shows no evident systematic bias in predicted aboveground dry mass, *M*, relative to trunk diameter (n = 1,504 trees). **b**, In contrast, our simplest form of allometric equation—used for 22% of our species and here applied to nine temperate species—shows an apparent bias towards overestimating *M* for large trees (n = 1,358 trees). **c**, New allometries that we created for the nine temperate species removed the apparent bias in predicted *M*.



Extended Data Figure 5 | **Estimated mass growth rates of the nine temperate species of Extended Data Fig. 4.** Growth was estimated using the simplest form of allometric model [log(M) = a + blog(D)] (a) and our allometric models fitted with piecewise linear regression (b). Regardless of the allometric model form, all nine species show increasing *G* in the largest trees.

Supplementary Table 1 | Results by species.

					Max.					
Country	Data ref.	Family	Species	# of trees	tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
Cameroon	51	Achariaceae	Scottellia klaineana	153	70.6	34	+	+		
Cameroon	51	Annonaceae	Annickia chlorantha	106	51.2	34	+			
Cameroon	51	Annonaceae	Xylopia aethiopica	71	53.3	34	+			
Cameroon	51	Combretaceae	Strephonema pseudocola	55	130.7	34	(+)	+		
Cameroon	51	Dichapetalaceae	Tapura africana	57	74.9	34	+			
Cameroon	51	Ebenaceae	Diospyros gabunensis	744	50.4	34	(+)	+	+	
Cameroon	51	Erythropalaceae	Strombosia pustulata	684	46.5	34	+	+		
Cameroon	51	Erythropalaceae	Strombosia scheffleri	119	69.9	34	+			
Cameroon	51	Erythropalaceae	Strombosiopsis tetrandra	230	68.9	34	+			
Cameroon	51	Euphorbiaceae	Dichostemma glaucescens	1771	44.5	34	+			
Cameroon	51	Euphorbiaceae	Discoglypremna caloneura	43	64.9	34	+			
Cameroon	51	Euphorbiaceae	Klaineanthus gaboniae	355	55.7	34	+			
Cameroon	51	Fabaceae	Hymenostegia afzelii	476	44.3	34	+			
Cameroon	51	Fabaceae	Talbotiella eketensis	132	51.2	34	+			
Cameroon	51	Lamiaceae	Vitex grandifolia	80	46.6	34	+			
Cameroon	51	Lamiaceae	Vitex sp.1	48	126.5	34	+			
Cameroon	51	Lauraceae	Hypodaphnis zenkeri	129	91.8	34	+			
Cameroon	51	Lecythidaceae	Oubanguia alata	2639	73.8	34	+	+		
Cameroon	51	Lecythidaceae	Scytopetalum klaineanum	45	76.0	34	+			
Cameroon	51	Phyllanthaceae	Protomegabaria stapfiana	384	58.4	34	+			
Cameroon	51	Phyllanthaceae	Uapaca staudtii	90	69.0	34	(+)			
Cameroon	51	Rubiaceae	Pausinystalia macroceras	49	58.5	34	+			
Cameroon	51	Rutaceae	Zanthoxylum gilletii	120	87.4	34	+			
Cameroon	51	Salicaceae	Homalium longistylum	51	63.2	34	+			
Cameroon	51	Sapotaceae	Lecomtedoxa klaineana	142	185.0	34	(+)	+		
Cameroon	51	Vochysiaceae	Erismadelphus exsul	58	85.0	34	+			
Dem. Rep. Congo	52	Apocynaceae	Alstonia boonei	42	116.3	34	+			
Dem. Rep. Congo	52	Fabaceae	Anthonotha macrophylla	41	60.1	34	(+)			
Dem. Rep. Congo	52	Fabaceae	Cynometra alexandri	1311	123.3	34	+	+		
Dem. Rep. Congo	52	Fabaceae	Erythrophleum suaveolens	101	112.9	34	(-)	+		
Dem. Rep. Congo	52	Fabaceae	Gilbertiodendron dewevrei	3492	142.3	34	+	+	+	
Dem. Rep. Congo	52	Fabaceae	Julbernardia seretii	988	122.3	34	+	+		

