BOARD OF APPEALS, CITY & COUNTY OF SAN FRANCISCO

Appeal of CURTIS SPECK & ARIANE EROY, Ph. D	Appellant(s)))	Appeal No. 15-085
vs.) }	
DEPARTMENT OF PUBLIC WORKS BUREAU OF URBAN FORESTRY,)))	
	Respondent	,	

NOTICE OF APPEAL

NOTICE IS HEREBY GIVEN THAT on May 29, 2015, the above named appellant(s) filed an appeal with the Board of Appeals of the City and County of San Francisco from the decision or order of the above named department(s), commission, or officer.

The substance or effect of the decision or order appealed from is the ISSUANCE on May 19, 2015, to Dept. of Public Works, Arts Commission & Municipal Transportation Agency, of a Tree Removal Permit (approval of request to remove forty-four (44) street trees with replacement of one-hundred eighty-five (185) street trees) along Masonic Avenue.

ORDER NO. 183617

FOR HEARING ON July 22, 2015

Address of Appellant(s):	Address of Other Parties:
Curtis Speck & Ariane Eroy, Ph.D, Appellants	DPW, Arts Commission & MTA, Permit Holders
2622 McAllister Street	c/o J. Dennis & D. Froehlich, Agents for Permit Holders
San Francisco, CA 94118	1155 Market Street
	San Francisco, CA 94103



Date Filed:

MAY 29 2015 APPEAL # 15-085

CITY & COUNTY OF SAN FRANCISCO BOARD OF APPEALS

PRELIMINARY STATEMENT OF APPEAL

I / We, Curtis Speck and Ariane Eroy, Ph. D., hereby appeal the following departmental action: ISSUANCE of Tree Removal Permit - ORDER NO. 183617 by the Department of Public Works -Bureau of Urban Forestry which was issued or became effective on: May 19, 2015, to: DPW, Arts Commission & MTA, for the property located at along Masonic Avenue.

BRIEFING SCHEDULE:

The Appellant may, but is not required to, submit a one page (double-spaced) supplementary statement with this Preliminary Statement of Appeal. No exhibits or other submissions are allowed at this time.

Appellant's Brief is due on or before: July 02, 2015, (no later than three (3) Thursdays prior to the hearing date), up to 12 pages in length, double-spaced, with unlimited exhibits, with eleven (11) copies delivered to the Board office by 4:30 p.m., and with additional copies delivered to the other parties the same day.

DEVICE PROBLEM FROM HOLLING (1) Thursday prior

Respondent's and Other Parties' Briefs are due on or before: **July 16, 2015, (no later than one (1) Thursday prior to hearing date)**, up to 12 pages in length, doubled-spaced, with unlimited exhibits, with eleven (11) copies delivered to the Board office by 4:30 p.m., and with additional copies delivered to the other parties the same day.

Only photographs and drawings may be submitted by the parties at hearing.

Hearing Date: Wednesday, July 22, 2015, 5:00 p.m., City Hall, Room 416, One Dr. Carlton B. Goodlett Place.

All parties to this appeal must adhere to the briefing schedule above, however if the hearing date is changed, the briefing schedule MAY also be changed. Written notice will be provided of any change to the briefing schedule.

In order to have their documents sent to the Board members prior to hearing, **members of the public** should submit eleven (11) copies of all documents of support/opposition no later than one (1) Thursday prior to hearing date by 4:30 p.m. Please note that names and contact information included in submittals from members of the public will become part of the public record. Submittals from members of the public may be made anonymously.

Please note that in addition to the parties' briefs, any materials that the Board receives relevant to this appeal, including letters of support/opposition from members of the public, are distributed to Board members prior to hearing. All such materials are available for inspection at the Board's office. You may also request a copy of the packet of materials that are provided to Board members at a cost of 10 cents per page, per S.F. Admin. Code Ch. 67.28.

If you have any questions please call the Board of Appeals at 415-575-6880

The reasons for this appeal are as follows:

see attached

Appellant or Agent (Circle One):

Eng PhD

Signature: Maue

Print Name: Hrane

Curtis Speck

May 26, 2015 BOARD OF APPEALS

to whom concerned:

MAY 2 9 2015 APPEAL # 15-085

We write to farmally appeal the recent ruling concerning the Masonic Street Project in San Francisco. Over 100 signitures and letters have been submitted in protest of the cutting of 40+ trees both before and after the hearing.

We will raise the following issues in the appeal:

why was the neighborhood not presented why was the neighborhood not presented the facts of the number of healthy trees scholuled for cutling during the planning sessions 2010-2014?

How to find better communication with the Masonie neighborhood? How in the severe drought can a neighborhood contribute to saving of healthy 20-25 year old trees?

We welcome the apportunity to Curtis Speck

Anané Eroy, PhD.

City and County of San Francisco

San Francisco Public Works

GENERAL - DIRECTOR'S OFFICE City Hall, Room 348 Tor. Carlton B. Goodlett Place, S.F., CA 94102 (415) 554-6920 www.sfdpw.org



Edwin M. Lee, Mayor Mohammed Nuru, Director

DPW Order No: 183617

The Director of Public Works held a Public Hearing on Monday, April 27th, 2015 commencing at 5:30 PM at City Hall, Room 416, 1 Dr. Carlton B. Goodlett Place, San Francisco, CA 94102. The hearing was to consider Order No. 183520 to consider the removal of forty-four (44) street trees with replacement of one hundred eighty-five (185) street trees along Masonic Avenue.

Based upon the testimony and facts submitted at the hearing, the recommendation to the Director is as follows:

Findings

Part of the Masonic Avenue Streetscape Improvement project, initiated in 2010, involves numerous City agencies including Public Works, Arts Commission, and Municipal Transportation Agency, and public involvement through various community outreach workshops. Part of the project entails removing a significant number of mature trees in order to re-align and re-grade the street, sidewalk, and plaza areas. The trees are identified as needing removal for either construction/road alignment reasons or due to tree health issues. Per the public process, the trees slated for removal were posted and the public was given the opportunity to appeal the removal at the hearing on April 27, 2015.

At the hearing, there were several members of the public who showed up to appeal the proposed removal of trees; there were no public advocates for the project besides the project manager and design lead. Although the project is several blocks long, most of the objections raised pertain to the trees located at the triangle bus stop plaza and median at the south side of the intersection of Masonic Avenue and Geary Street. The project manager explained the need to remove the trees in a well organized slideshow presentation made at the hearing. The project manager also attempted to address several of the community objections made during the hearing.

The prevailing complaint made during the hearing was the lack of community awareness that the trees were going to be removed. Despite multiple community meetings and partnering workshops held during the project development, the proposed removal of trees was not brought up in the discussions, as this need was not discovered until later phases of design.



Making San Francisco a beautiful, livable, vibrant, and sustainable city.

An appellant, Mr. Larry Griffin stated that he resides one and a half blocks from the project site and was not informed about the project. (Apparently, the public outreach only extends to the community within one block of the project site.)

An appellant, Ms. Rupa Rose, stated that there was no mention of tree removal in public meetings she attended.

An appellant, Mr. Curtis Speck presented a petition with dozens of signatures which requests that a public meeting be set for the citizens of San Francisco to offer better proposals than cutting the healthy trees.

An appellant, Ms. Anastasia Glickshtern, was not convinced by the presentation that the re-alignment requires the trees at the plaza be removed and cited slides from the public presentation that indicated many mature trees at the plaza would remain in place.

An appellant, Ms. Tonya Sabatino, expressed confusion and was not convinced by the presentation that the tree health issues raised requires the trees at the plaza be removed.

An appellant, Ms. Amber Yada, made an emotional appeal regarding the love her children experienced growing up alongside the trees in the plaza and did not understand the City's intention to remove them without further consideration.

Numerous appeal letters were submitted by the public carrying a similar sentiment as well as expressing other concerns including cost of removal, drought consideration, CO2 sequestration, loss of shade, wind and dust filtering, and a bird habitat. Additionally, one appellant feels the net gain of new trees is falsely advertised since the new trees are much smaller than the mature ones being removed.

I feel that the project manager has adequately explained the technical reasons for the need to remove the trees as part of the re-alignment and re-grading process. Given the testimony presented by multiple appellants, I feel this technical information has not yet been adequately clarified to the affected residents and further public outreach is needed to garner more public support for the tree removal. I also feel the project manager should verify that preserving any of the trees has a constructability limitation or negative impact on the project, and showcase how the project will best address the problem as currently designed.

Recommendation

APPROVE the removal of all of the street trees posted for removal, with the following conditions:

- 1. The project manager shall verify that the mature trees slated for removal cannot be practically preserved within the program of the new project.
- 2. Clarify for the public, the scope of tree removal and explain why the trees need to be removed.

BOARD OF APPEALS



MAY 2 9 2015 APPEAL # 15-085

Appeal:



This Order may be appealed to the Board of Appeals within 15 days of May 19th, 2015.

Board of Appeals 1650 Mission, Room 304 San Francisco, CA 94103 (between Van Ness and Duboce Avenues)

Phone: 415.575.6880 Fax: 415.575.6885

Regular office hours of the Board of Appeals are Monday through Friday from 8am to 5pm. Appointments may be made for filing an appeal by calling 415-575-6880. All appeals must be filed in person. For additional information on the San Francisco Board of Appeals and to view the Appeal Process Overview, please visit their website at http://sfgov.org/bdappeal/

5/14/2015



Nuru, Mohammed Approver 1 Signed by: Nuru, Mohammed

MAY 29 2015 APPEAL # 15-085



HD 9/2/15

JUL 3 0 2015

APPEAL # 15-065

One of Leonardo Da Vinci's principles is entitled "Demonstration" which means to "to test, to experience with persistence and willingness, to learn from mistakes". We are here tonight because we believe it to be a mistake to cut 40+ mature trees as part of the Masonic Street Project. We would like to see this mistake corrected.

BENEFITS OF MATURE TREES

THE MATURE TREE IS A LIVING ORGANISM THAT IS COMPLETELY SELF-CONSTRUCTING, COMPLETELY SELF-MAINTAINING, COMPLETELY SELF-DIRECTING, COMPLETELY SELF-REPAIRING, COMPLETELY SELF-DEFENDING, COMPLETELY SELF-HEALING.

Environmental groups and urban foresters maintain too few mature trees are being saved and replenishing is not sufficient. The benefits of mature trees are:

- 1. Mature trees absorb and block noise and reduce glare. A well placed tree can reduce noise by as much as 40 percent.
- 2. Trees absorb carbon dioxide and potentially harmful gasses, such as sulfur dioxide, carbon monoxide, from air and release oxygen.

One large tree can supply a day's supply of oxygen for four people.

A healthy tree can store 13 pounds of carbon each year.

Each gallon of gasoline burned produces almost 20 pounds of carbon dioxide.

For every 10,000 miles you drive, it take 7 trees to remove the amount of

carbon dioxide produced if your car gets 40 miles per gallon.

- 3. Most of us respond to the presence of trees beyond simply observing their beauty. We feel serene, peaceful, restful, and tranquil-we are "at home" with the tree's presence.
- * Trees of Strength, North Caroline State University College of Agriculture

 Observe the draft #1 on Projected mature tree size and soil volume and
 stormwater storage.

The mature tree reduces surface water runoff thus decreasing soil erosion and enabling the tree to withstand drought conditions. Peter MacDonagh sited in San Francisco at the Greenbuild Show November 15, 2012, "The most significant problem urban trees face is the inadequate quantity of soil useable for root growth". MacDonagh states that trees are unlikely to grow large enough to produce anywhere near the level of ecological services that are capable of providing. But we have 40+ mature trees now producing, why would one want to cut them?

A very detailed study entitled "Rate of Tree Carbon Accumulation Increases Continuously With Tree Size" states that "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."