Country	Data ref.	Family	Species	# of trees	Max. tree diam.	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
					(cm)					
Dem. Rep. Congo	52	Malvaceae	Cola lateritia	186	67.7	34	+	+		
Dem. Rep. Congo	52	Phyllanthaceae	Cleistanthus michelsonii	197	88.0	34	+	+		
Dem. Rep. Congo	52	Rhizophoraceae	Comiphyton gabonense	44	75.2	34	+			
Dem. Rep. Congo	52	Rubiaceae	Hallea stipulosa	88	84.0	34	(+)	+		
Dem. Rep. Congo	52	Rubiaceae	Sarcocephalus pobeguinii	47	76.8	34	+			
China	53	Betulaceae	Betula platyphylla	90	46.4	54,55	+	+		
China	53	Fagaceae	Quercus mongolica	770	104.2	54,55	+	+		
China	53	Malvaceae	Tilia amurensis	2185	104.4	54,55	+	+		
China	53	Malvaceae	Tilia mandshurica	142	76.5	54,55	(+)			
China	53	Oleaceae	Fraxinus mandshurica	648	100.3	54,55	(+)	+	+	(-)
China	53	Pinaceae	Pinus koraiensis	2387	98.5	54,55	(-)	+	+	(-)
China	53	Rosaceae	Malus baccata	50	48.3	54,55	(+)			
China	53	Sapindaceae Ulmaceae	Acer mono	1625	61.0	54,55	(+)	+		
China Malaysia	53 56	Anacardiaceae	Ulmus japonica Gluta laxiflora	395 458	100.1 50.9	54,55 34	+ +	+	+	
Malaysia	56	Anacardiaceae	Gluta macrocarpa	408	<u> </u>	34	+ +	+		
Malaysia	56	Anacardiaceae	Gluta wallichii	72	97.4	34	+	+	(+)	
Malaysia	56	Anacardiaceae	Gluta woodsiana	78	80.2	34	+		(.)	
Malaysia	56	Anacardiaceae	Mangifera foetida	81	62.0	34	+			
Malaysia	56	Anacardiaceae	Mangifera parvifolia	293	50.8	34	(+)	+		
Malaysia	56	Anacardiaceae	Swintonia foxworthyi	62	66.5	34	+			
Malaysia	56	Anacardiaceae	Swintonia schwenkii	211	86.1	34	(+)	+		
Malaysia	56	Burseraceae	Canarium pseudopatenti- nervium	54	69.9	34	(+)			
Malaysia	56	Burseraceae	Dacryodes aff. incurvata	161	54.7	34	+			
Malaysia	56	Burseraceae	Dacryodes expansa	507	49.6	34	+			
Malaysia	56	Burseraceae	Dacryodes incurvata	90	64.2	34	+			
Malaysia	56	Burseraceae	Dacryodes rostrata	403	51.6	34	+			
Malaysia	56	Burseraceae	Santiria grandiflora	51	68.0	34	+	+		
Malaysia	56	Burseraceae	Santiria laevigata	263	64.5	34	+	+		
Malaysia	56	Burseraceae	Santiria mollis	81	65.8	34	+			
Malaysia	56	Burseraceae	Santiria rubiginosa	44	89.6	34	+			
Malaysia	56	Burseraceae	Santiria tomentosa	128	62.8	34	(+)	(+)	(+)	(+)
Malaysia	56	Clusiaceae	Calophyllum soulattri	40	95.4	34	(+)	+		
Malaysia	56	Clusiaceae	Garcinia caudiculata	54	58.9	34	+			
Malaysia	56	Clusiaceae	Kayea macrantha	80	46.8	34	+			
Malaysia	56	Crypteroniaceae	Crypteronia macrophylla	105	48.2	34	(+)			
Malaysia	56	Ctenolophonaceae	Ctenolophon parvifolius	74	82.6	34	(+)	+		
Malaysia	56	Dipterocarpaceae	Cotylelobium melanoxylon	48	85.1	34	(+)	+		

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
Malaysia	56	Dipterocarpaceae	Dipterocarpus confertus	47	137.0	34	+	+		
Malaysia	56	Dipterocarpaceae	Dipterocarpus crinitus	51	125.5	34	(+)	+	+	
Malaysia	56	Dipterocarpaceae	Dipterocarpus geniculatus	62	118.2	34	+	+		
Malaysia	56	Dipterocarpaceae	Dipterocarpus globosus	624	118.1	34	+	+		
Malaysia	56	Dipterocarpaceae	Dipterocarpus palembanicus subsp. borneensis	47	116.7	34	+			
Malaysia	56	Dipterocarpaceae	Dipterocarpus palembanicus subsp. palembanicus	43	93.2	34	(-)	+		
Malaysia	56	Dipterocarpaceae	Dryobalanops aromatica	705	144.4	34	+	+		
Malaysia	56	Dipterocarpaceae	Dryobalanops lanceolata	43	123.4	34	+	+		
Malaysia	56	Dipterocarpaceae	Parashorea parvifolia	58	124.5	34	+	+		
Malaysia	56	Dipterocarpaceae	Shorea acuta	361	79.5	34	+	+		
Malaysia	56	Dipterocarpaceae	Shorea amplexicaulis	146	87.4	34	+			
Malaysia	56	Dipterocarpaceae	Shorea beccariana	218	110.2	34	+	+		
Malaysia	56	Dipterocarpaceae	Shorea curtisii	67	136.7	34	+			
Malaysia	56	Dipterocarpaceae	Shorea falciferoides	70	141.4	34	+	+	+	
Malaysia	56	Dipterocarpaceae	Shorea kunstleri	104	127.8	34	(+)	+		
Malaysia	56	Dipterocarpaceae	Shorea laxa	375	114.1	34	+	+		
Malaysia	56	Dipterocarpaceae	Shorea macroptera subsp. baillonii	136	97.3	34	+	+		
Malaysia	56	Dipterocarpaceae	Shorea macroptera subsp. macropterifolia	131	74.0	34	+	+		
Malaysia	56	Dipterocarpaceae	Shorea ovata	57	81.1	34	+			
Malaysia	56	Dipterocarpaceae	Shorea parvifolia	126	126.3	34	+			└──
Malaysia	56	Dipterocarpaceae	Shorea quadrinervis	110	69.2	34	+			
Malaysia	56	Dipterocarpaceae	Shorea rubella	53	125.7	34	+	+		
Malaysia	56	Dipterocarpaceae	Shorea scaberrima	56	125.5	34	+	+	(.)	
Malaysia	56	Dipterocarpaceae	Shorea scrobiculata	76	97.6 130.0	34	+	+	(+)	
Malaysia Malaysia	56 56	Dipterocarpaceae Dipterocarpaceae	Shorea smithiana Vatica badiifolia	129 80	81.1	34 34	+ (+)	+ +	+	
Malaysia	56	Ebenaceae	Diospyros diepenhorstii	132	58.7	34 34	(+)	+		
Malaysia	56	Euphorbiaceae	Chaetocarpus castanocarpus	174	48.0	34	+			
Malaysia	56	Euphorbiaceae	Elateriospermum tapos	449	51.0	34	+			
Malaysia	56	Fabaceae	Dialium indum	98	72.0	34	+			
Malaysia	56	Fabaceae	Koompassia malaccensis	68	103.0	34	+			
Malaysia	56	Fabaceae	Millettia vasta	44	79.1	34	+			
Malaysia	56	Ixonanthaceae	Allantospermum borneense	714	58.0	34	+	+		
Malaysia	56	Kiggelariaceae	Hydnocarpus pinguis	87	46.6	34	(-)	+		