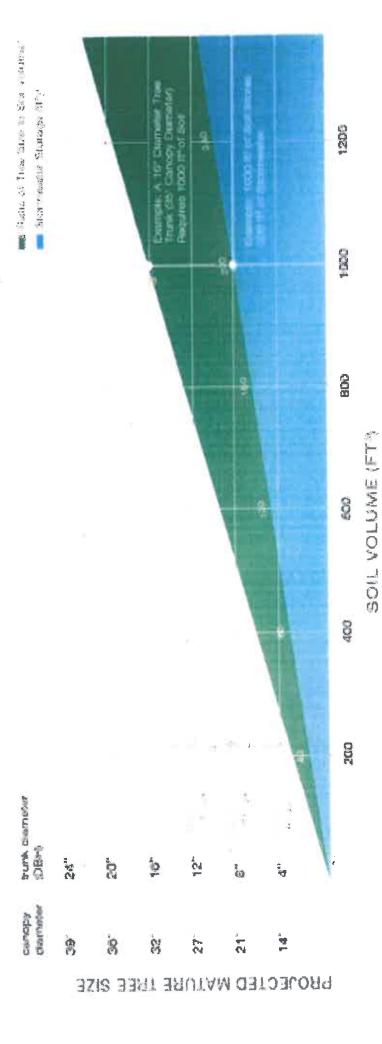
"In absolute terms, trees 100 cm in trunk diameter typically add from 10 kg to 200 kg of aboveground dry mass each year, averaging 103 kg per year. This is nearly three times the rate for trees of the same species at 50 cm in diameter and is the mass equivalent to adding an entirely new tree of 10-20 cm in diameter

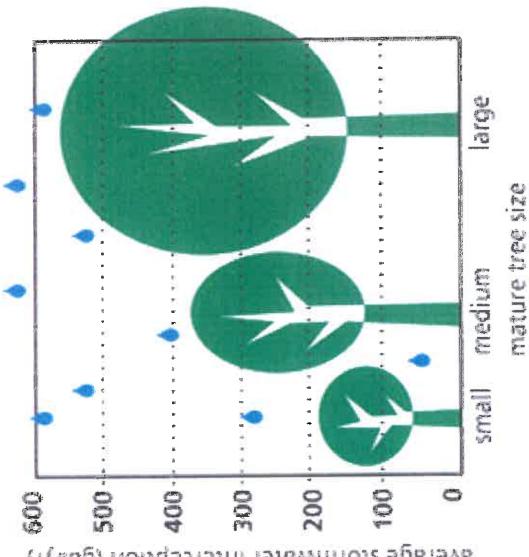
to the forest each year." See figure #3

This study also concluded,"Lastly, the rapid growth of large trees indicates that relative to their numbers, the mature trees could play a disproportional important role in these feedbacks. For example, in our western USA old growth forest plots, trees 100 cm in diameter comprised 6% of the trees, yet contributed 33% of the annual forest mass growth."

In closure, by looking at the total benefits of the mature tree, we see even other benefits: the CO2 reduction = 4% and air quality improvement = 5%. The other 3 benefits are stormwater runoff reduction = 28%, energy savings = 29% and property value increase = 34%. See **draft**#4

THE MATURE TREE IS A LIVING ORGANISM THAT IS COMPLETE.... HELP CORRECT THE MISTAKE.