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
Malaysia	56	Kiggelariaceae	Hydnocarpus woodii	62	71.0	34	+			
Malaysia	56	Lauraceae	Alseodaphne bancana	110	85.0	34	+			
Malaysia	56	Lauraceae	Alseodaphne insignis	115	98.0	34	(-)	(+)	(+)	
Malaysia	56	Malvaceae	Durio acutifolius	71	71.0	34	+			
Malaysia	56	Malvaceae	Durio crassipes	66	104.3	34	+			
Malaysia	56	Malvaceae	Pentace adenophora	82	88.1	34	(+)	+		
Malaysia	56	Moraceae	Artocarpus anisophyllus	116	52.5	34	+			
Malaysia	56	Moraceae	Artocarpus nitidus	89	46.0	34	+			
Malaysia	56	Myristicaceae	Myristica villosa	77	45.8	34	+			
Malaysia	56	Myrtaceae	Cleistocalyx cf. barringtonioides	70	67.2	34	+			
Malaysia	56	Myrtaceae	Syzygium cf. attenuatum	62	65.0	34	+			
Malaysia	56	Myrtaceae	Syzygium cf. grande	221	62.0	34	+			
Malaysia	56	Myrtaceae	Syzygium sp. incert. c	41	75.4	34	(-)	+		
Malaysia	56	Myrtaceae	Whiteodendron moultonianum	576	70.7	34	+			
Malaysia	56	Oxalidaceae	Sarcotheca diversifolia	47	50.9	34	+			
Malaysia	56	Rutaceae	Melicope glabra	58	54.2	34	+			
Malaysia	56	Sapotaceae	Palaquium microphyllum	91	62.7	34	+			
Malaysia	56	Verbenaceae	Teijsmanniodendr on simplicifolium	281	60.2	34	+			
Taiwan	57	Anacardiaceae	Rhus succedanea	61	54.0	34	+			
Taiwan	57	Araliaceae	Schefflera octophylla	472	84.1	34	+			
Taiwan	57	Ebenaceae	Diospyros morrisiana	492	60.9	34	+	+		
Taiwan	57	Elaeocarpaceae	Elaeocarpus japonicus	375	72.4	34	(+)	+	+	
Taiwan	57	Fagaceae	Castanopsis cuspidata	1311	99.0	34	+	+	-	
Taiwan	57	Fagaceae	Cyclobalanopsis gilva	118	88.4	34	+			
Taiwan	57	Fagaceae	Cyclobalanopsis longinux	246	52.9	34	+			
Taiwan	57	Fagaceae	Limlia uraiana	1108	171.5	34	(+)	+	1	<u> </u>
Taiwan	57	Fagaceae	Lithocarpus harlandii	49	59.2	34	+			
Taiwan	57	Juglandaceae	Engelhardia	561	93.3	34	+	+	+	
Taiwan	57	Lauraceae	Cinnamomum micranthum	204	90.6	34	+			
Taiwan	57	Lauraceae	Litsea acuminata	986	67.5	34	+	+	(+)	<u> </u>
Taiwan	57	Lauraceae	Machilus thunbergii	1223	90.0	34	(+)	+		
Taiwan	57	Lauraceae	Machilus zuihoensis	613	79.5	34	+	-		
Taiwan	57	Lythraceae	Lagerstroemia subcostata	83	48.0	34	(+)			
Taiwan	57	Phyllanthaceae	Glochidion acuminatum	394	39.6	34	+			
Taiwan	57	Sabiaceae	Meliosma squamulata	1814	74.8	34	+	+		

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
Taiwan	57	Theaceae	Pyrenaria shinkoensis	1679	43.3	34	+	+	+	
Thailand	58	Anacardiaceae	Gluta obovata	172	90.8	34	+	+		
Thailand	58	Annonaceae	Alphonsea ventricosa	566	71.7	34	+			
Thailand	58	Annonaceae	Polyalthia viridis	2207	46.4	34	+			
Thailand	58	Annonaceae	Saccopetalum lineatum	999	114.6	34	+	+	+	
Thailand	58	Burseraceae	Garuga pinnata	53	87.4	34	+			
Thailand	58	Clusiaceae	Garcinia speciosa	454	68.9	34	+			
Thailand	58	Datiscaceae	Tetrameles nudiflora	205	219.4	34	(+)	+		
Thailand	58	Dipterocarpaceae	Anisoptera costata	75	138.1	34	+	+		
Thailand	58	Dipterocarpaceae	Dipterocarpus alatus	195	149.2	34	(+)	+		
Thailand	58	Dipterocarpaceae	Hopea odorata	182	189.9	34	+	+		
Thailand	58	Dipterocarpaceae	Vatica harmandiana	692	126.8	34	+	+		
Thailand	58	Ebenaceae	Diospyros variegata	381	74.8	34	+	+		
Thailand	58	Ebenaceae	Diospyros winitii	786	45.0	34	+			
Thailand	58	Euphorbiaceae	Macaranga siamensis	90	52.0	34	+			
Thailand	58	Euphorbiaceae	Mallotus philippenensis	121	51.4	34	+			
Thailand	58	Euphorbiaceae	Trewia nudiflora	159	61.7	34	+			
Thailand	58	Irvingiaceae	Irvingia malayana	95	113.0	34	+	+		
Thailand	58	Lamiaceae	Vitex peduncularis	54	71.8	34	+			
Thailand	58	Lauraceae	Neolitsea obtusifolia	500	66.6	34	+	+		
Thailand	58	Lauraceae	Persea sp.	138	63.9	34	+			
Thailand	58	Lythraceae	Lagerstroemia tomentosa	188	137.6	34	+	+		
Thailand	58	Malvaceae	Pterospermum grandiflorum	118	65.1	34	+			
Thailand	58	Meliaceae	Aglaia spectabilis	110	67.2	34	(-)	+	+	
Thailand	58	Meliaceae	Aphanamixis polystachya	71	76.9	34	+			
Thailand	58	Meliaceae	Chukrassia tabularis	96	87.0	34	(+)	+		
Thailand	58	Meliaceae	Dysoxylum grande	72	39.3	34	+			
Thailand	58	Myrtaceae	Syzygium syzgioides	75	68.0	34	+			
Thailand	58	Phyllanthaceae	Baccaurea ramiflora	907	41.4	34	+			
Thailand	58	Polygalaceae	Xanthophyllum flavescens	88	56.7	34	+			
Thailand	58	Sapindaceae	Acer oblongum	175	131.4	34	(+)	+		
Thailand	58	Sapindaceae	Arytera littoralis	818	42.5	34	(-)	+		
Thailand	58	Sapindaceae	Dimocarpus longan	999	92.2	34	+	+		
Thailand	58	Sapindaceae	Harpullia arborea	186	48.6	34	+	-		
New Zealand	59	Cunoniaceae	Weinmannia racemosa	9277	173.8	60	+	+	+	
New Zealand	59	Cupressaceae	Libocedrus bidwillii	56	83.2	60	+			
New Zealand	59	Elaeocarpaceae	Elaeocarpus dentatus	56	85.4	60	+			
New Zealand	59	Elaeocarpaceae	Elaeocarpus hookerianus	91	95.0	60	(-)	+		