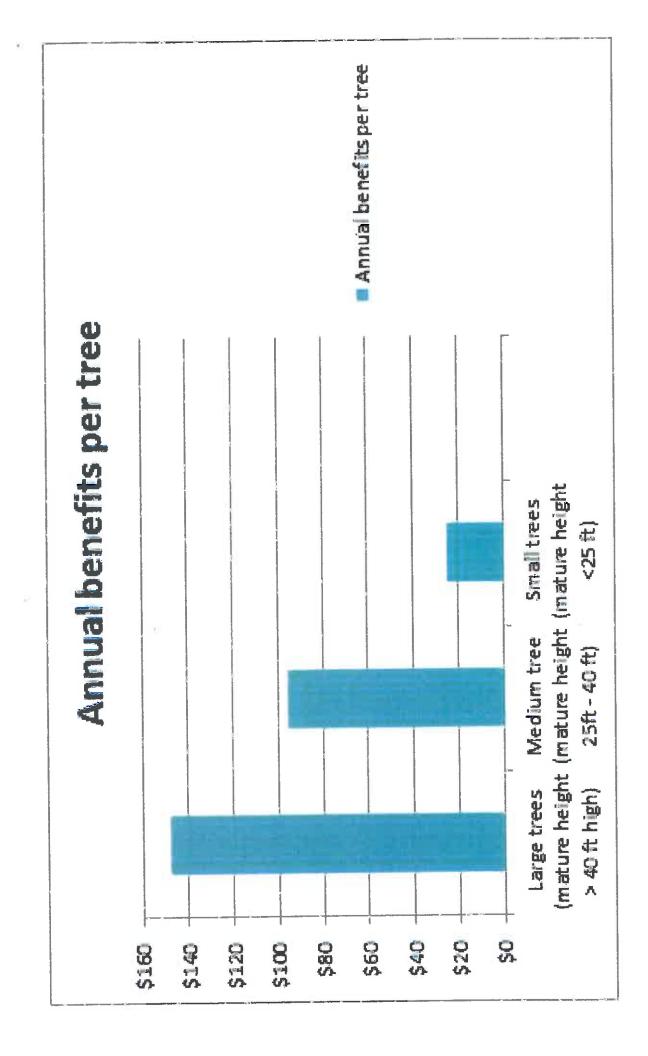


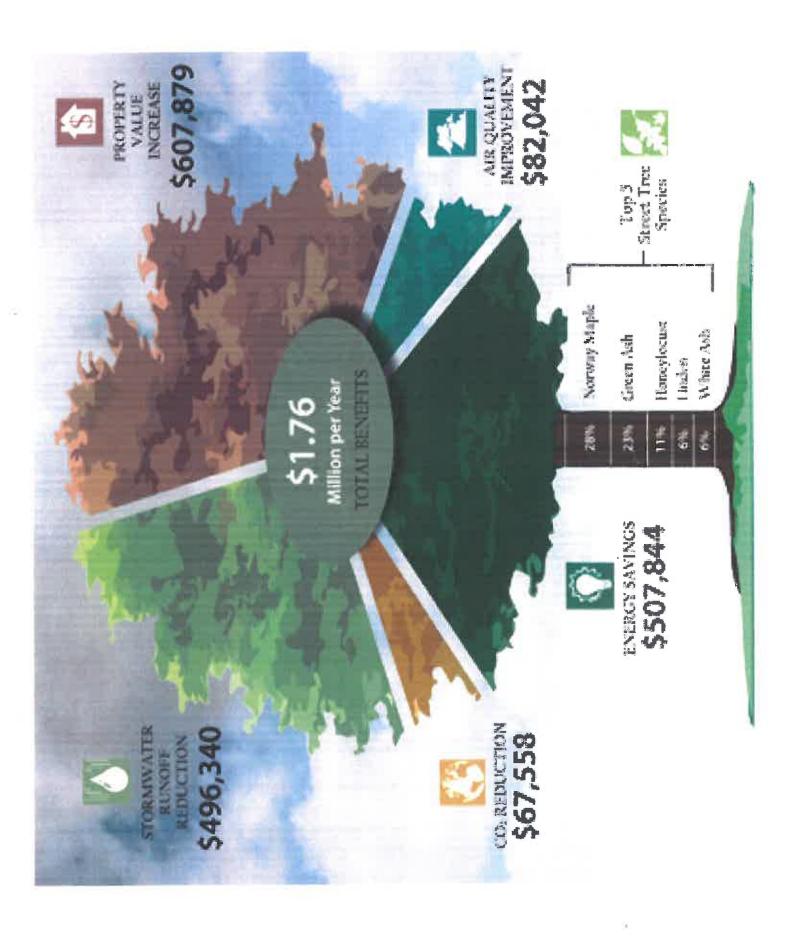
average stormwater interception (gallyr)

stormwater it

can manage.

The larger the tree, the more







Rate of tree carbon accumulation increases continuously with tree size

N. L. Stephenson¹, A. J. Das¹, R. Condit², S. E. Russo³, P. J. Baker⁴, N. G. Beckman³t, D. A. Coomes⁵, E. R. Lines⁶, W. K. Morris⁷, N. Ruger^{2,9}t, E. Álvarez³, C. Blundo¹⁰, S. Bunyavejchewin¹¹, G. Chuyong¹², S. J. Davies¹³, Á. Duque¹⁴, C. N. Ewango¹⁵, O. Flores¹⁶, J. F. Franklin¹⁷, H. R. Grau¹⁰, Z. Hao¹⁸, M. E. Harmon¹⁹, S. P. Hubbell^{2,20}, D. Kentack¹³, Y. Lin²¹, J.-R. Makana¹⁵, A. Malizia¹⁰, L. R. Malizia²², R. J. Pabst¹⁹, N. Pongpattananurak²³, S.-H. Su²⁴, I-F. Sun²⁵, S. Tan²⁶, D. Thomas²⁷, P. J. van Mantgem²⁸, X. Wang¹⁸, S. K. Wiser²⁹ & M. A. Zavala³⁰

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 stands23. 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, 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-level^{8–10} 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. Although the results of a few single-species studies have been consistent with this assumption. 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 stands. (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 reproduction¹¹⁻¹⁶. 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 theory" (Extended Data Fig. 2). Similar to the results of our main

1US Geological Survey, Western Ecological Research Conter. Three Rivers. California 93,271, USA. Smithson an Tropical Research Institute Apertado 0843-03092, Balboa Republic of Panama. School of Biological Sciences, University of Nebraska, Lincoln, Nebracka 68508, USA, 300 pirtment of Firestand Ecosystical Science University of Melbourne, Victoria 3121 Justralia 50 pirtment of Plant Sciences, University of Cambridge CB2 3EA UK. Department of Geography, University College London, Landon WC1E 5BT, UK. School of Setany, University of Melbourne, Victoria 3010, Justialia. ^aSpezialle Botanik und Funktionalle Blockversnat, Universität traipzig, 94103 Leipzig, Germany, ⁹Jardín polán podá Medellin, Calle 73, No. 510-14, Medellin. Colombin. ¹⁰Instituto de Ecologia Regiona i, Universidad Nicional de Tucumán, 4107 Yerba Buen a, Tucumán, Argentina. *18 scarch Office, Department of Flational Perks, Wildlife and Plant Concervation, Bangkok 10300, Thailand. *20 partment of Botany and Plant Physiology, Buea, Southwest Province, Cameroon, 195% this on an Institution Global Earth Observatory—Center for Tropical Forest Science, Smithconian Institution PO Box 37012, Washington, DC 20013, USA 14 Universidad Nacional de Colombia, Departamento de Ciencias Forestalas Medicilin Lolombia, 14 Wildlife Conservition Jociety, kinstiasa/Gombe, Democratir, Republic of the Congo, 16 Unité Mixte de Reche: the Peuplements Végétaux et Froagres eurs et Miliau Tropical, Université de la Réunion/CIRAD 97410 Saint Pierre, France, 1 School of Environmental and Format Sciences, University of Washington, Seattle, Washington 98195, USA, 18 State Key Laboratory of Forest and Suil Englogy Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 1101.4. Chura, "Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331, USA "Department of Ecology and evolutionary Biology, University of California, Loc Angeles, California 90095, USA. **Department of Life Science, Tunghai University, Taichung City 40704, Taiwan. 22Fauilled dis Ciences Agreement of Life Science, Tunghai University, Taichung City 40704, Taiwan. 22Fauilled dis Ciences Agreement of Life Science, Tunghai University, Taichung City 40704, Taiwan. Argentina 23 Foculty of Forestry, Nasetsart University, Chalu Chak Bangkok 10900, Thailand. 11 Farwan Forestry Research Institute, Toipei 10066, Taiv an. 25 Department of Natural Resources and Environmental Studies Institute Deng Hwa University, Huasien 97401, Tsirvan. Sarawak Forestry Department, Kirching Sarawak 93669, Malagrat. Papertment of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 273-31, USA 2 US Geological Survey, Western Ecological Research Center, Ameria, California 95-21. USA 2 Landcare Research, PD Box 40, Lincolin 7640, New Zealand, For: st Ecology and Restoration Group, Department of Life Sciencus, University of Alcalé, Alcalé de Honares, 28905 Madrid, Sprint, Present addresses: Mathematical Birisciences Institute, Ohio State University, Columbus, Ohio 43210, USA (id.G.B.); German Centre for Integrative Biodiversity Research (IDIV), Halfe-Jena-Lupzia, 04103 Leipzig, Germany (N.R.).