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
New Zealand	59	Escalloniaceae	Carpodetus serratus	628	48.3	60	+			
New Zealand	59	Escalloniaceae	Ixerba excelsa	98	58.8	60	+			
New Zealand	59	Escalloniaceae	Quintinia acutifolia	368	39.8	60	+			
New Zealand	59	Fagaceae	Nothofagus fusca	2381	203.5	60	+	+	+	-
New Zealand	59	Fagaceae	Nothofagus menziesii	6855	158.0	60	+	+	+	+
New Zealand	59	Fagaceae	Nothofagus solandri	17595	121.0	60	+	+	+	+
New Zealand	59	Fagaceae	Nothofagus truncata	89	124.5	60	+			
New Zealand	59	Griseliniaceae	Griselinia littoralis	1636	106.3	60	+	+		
New Zealand	59	Lauraceae	Beilschmiedia tawa	304	95.0	60	+			
New Zealand	59	Myrtaceae	Kunzea ericoides	599	78.4	60	(+)	+	+	
New Zealand	59	Myrtaceae	Metrosideros umbellata	1196	267.5	60	+	+		
New Zealand	59	Onagraceae	Fuchsia excorticata	241	66.5	60	+	+		
New Zealand	59	Podocarpaceae	Dacrydium cupressinum	860	193.0	60	+	+	+	
New Zealand	59	Podocarpaceae	Podocarpus hallii	1277	147.7	60	(+)	+		
New Zealand	59	Podocarpaceae	Prumnopitys ferruginea	444	90.5	60	+			
New Zealand	59	Podocarpaceae	Prumnopytis taxifolia	72	65.7	60	+			
New Zealand	59	Proteaceae	Knightia excelsa	175	90.5	60	+	+		
New Zealand	59	Violaceae	Melicytus ramiflorus	1120	138	60	+			
Argentina	61	Anacardiaceae	Astronium urundeuva	212	90.0	34	+	+		
Argentina	61	Betulaceae	Alnus acuminata	145	66.2	34	+			
Argentina	61	Bignoniaceae	Tabebuia impetiginosa	107	62.3	34	+	+		
Argentina	61	Boraginaceae	Cordia trichotoma	100	54.6	34	+			
Argentina	61	Boraginaceae	Patagonula americana	277	77.5	34	+	+		
Argentina	61	Caprifoliaceae	Sambucus nigra	102	50.6	34	(+)			
Argentina	61	Combretaceae	Terminalia triflora	371	85.4	34	+			
Argentina	61	Elaeocarpaceae	Crinodendron tucumanum	175	113.4	34	+	+	(-)	
Argentina	61	Fabaceae	Anadenanthera colubrina	616	127.0	34	+	+		
Argentina	61	Fabaceae	Gleditsia amorphoides	181	45.0	34	+			
Argentina	61	Fabaceae	Myroxylon peruiferum	68	64.0	34	+			
Argentina	61	Fabaceae	Parapiptadenia excelsa	499	89.2	34	(-)	+		
Argentina	61	Fabaceae	Tipuana tipu	46	152.2	34	+	+		
Argentina	61	Juglandaceae	Juglans australis	98	56.7	34	+			
Argentina	61	Lauraceae	Cinnamomum porphyrium	627	174.5	34	+			
Argentina	61	Lauraceae	Ocotea puberula	318	82.5	34	+			

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
Argentina	61	Malvaceae	Heliocarpus popayanensis	56	55.7	34	+			
Argentina	61	Meliaceae	Cedrela balansae	69	100.5	34	+			
Argentina	61	Meliaceae	Cedrela lilloi	75	82.8	34	(-)	+		
Argentina	61	Moraceae	Morus alba	179	76.1	34	(+)	+	(+)	(+)
Argentina	61	Myrtaceae	Blepharocalyx salicifolious	174	132.5	34	(+)	+	+	
Argentina	61	Myrtaceae	Myrcianthes pungens	516	72.6	34	+			
Argentina	61	Nyctaginaceae	Pisonia zapallo	365	84.7	34	+			
Argentina	61	Podocarpaceae	Podocarpus parlatorei	299	151.9	34	+	+		
Argentina	61	Polygonaceae	Ruprechtia laxiflora	93	104.8	34	+	+		
Argentina	61	Primulaceae	Myrsine laetevirens	149	134.4	34	+			
Argentina	61	Rhamnaceae	Phyllostilon rhamnoides	441	88.2	34	+	+		
Argentina	61	Rubiaceae	Callycophylum multiflorum	287	83.7	34	(-)	+		
Argentina	61	Sapindaceae	Cupanea vernalis	128	57.5	34	+			<u> </u>
Argentina	61	Sapindaceae	Diatenopterix sorbifolia	291	54.9	34	(+)	+		
Argentina	61	Sapotaceae	Chrysophyllum gonocarpun	172	75.0	34	+	+		
Colombia	62	Anacardiaceae	Astronium graveolens	290	50.2	63	(+)	+		
Colombia	62	Burseraceae	Bursera simaruba	186	64.9	63	+			
Colombia	62	Dipterocarpaceae	Pseudomonotes	58	72.9	63	+			
			tropenbosii				-			
Colombia	62	Euphorbiaceae	Croton magdalenensis	52	52.0	63	+			
Colombia	62	Fagaceae	Quercus humboldtii	509	92.5	63	+	+	-	
Colombia	62	Lecythidaceae	Eschweilera punctata	115	69.7	63	+			
Colombia	62	Moraceae	Brosimum utile	115	97.1	63	+			
Panama	64	Anacardiaceae	Spondias radlkoferi	57	93.9	34	(+)	+		
Panama	64	Annonaceae	Guatteria dumetorum	160	67.3	34	(-)	+		
Panama	64	Apocynaceae	Aspidosperma spruceanum	50	111.2	34	+	+		
Panama	64	Apocynaceae	Tabernaemontana arborea	292	82.7	34	+			
Panama	64	Araliaceae	Dendropanax arboreus	64	66.9	34	+	+		
Panama	64	Bignoniaceae	Jacaranda copaia	205	91.6	34	+			<u> </u>
Panama	64	Bignoniaceae	Tabebuia rosea	55	82.5	34	+		1	<u> </u>
Panama	64	Boraginaceae	Cordia alliodora	49	64.2	34	+			
Panama	64	Boraginaceae	Cordia bicolor	289	45.8	34	+			
Panama	64	Burseraceae	Protium tenuifolium	331	46.3	34	+			
Panama	64	Burseraceae	Tetragastris panamensis	356	74.2	34	+			
Panama	64	Chrysobalanaceae	Hirtella triandra	646	41.0	34	+			
Panama	64	Erythropalaceae	Heisteria concinna	255	38.0	34	+			
Panama	64	Euphorbiaceae	Alchornea costaricensis	87	60.3	34	(+)			
Panama	64	Euphorbiaceae	Hura crepitans	87	246.8	34	(-)	+	+	
Panama	64	Fabaceae	Lonchocarpus heptaphyllus	86	55.7	34	+		Ī	[

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
Panama	64	Fabaceae	Tachigali versicolor	78	63.2	34	(+)	+	+	
Panama	64	Lauraceae	Beilschmiedia pendula	228	79.2	34	+	+		
Panama	64	Lauraceae	Ocotea whitei	97	82.7	34	+			
Panama	64	Lecythidaceae	Gustavia superba	547	44.8	34	+			
Panama	64	Malvaceae	Apeiba membranacea	174	114.3	34	+			
Panama	64	Malvaceae	Luehea seemannii	62	113.9	34	+			
Panama	64	Malvaceae	Quararibea asterolepis	525	92.5	34	+			
Panama	64	Meliaceae	Guarea guidonia	296	44.5	34	+			
Panama	64	Meliaceae	Trichilia tuberculata	1306	64.3	34	+	+		
Panama	64	Moraceae	Brosimum alicastrum	162	129.5	34	(-)	+		
Panama	64	Moraceae	Poulsenia armata	480	80.0	34	+			
Panama	64	Myristicaceae	Virola sebifera	495	42.3	34	+			1
Panama	64	Myristicaceae	Virola surinamensis	107	88.5	34	(-)	+		
Panama	64	Nyctaginaceae	Guapira standleyana	78	108.7	34	+			
Panama	64	Putranjivaceae	Drypetes standleyi	276	60.6	34	+	+		
Panama	64	Rubiaceae	Alseis blackiana	881	89.2	34	(+)	+	+	
Panama	64	Rutaceae	Zanthoxylum ekmanii	111	67.4	34	+			
Panama	64	Salicaceae	Casearia arborea	69	54.7	34	+			
Panama	64	Sapotaceae	Pouteria reticulata	169	85.0	34	(+)	+		
Panama	64	Simaroubaceae	Simarouba amara	207	76.7	34	+	+		
Panama	64	Urticaceae	Cecropia insignis	155	56.2	34	+			
Spain	65,66	Aquifoliaceae	Ilex aquifolium	295	51.6	65,66	+			
Spain	65,66	Aquifoliaceae	Ilex canariensis	272	71.6	65,66	+			
Spain Spain	65,66	Betulaceae Betulaceae	Alnus glutinosa	1177	118.4	65,66	+	+	+	
Spain Spain	65,66 65,66	Cupressaceae	Betula spp. Chamaecyparis lawsoniana	2343 724	79.6 50.4	65,66 65,66	++	++	+	
Spain	65,66	Cupressaceae	Juniperus communis	684	75.8	65,66	+	+		
Spain	65,66	Cupressaceae	Juniperus thurifera	5900	127.3	65,66	+	+	+	
Spain	65,66	Fagaceae	Castanea sativa	4775	240.6	65,66	(+)	+	+	
Spain	65,66	Fagaceae	Fagus sylvatica	20676	164.9	65,66	+	+	+	(+)
Spain	65,66	Fagaceae	Quercus ilex	40451	141.6	65,66	+	+	+	-
Spain	65,66	Fagaceae	Quercus petraea	5145	187.8	65,66	(-)	+	+	
Spain	65,66	Fagaceae	Quercus pyrenaica	20466	172.4	65,66	(+)	+	+	(+)
Spain	65,66	Fagaceae	Quercus robur	8866	146.4	65,66	(-)	+	+	-
Spain	65,66	Fagaceae	Quercus suber	10907	146.5	65,66	-	+	+	+
Spain	65,66	Juglandaceae	Juglans regia	68	77.0	65,66	(+)			
Spain	65,66	Lauraceae	Persea indica	201	105.0	65,66	+			
Spain	65,66	Malvaceae	Tilia spp.	97	79.9	65,66	+			
Spain	65,66	Myricaceae	Myrica faya	786	108.2	65,66	+	+	+	
Spain	65,66	Myrtaceae	Eucalyptus camaldulensis	1189	89.1	65,66	-	+	+	+
Spain	65,66	Myrtaceae	Eucalyptus globulus	3465	117.8	65,66	-	+	+	+
Spain	65,66	Myrtaceae	Eucalyptus nitens	189	101.2	65,66	(+)	+		
Spain	65,66	Oleaceae	Olea europaea	389	81.2	65,66	(+)	-	+	
Spain	65,66	Pinaceae	Abies alba	2276	140.1	65,66	(+)	+		
Spain	65,66	Pinaceae Pinaceae	Larix spp. Picea abies	794 94	47.9 75.4	65,66 65,66	(-)	(+) +	+	+
Spain	65,66									