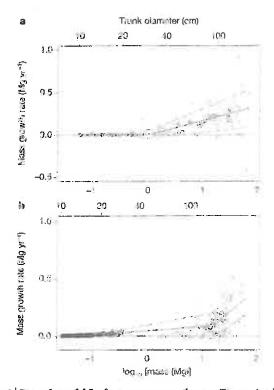


Figure 1 | Example model fits for tree mass growth rates. The species shown are the angiosperm species (Lecontedoxa klaineina, Cameroon, 142 trees) (a) and gymnosperm species (Picca sitchesis), USA, 409 trees) (b) in our data set that had the most massive trees (defined as those with the greatest cumulative aboveground dry mass in their five most massive tree). Each point represents a single tree; the solid ted 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, 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. I'o 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 size³⁻¹⁰, empirical observations and metabolic scaling theory both indicate that, on average, total tree leaf mass increases as the square of trunk diameter. 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

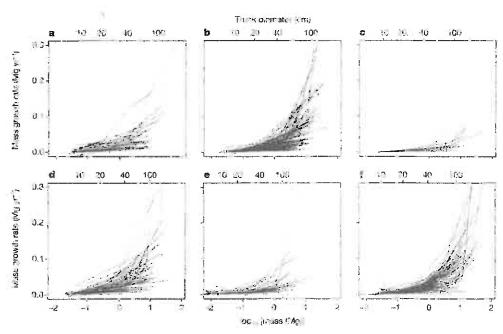


Figure 2 | Aboveground mass growth rates for the 403 tree species, by continent. a, Africa (Cameroon, Democratic Republic of the Congo); b, Asia (China, Malaysia, Taiwan, Thailand); c, Australa ia (New Zealand); d, Central and South America (Argentina, Colombia, Panama); e, Europe (Spain); and

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

Contineat	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)
Australosia	35,413	22	95.5 (95.5)
Central and South America	18,530	77	97.4 (92.2)
Europe	439.859	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 9,19,72}. 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 ^{16,23}, several factors (including the interplay of changing growth efficiency and tree dominance hierarchies²³) 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 ^{25,25}. 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

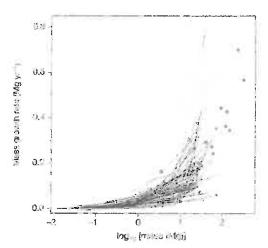


Figure 3 Aboveground mass growth rates of species in our data set compared with *E. regnans* and *S. sempervirens*. For clarity, only the 58 species in our data set having at least one tree exceeding 20 Mg are shown (lines). Data for *E. regnans* (green dots, 15 trees) and *S. sempervirens* (red dots, 21 trees) are from an intensive study that included some of the most massive individual trees on Earth. 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 percannal 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 ^{8,29}. The rapid growth of large trees indicates that, relative to their numbers, they could play a disproportionately important role in these feedbacks ¹⁰. 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.

WETHODS 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 treas with trunk diameter ≥10 cm, and to species having ≥ 10 trees in total and ≥15 trees with trunk diameter ≥30 cm Maximum trunk diameters ranged from 38 cm to 270 cm among species, averaging 92 cm. We converted each drameter 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 Gas 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 ritted to G versus log(M) in each bin so that the line regments 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 Akailæ's Information Criterion for each species. Our approach thus makes no assumptions about the shape of the relationship between C and log(M), and can accommodate increasing, decreasing or hump-shaped relationships. Parameters were fitted with a Gibbs sampler based on Metropolis updates, poducing 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 rits failing to detect a final growth decline in the largest trees, possible biases introduced by the 47% or 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 and available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 5 August; accepted 27 November 2013. Published online 15 January 2014.

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

- Medvigy, D., Weisy, S. C., Munger, J. W., Hollinger, D. Y. & Moorcroft, P. R. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. I. Geophys. Res. 114, G01002 (1009).
- Caspersen, J. P., Vonderwel, M. C., Coln, W. G. & Pürves, D. W. How stand productivity results from size- and competition-dependent growth and mortality. PLos ONE 6, e28660 (2011).
- 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. & Dzwson, T. E. (eds) Jize- and Age-Related Changes in Tree Structure and Function (Springer, 2011).
- Enquist, B. J. West, G. P. Charnov, E. L. & Brown, J. H. Mometric scaling of production and life-history variation in vascular plants. Nature 401, 907–911 (1999).
- Sillett, S. C. et al. Increasing wood production through old age in tall trees. For. Ecol. Manage. 259, 976–994 (2010).
- Mencuccini, M. et al. Size-mediated ageing reduces vigour in frees, Ecol. Lett. 8, 1183–1190 (2005).
- Drake, J. E., Reetz, L. M., Davis, S. C. & DeLucia, E. H. Hydraufic limitation not declining nitrogen availability causes the age-related photosynthetic decline in loblolly pine (*Pinus taeda L.*). *Plant Cell Environ.* 33, 1756–1766 (2010).
- Ryan, M. 3. Binkley, D. & Fownes, J. H. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Rev. 27, 213–262 (1997).
- Thomas, S. C. in Size- and Age-Related Changes in Tree Structure and Function (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, 695–711 (2013).
- Carey, E. V., Sals, 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 frees tri respond to environmental change. J. Integr. Plant Biol. 50, 1355–1364 (2008)
- Piper, F.I. & Fajardo, A No evidence of carbon limitation with tree age and neight in Nothofag is cumillo 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 forest productivity". *Otins* 94, 374–376 (2001).
 Johans, J. C., Chojnacky, D. C., Heath, L. S. & Birdsey, R. A. Comorehensive Database
- Johans, J.C., Chojnac'ry, D.C., Heath, L.S. & Birdsey, R.A. Comprehensive Estabase of Diameter-based Biomess Regressions for North American Tice Species General Technical Report NE-319, http://www.nrs.fs.fed.us/pubs/6/25 (USDA Forest Service, Northeastern Research Station, 2004).
 Niklas, K.J. & Enquist B.J. Canonical rules for plant organ biomass partitioning
- Niklas, K. J. & Enquist, B. J. Canonical rules for plant organ biomass partitioning and annual allocation. Im. J. Bot. 89, 312–819 (2002).
- Thomas, S. C. Photosynthetic capacity peaks at intermediate size in termograte decirbuous it ies. Tree Physiol. 30, 555-573 (2010).
 Steppe K., Minemets, U. & Teckey, R. C. in Size- and Age-Related Changes in Tree
- Steppe K., Nimemets, U. & Teskey, R. C. in Size- and Age-Related Changes in Tree Substance and Function (eds Meinzer, F. C., Lachenbruch, B. & Davison, T. E.). 235–253 (Springer, 2011).
- Gilmore, D. W. & Seymour, P. S. Alternative measures of stem growth efficiency applied to Ables balsacines from four canopy positions in central Walne, USA. For. Ecol. Manage 84, 209–218 (1996).
- Naumann, M.R. & Ryan, M. G. Physiographic stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests. Tree Physiol. 2, 47–59 (1986).
- Coornes, D.A. Holdaway S. J. hobe P. K. Lines: E. P. & Allen R. B. Algebraid Integrative frainc work for mudelling woody piornass production and earborn sequestration races in icrosts. J. Ecol. 100, 42–64 (2012)
- Binkley, D. A hypothesis about the interaction of the dominance and stand production through stand development. For. Ecol. Manage 190, 255–271 (2004).

- Pretzsch, H. & Biber, P. A re-evaluation of Raineke's rule and stand density index. For. Sci. 51, 204–320 (2005).
- Kashian D. M., Turner, M. G. Romme, W. H. & Lorimer, C. G. Variability and contergence in stand structural development on a fire-dominated subalpine landscape. Ecology 86, 643–654 (2005).
- Munné-Posch, S. Do perennials really senesce? Trends Plant Sci. 13, 215–220 (2008).
- Jump A S., Hunt J. M. & Pefiuelas, J. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Glob. Change Biol. 12, 2163–2174 (2006).
- 29 Lindenmayer D.B. Laurania, W.F. & Franklin, J.F. Global decline in large oid trees, Science 338, 1305–1306 (2012).
- Enguist, B. J., West, G. B. & Brown, J. H. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proc. Netl Acad. Sci. USA* 106, 7046–7051 (2009).

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

Acknowledgements We thank the hundreds of people who have established and maintained the forest plots and their associated databases; M. G. Ryan for comments on the manuscript; C. D. Canham and T. Hart for supplying data; C. D. Canham for dis russions and fleetback: J. S. Baron for hosting our workshops; and Spain's Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA) for granting access to the Spanish Forest Inventory Data. Our analyses were supported by the United States Geological Survey (USGS) John Wesley Powell Center for Analysis and Synthesis, the USGS Ecosystems and Climate and Land Lise Change mission aleas, the Smithsonian Institution Global Earth Observatory—Center for Tropical Folest Science (CTFS), and a University of Neoraska-Lincoln Program of Excellence in Population Biology Postdocforal Fellowship (to N.G.B.), In addition, X.V., was supported by Netional Natural Science Foundation of China (31370444) and State Key Laborator, of Forest and Soil Ecology (LFSF2013-11). Data collection was funded by a broad range of organizations including the USGS, the CTFS, the US National Science Foundation, the Andrews LTER (NSF-LTER DEB-0823380), the US National Park Service, the US Forest Service (USFS), the USFS Forest Inventory and Analysis Program, the John D. and Catherine T. MacArthur Founcation, the Andrew W. Mellon Foundation, MAGRAMA, the Council of Agriculture of Taiwan, the National Science Council of Taiwan, the National Natural Science Foundation of China, the Knowledge Innovation Program of the Chinese / cademy of Scionces, Landcale Research and the National Regetation Survey Database (IVVS) of New Zealand the French Fund for the Global Environment and Fundación ProYungas. This paper is a contribution from the Western Mountain Initiative, a USGS global change research project. Any use of trade names is fur descriptive purposes only and does not imply endorsement by the USA government.

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 phalytical approach and wrote the computer code. N.L.S., A.J.D., R.C., S.E.R. P.J.B., N.C.P. D.A.C., E.R.L., W.K.M. and N.P. 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.A., C.B., S.B., G.C., S.J.D., A.D., C.N.E., D.F., J.F.F., H.R.G., Z.H., M.E.H., S.P.H., D.K., Y.L., J.-R. I.A., A.M., L.R.M., R.J.P., N.P., S.-H.S., I-F.S., S.T., I.T., P.J.V.M., X.W., S.K.W. and M.A.T. supplied data and sources of allometric equations appropriate to their data.

Author Information Fitted niodel 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 w. w. nature com/reprints. The authors declare no combeting linancial interests, Readers are welcome to comment on the online version of the paper. Correspondince and requests for materials should be addressed to N.L.S. (instephenson@usps.gor).



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. Ploty 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 Tree height.