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
Spain	65,66	Pinaceae	Pinus halepensis	43615	102.8	65,66	(+)	+	+	+
Spain	65,66	Pinaceae	Pinus nigra	44291	95.5	65,66	+	+	+	+
Spain	65,66	Pinaceae	Pinus pinaster	76024	96.4	65,66	+	+	+	+
Spain	65,66	Pinaceae	Pinus pinea	14112	130.5	65,66	+	+	+	-
Spain	65,66	Pinaceae	Pinus radiata	11331	90.7	65,66	(-)	+	+	+
Spain	65,66	Pinaceae	Pinus sylvestris	87225	128.3	65,66	+	+	+	+
Spain	65,66	Pinaceae	Pinus uncinata	10735	127.3	65,66	-	+		
Spain	65,66	Rosaceae	Prunus spp.	223	49.3	65,66	(+)	+		
Spain	65,66	Rosaceae	Sorbus spp.	327	65.3	65,66	(-)	(+)		
Spain	65,66	Salicaceae	Populus alba	209	91.7	65,66	(-)	+		
Spain	65,66	Salicaceae	Populus nigra	1189	101.9	65,66	(-)	+		
Spain	65,66	Salicaceae	Populus tremula	454	90.5	65,66	+			
Spain	65,66	Salicaceae	Salix spp.	636	105.0	65,66	(-)	+	(+)	
Spain	65,66	Sapindaceae	Acer campestre	1091	89.1	65,66	(+)	+		
Spain	65,66	Taxaceae	Taxus baccata	40	107.6	65,66	(-)	+		
Spain	65,66	Ulmaceae	Ulmus minor	114	111.4	65,66	+			
United States (east)	67	Betulaceae	Betula alleghaniensis	1245	102.4	17	(+)	+		
United States (east)	67	Betulaceae	Betula lenta	244	60.2	17	+			
United States (east)	67	Betulaceae	Betula nigra	212	81.0	17	+	+		
United States (east)	67	Betulaceae	Betula papyrifera	1506	63.0	17	+	+	+	
United States (east)	67	Cornaceae	Nyssa aquatica	53	101.1	17	-			
United States (east)	67	Cornaceae	Nyssa sylvatica	682	75.7	17	+			
United States (east)	67	Cupressaceae	Juniperus virginiana	800	60.7	17	(-)	+		
United States (east)	67	Cupressaceae	Thuja occidentalis	4337	80.8	17	+	+		
United States (east)	67	Fabaceae	Gleditsia triacanthos	304	103.9	17	+	+		
United States (east)	67	Fabaceae	Robinia psuedoacacia	443	64.8	17	+	+		
United States (east)	67	Fagaceae	Fagus grandifolia	2130	109.5	17	+	+	+	
United States (east)	67	Fagaceae	Quercus alba	6583	127.8	17	(+)	+	+	+
United States (east)	67	Fagaceae	Quercus bicolor	210	100.6	17	+	+		
United States (east)	67	Fagaceae	Quercus coccinea	878	68.1	17	-	+	+	+
United States (east)	67	Fagaceae	Quercus ellipsoidalis	226	76.7	17	+	+	+	

					Max.					
Country	Data ref.	Family	Species	# of trees	tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
United States	67	Fagaceae	Quercus falcata var. falcata	249	100.1	17	+	+		
(east)	07	F	Overeve feleete	00	00.0	47				
United States	67	Fagaceae	Quercus falcata var. pagodaefolia	60	80.8	17	(-)	+		
(east) United	67	Fagaceae	Quercus	310	72.1	17	-	+	+	
States (east)	07	Гауасеае	imbricaria	310	72.1	17	-	+	+	
United States (east)	67	Fagaceae	Quercus macrocarpa	224	116.8	17	+	+		
United States (east)	67	Fagaceae	Quercus michauxii	45	107.7	17	+	+		
United States (east)	67	Fagaceae	Quercus muehlenbergii	439	94.5	17	(+)	+	+	+
United States (east)	67	Fagaceae	Quercus palustris	584	138.7	17	(+)	+	+	
United States (east)	67	Fagaceae	Quercus prinus	1900	93.7	17	+	+	+	+
United States (east)	67	Fagaceae	Quercus rubra	4477	157.7	17	+	+	+	
United States (east)	67	Fagaceae	Quercus shumardii	62	104.9	17	+			
United States (east)	67	Fagaceae	Quercus stellata	711	74.4	17	+	+	+	
United States (east)	67	Fagaceae	Quercus velutina	3867	104.4	17	+	+	+	+
United States (east)	67	Hamamelidaceae	Liquidambar styraciflua	777	72.6	17	(+)	+		
United States (east)	67	Juglandaceae	Carya cordiformis	774	81.0	17	+	+		
United States (east)	67	Juglandaceae	Carya glabra	2060	95.8	17	(+)	+	+	
United States (east)	67	Juglandaceae	Carya laciniosa	74	68.3	17	+			
United States (east)	67	Juglandaceae	Carya ovata	1602	82.6	17	(-)	+	+	
United States (east)	67	Juglandaceae	Carya tomentosa	975	93.5	17	+	+		
United States (east)	67	Juglandaceae	Juglans nigra	1108	82.6	17	-	+	+	+
United States (east)	67	Lauraceae	Sassafras albidum	895	75.7	17	+	+	+	(+)
United States (east)	67	Magnoliaceae	Liriodendron tulipifera	3239	117.1	17	-	+	+	+

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
United States (east)	67	Magnoliaceae	Magnolia acuminata	98	55.1	17	+			
United States (east)	67	Malvaceae	Tilia americana	1571	122.7	17	+	+	+	
United States (east)	67	Moraceae	Maclura pomifera	174	61.7	17	+	+		
United States (east)	67	Oleaceae	Fraxinus americana	2354	137.2	17	-	+	+	+
United States (east)	67	Oleaceae	Fraxinus nigra	712	58.2	17	+	+		
United States (east)	67	Oleaceae	Fraxinus pennsylvanica	906	115.6	17	+	+		
United States (east)	67	Pinaceae	Abies balsamea	1227	40.1	17	+			
United States (east)	67	Pinaceae	Larix laricina	646	57.2	17	+	+		
United States (east)	67	Pinaceae	Picea glauca	759	73.9	17	(+)	+		
United States (east)	67	Pinaceae	Picea mariana	1124	49.8	17	+	+		
United States (east)	67	Pinaceae	Picea rubens	412	46.5	17	+			
United States (east)	67	Pinaceae	Pinus banksiana	1245	47.5	17	+	+		
United States (east)	67	Pinaceae	Pinus echinata	596	71.4	17	(-)	+		
United States (east)	67	Pinaceae	Pinus resinosa	2173	65.5	17	(-)	+	+	+
United States (east)	67	Pinaceae	Pinus rigida	299	46.2	17	+	+		
United States (east)	67	Pinaceae	Pinus strobus	2728	108.0	17	+	+		
United States (east)	67	Pinaceae	Pinus taeda	597	58.2	17	(+)	+		
United States (east)	67	Pinaceae	Pinus virginiana	921	55.4	17	+	+		
United States (east)	67	Pinaceae	Tsuga canadensis	2071	100.1	17	+	+	+	
United States (east)	67	Platanaceae	Platanus occidentalis	1073	133.9	17	-	+	+	
United States (east)	67	Rosaceae	Prunus serotina	1532	88.9	17	+	+	+	

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
United States (east)	67	Salicaceae	Populus balsamifera	381	82.8	17	+	+	+	
United States (east)	67	Salicaceae	Populus deltoides	648	147.1	17	-	+		
United States (east)	67	Salicaceae	Populus grandidentata	1242	66.5	17	+	+		
United States (east)	67	Salicaceae	Populus tremuloides	2270	62.5	17	+	+	+	
United States (east)	67	Salicaceae	Salix nigra	164	88.4	17	+			
United States (east)	67	Sapindaceae	Acer negundo	417	100.8	17	+	+		
United States (east)	67	Sapindaceae	Acer rubrum	7448	124.0	17	+	+	+	+
United States (east)	67	Sapindaceae	Acer saccharinum	1386	121.2	17	(+)	+	+	+
United States (east)	67	Sapindaceae	Acer saccharum	8681	113.3	17	+	+	+	
United States (east)	67	Sapindaceae	Aesculus glabra	85	61.7	17	(+)	+		
United States (east)	67	Ulmaceae	Celtis occidentalis	552	130.6	17	(+)	+	+	(+)
United States (east)	67	Ulmaceae	Ulmus americana	884	72.4	17	+	+		
United States (east)	67	Ulmaceae	Ulmus rubra	415	72.9	17	(+)	+	+	
United States (west)	68,69	Cupressaceae	Calocedrus decurrens	1587	176.0	17	(+)	+	+	+
United States (west)	68,69	Cupressaceae	Chamaecyparis nootkatensis	572	210.0	17	+	+	+	
United States (west)	68,69	Cupressaceae	Thuja plicata	284	240.7	17	+	+		
United States (west)	68,69	Fagaceae	Quercus kelloggii	422	97.8	17	(+)	+		
United States (west)	68,69	Pinaceae	Abies amabilis	2595	124.7	17	+	+	+	(+)
United States (west)	68,69	Pinaceae	Abies concolor	3248	166.8	17	+	+	+	
United States (west)	68,69	Pinaceae	Abies magnifica	1644	249.7	17	+	+	+	+
United States (west)	68,69	Pinaceae	Abies procera	205	230.2	17	+	+		