We excluded tiecs exhibiting extreme diameter growth, defined as trunks where D increased by ≥ 40 mm yr⁻¹ or that shrank by $\geq 12s$, where s is the standard deviation of the D measurement error, $s = 0.9036 \pm 0.006214D$ (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 error.³

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 aboveg ound 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 specific and others were specific to higher texonomic levels or forest type's, described in the references in Supplementary Table 1. The single tropical moist forest equation of ref. 24 was applied to most tropical species, whereas most temperate species had unique species-specific equations. Most ailometric equations are broadly similar, relating $\log M$ to $\log (D)$ linearly, or nearly linearly—a familiar relationship in allometric scaling of both animals and plants ¹⁵. Equations can show a variety of differences in detail, nowever, with some adding $\log (D)$ squared and cubed terms. All equation 3 make use of the wood density of individual species, but when wood density was not available for a given species we used mean would density for a genus of family.

Using a single, average allometry for most cropical species, and mean wood density for a genus or family for several species, limits the activacy of our estimates of M. However, because we treateach species reparately, 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 contelated and their growth rates are expected to scale isomethically both within and among species $^{(4)}$, $^{(5)}$, resulte from those two regions should not after 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 above ground dry mass growth rate, C_s and above ground dry mass, M_s 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 litted as a function of X by linear regression. The position of the bins is adaptive; it is flitted 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_s is fixed. For example, if B = 2, there are four parameters to be litted for a single species: the location of the boundary between bins, X_1 ; the slope of the regression in the drst bin, S_1 ; the slope in the second bin, S_2 ; and an intercept term. Those four parameters completely define the model. In general, there are 2B 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, $\sigma_{\rm c}$, as a function of log(M). The increase of $\sigma_{\rm c}$

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 Malkov chain Monte Carlo chain of parameter estimates was created using a Gibbs sampler with a Metropolis update with written in the programming language R (-ef. 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 rurs, 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_0 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 piecise 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 outhers. 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 model.

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 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 enaggerated. This might occur because trees on less-productive sites—presumably the sites having the slowest-growing treer within any given size class—could be under-represented 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 trank 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, 7.4% (dominated by cropical species) had no trees in our data set with D exceeding that used in calibrating the allometric equations, with the remaining 2.6% (dominated by temperate species) having at least one tree with D exceeding that used in calibration. The percentage of species with increasing C 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 C 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 trees." Por 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[(RSF)³/2] for the error 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 tixon specific constants. For nine of our species that used equations of this form (all from the temperate western USA: Abies anabilis, A. Loncolor, A. procera, Pinus lambertiana, Pinus ponderosa, Picea sitchensis, Pecudoisuga mencietii, Isuga 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 treated 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 tother 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 piecewire regressions led to predictions of M with no apparent bias relative to D (Extended Data Fig. 1c). This new, unbiased ellometry 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 (Fxiended 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 equations'. 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 relation hips), 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 years'. E. regnuns 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 F regnans and S sempervirons—15 and 21 trees, respectively—fell below our required ≥40 trees for fitting piecewise linear regressions, so we simply plotted data points for individual E. regnant 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 litted 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 $G \leq 0$. 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 $G \leq 0$ caused several species to fall below our threshold sample size, reducing the total number of species analysed to 381 (Extended Data Fig. 2).

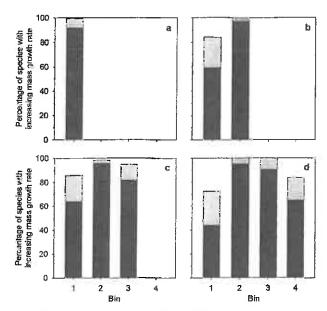
Growth in the absence of competition. We obtained published equations for 41 North American and European species, in 16 species-site combinations, elating species-specific tree diameter growth rates to trunk diameter D and to neighbourhood competition"-13. Setting neighbourhood competition to zero gave 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} , (5) used in appropriate taxon-specific allometric equation to calculate the associated free masses M_t and M_{t-1} , and (11) calculated is see 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 Nino dry season. J. Trop. Ecol. 20, 51–72 (2004).
- Condit, R. et al. The importance of demographic niches to tree diversity. Science 313, 95–101 (2006).
- Rüger, N., Berger, U., Hubbell, S. P., Vibilledent, G. & Condit, R. Growth strategies of tropical tree species: disentangling light and size effects. PLoS ONE 6, a25330 (2011).
- Chave, J. et al. Tree allornetry and improved estimation of carbon stocks and balance in tropical forests. Oecologie 145, 87–99 (2005).
- Sibly, R. M., Brown, J. H. & Kodric-Brown, A. (eds) Metabolic Ecology: A Scaling Approach (John Wiley & Sons, 2012).
- Zanni, 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).



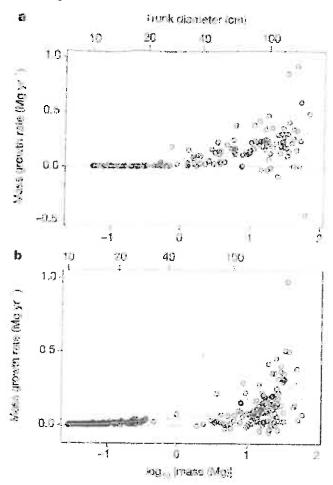
- 38. Niklas, K. J. Plant allometry: is there a grand unifying theory? Biol. Rev. 79, 871-889 (2004).
- 39. Metropolis, N., Rosembluth, A. W., Rosembluth, M. N., Teller, A. H. & Teller, E. Equation of stat- calculations by fast computing machines. J. Cheni. Phys. 21, 1087-1092 (1953).
- Rüger, N., Muth, A., Hubbell, S. P. & Condit, R. Determinants of mortality across a tropical lowland rainfurest community. *Oikos* 120, 1047-1056 (2011).
 R Development Core Team, R. A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, 2009).
- 42. Hilborn, R. & Mangel, M. The Ecological Detective: Confronting Models with Data (Princeton Univ. Piess, 1997).
- 43. Chambers, J. Q. Dos Santos, J., Ribeiro, R. J. & Higuchi, N. Tree damage allometric 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, N. D., Canham, C. D. & LeFage, P. T. Above- versus below-ground competitive effects and responses of a guild of tempe vite tree species. J. Ecol. 97, 118-130 (2009).
- 47. Pretzsch, H. & Biper, P. Silie symmetric versus size-asymmetric competition and growth partitioning among trees in lorest stands along an ecological gradient in central Europe Can. J. For Res. 40, 370–384 (2010).
- 48. Gómez-Aparicio, L., García-Valdés, R., Ruiz-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).
 49. Das, A. The affect of size and competition on tree growth rate in old-growth coniterous forests. *Can. J. For. Res.* 42, 1983–1995 (2012).
 50. Zianis, D., Muskkonen, P., Makiova, R. & Mancuccini, 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).

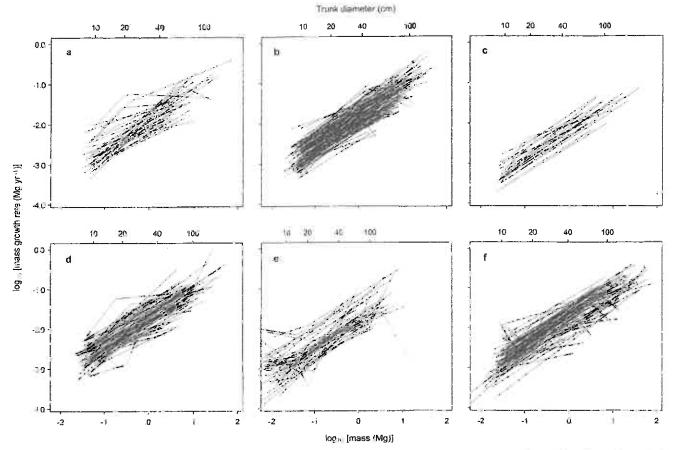
Figure 1: Example model fits for tree mass growth rates.



The species shown are the angiosperm species (Lecomredox a 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.

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).

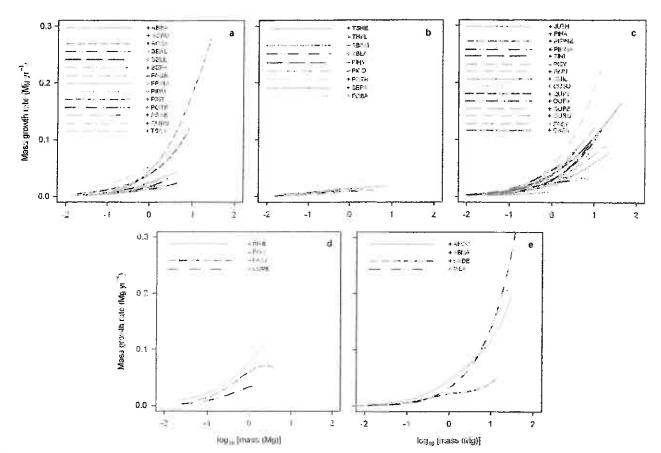
Figure 2: Aboveground mass growth rates for the 403 tree species, by continent.



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, Austraiasia

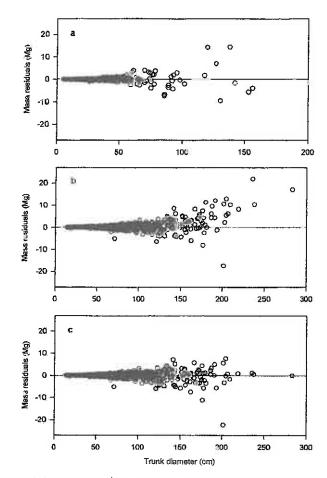
(22 species); d, Central and South America (73 species); e, Europe (41 species); and f, North America (89 species). Trunk diameters are approximate values for reference, based on the average diameters of trees of a given mass.



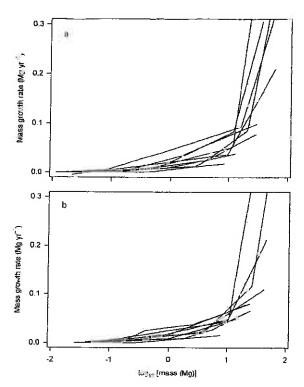


Extended Data Figure 3 | Aboveground mass growth rates for 41 tree species in the absence of competition. The '+' or '-' symbol preceding each species code indicates, respectively, species with mass growth rates that increased continuously with tree size or species with mass growth rates that declined in the largest trees. Sources of the diarneter growth equations used to calculate mass growth were a, rcf. 45; b, rcf. 46, c, rcf. 48; d, rcf. 47; and e, rcf. 49. ABAM, Abies amabilis; ABBA, Abies belsomea; ABCO, Abies concolor, ABIA, Abies insiocarpa. ABMA, Abies magnifica; ACRU, Aver rubrum; ACSA, Acr saccherum; BiAL, Betula alegianiensis; BELE, Betula lenta; BEPA, Betula papprijera; CADF, Calocedrus decurrens, CASA, Castanea sativa; † AGR, Fague grandifolia; † ASX, Fague sylvatica; † RAM, Fraxinus americana; JUTH,

Juniperus thurifera; PIAB, Picea abus, PICO, Pinus contortu; PIHA, Pinus nalepensis, PIHY, Picea hybrid (a complex of Picea glauco, P sichensis and P. engelmannii), PILA, Pinus lambertuana; PINI, Pinus nigra; PIPINA, Pinus pinaster, PIPINE, Pinus pince, PIRU, Picea vubens, PIST, Pinus strobus, PISY, Pinus sylvestris; PIUN, Pinus uncupata, POBA, Populus balsamifera ssptrichocarpa; POTR, Populus iremuloides; PRSE, Prunus serotina, QUFA, Quercus fagines; QUIL, Quercus ilex, QUPF, Quercus petraea, QUPY, Quercus pyrenaica; QURO, Quercus robar, QURU, Quercus rupra; QUSU, Quercus suber, TIPIL, Tinja plicata; TSCA, Isuga canadensis, and TSHE, Tsuga heterophylla



Extended Data Figure 4 Residuals of predicted minus observed tree mass. a. The allometric equation for moist tropical forests —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 nune 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 $[\log(M) = a + b \log(D)]$ (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.