Country	Data ref.	Family	Species	# of trees	Max. tree diam. (cm)	Allom. ref.	Bin 1	Bin 2	Bin 3	Bin 4
United States (west)	68,69	Pinaceae	Picea sitchensis	409	270.5	17	+	+	(+)	+
United States (west)	68,69	Pinaceae	Pinus albicaulis	550	41.8	17	+			
United States (west)	68,69	Pinaceae	Pinus balfouriana	152	153.0	17	(+)			
United States (west)	68,69	Pinaceae	Pinus contorta	155	70.0	17	(+)	+		
United States (west)	68,69	Pinaceae	Pinus jeffreyi	99	136.6	17	+			
United States (west)	68,69	Pinaceae	Pinus lambertiana	564	196.9	17	+	+	+	+
United States (west)	68,69	Pinaceae	Pinus monticola	215	234.2	17	+	+	+	
United States (west)	68,69	Pinaceae	Pinus ponderosa	2191	175.5	17	+	+	+	
United States (west)	68,69	Pinaceae	Pseudotsuga menziesii	744	225.6	17	(+)	+	+	+
United States (west)	68,69	Pinaceae	Tsuga heterophylla	2253	190.8	17	+	+	+	+
United States (west)	68,69	Pinaceae	Tsuga mertensiana	188	115.1	17	(+)	+		

Data ref. = publication(s) describing our data source for each species; **Allom. ref.** = publication(s) from which we obtained allometric equations for each species. A "+" or "-" symbol in a numbered **Bin** column indicates that the model receiving the greatest weight of evidence by AIC included that bin (line segment); for example, a species having a symbol under **Bin 1** and **Bin 2** but not under **Bin 3** and **Bin 4** was fit with two line segments. "+" indicates that the line segment had a positive slope (mass growth rate increased with tree size within the bin); "-" indicates a negative slope. Symbols without parentheses indicate that the slope for that bin for that particular species was significant at $P \le 0.05$.

- 51. Chuyong, G. B. *et al.* in *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network* (eds Losos, E. C. & Leigh, E. G. Jr.) 506–516 (University of Chicago Press, 2004).
- 52. Makana, J.-R. *et al.* in *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network* (eds Losos, E. C. & Leigh, E. G. Jr.) 492–505 (University of Chicago Press, 2004).

- 53. Wang, X. *et al.* Spatial distributions of species in an old-growth temperate forest, northeastern China. *Can. J. For. Res.* **40**, 1011–1019 (2010).
- Xu, Z., Li, X. & Dai, H. Study on biomass of species in broad-leaved Korean pine mixed forest in Changbai Mountain [in Chinese]. *Forest Ecosyst. Res.* 5, 33–46 (1985).
- 55. Wang, C. Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. *For. Ecol. Manage.* **222**, 9–16 (2006).
- 56. Lee, H. S. *et al.* in *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network* (eds Losos, E. C. & Leigh, E. G. Jr.) 527-539 (University of Chicago Press, 2004).
- 57. Su, S. H. et al. Fushan Subtropical Forest Dynamics Plot: Tree Species Characteristics and Distribution Patterns. (Taiwan Forestry Research Institute: Taipei, Taiwan, 2007).
- Bunyavejchewin, S., Baker, P. J., LaFrankie, J. V. & Ashton, P. S. in *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network* (eds Losos, E. C. & Leigh, E. G. Jr.) 482-491 (University of Chicago Press, 2004).
- 59. Wiser, S. K., Bellingham, P. J. & Burrows, L. E. Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *New Zealand J. Ecol.* **25**, 1–17 (2001).
- Coomes, D. A., Allen, R. B., Scott, N. A., Goulding, C. & Beets, P. Designing systems to monitor carbon stocks in forests and shrublands. *For. Ecol. Manage*. 164, 89–108 (2002).
- 61. Easdale, T. A., Healey, J. R., Grau, H. R. & Malizia, A. Tree life histories in a montane subtropical forest: species differ independently by shade-tolerance, turnover rate and substrate preference. *J. Ecol.* **95**, 1234–1249 (2007).
- 62. Phillips Bernal, J. F. *et al. Estimación de las Reservas Potenciales de Carbono Almacenadas en la Biomasa Aérea en Bosques Naturales de Colombia.* (Instituto de Hidrología, Meteorología, y Estudios Ambientales: Bogotá D.C., Colombia, 2011).
- 63. Alvarez, E. *et al.* Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia. *For. Ecol. Manage.* **267**, 297–308 (2012).
- 64. Leigh, E. G. Jr. *et al.* in *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network* (eds Losos, E. C. & Leigh, E. G. Jr.) 451-463 (University of Chicago Press, 2004).

- 65. Ministerio de Medio Ambiente (IFN2: MMA) Segundo Inventario Forestal Nacional (1986–1996): Bases de Datos e Información Cartográfica. (Banco de Datos de la Naturaleza, Ministerio de Medio Ambiente: Madrid, Spain, 1996).
- 66. Ministerio de Medio Ambiente (IFN3: MMA) *Tercer Inventario Forestal Nacional (1997-2007): Bases de Datos e Información Cartográfica.* (Banco de Datos de la Naturaleza, Ministerio de Medio Ambiente: Madrid, Spain, 2007).
- 67. Canham, C. D. & Thomas, R. Q. Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. *Ecology* **91**, 3433–3440 (2010).
- Acker, S. A., McKee, W. A., Harmon, M. E. & Franklin, J. F. in *Forest Biodiversity in North, Central and South America, and the Caribbean: Research and Monitoring* (eds Dallmeier, J. & Comisky, A.) 93–106 (Man and the Biosphere Series, Vol. 21, UNESCO and Parthenon Publishing Group: Paris & New York, 1998).
- 69. Stephenson, N. L. & van Mantgem, P. J. Forest turnover rates follow global and regional patterns of productivity. *Ecol. Lett.* **8**, 524–531 (2005).