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Title: CHARACTERIZING A LINK IN THE TERRESTRIAL CARBON CYCLE:
A GLOBAL OVERVIEW OF INDIVIDUAL TREE MASS GROWTH

Short Title: Tree mass growth

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Project Summary:

Forests sequester the majority of the terrestrial biosphere's carbon and are key components of the global carbon cycle, potentially contributing substantial feedbacks to ongoing climatic changes. It is therefore remarkable that no consensus yet exists about the fundamental nature of tree mass growth (and thus carbon sequestration rate). Specifically, does tree mass growth rate increase, decrease, or stay the same with increasing tree size? The answer could have profound implications for our ability to forecast the role of forests in the global carbon cycle and to devise appropriate adaptation and mitigation strategies for forests in the face of rapid climatic changes.

We will conduct the first global-scale characterization of the relationship between individual tree mass growth rate and tree size. To reach this end, we will analyze forest monitoring data from every forested continent, including millions of trees and more than 1,000 species. We have assembled an international team to accomplish this task, and have leveraged funds with the Smithsonian Tropical Research Institute's Center for Tropical Forest Science.

Proposed Start and End Dates: Jan. 2010 – Dec. 2011

Proposed Data Release Date: Feb. 2011

Is this a resubmission? No

Conflicts of Interest with Reviewers:

Stephenson, Das, and van Mantgem are PI/collaborators with Jill Baron (one of the Directors of the Powell Center) on the USGS Western Mountain Initiative climate change research project.

Problem statement

“Tree [mass] growth *must* be sigmoidal, and therefore growth rates *must* first increase and then decrease with tree size” (emphasis in the original).
– Weiner & Thomas (2001)

“[Metabolic theory predicts that] as an individual grows, $dM/dt \propto M^{3/4}$ [i.e., tree mass growth rate, dM/dt , increases indefinitely with increasing tree mass, M].”
– Enquist *et al.* (1999)

The preceding statements by respected ecologists highlight a remarkable fact: no consensus yet exists as to whether tree mass growth rate declines, remains constant, or increases with tree size. The debate remains lively because (1) logical arguments can be made supporting each of the possibilities (e.g., Enquist *et al.* 1999, Weiner & Thomas 2001, Binkley *et al.* 2002, Kutsch *et al.* 2009), but (2) explicit empirical tests that include a full range of tree sizes are virtually nonexistent.

Yet forests sequester the majority of the terrestrial biosphere’s carbon and are key components of the global carbon cycle, potentially contributing substantial feedbacks to ongoing climatic changes (Bonan 2008). If we are to forecast effects of climatic changes on forests and plan for adaptation and mitigation, we must first understand the basic nature of tree growth. For example, though forests play a central role in international treaties focused on carbon capture and sequestration, effective management approaches (e.g., thinning trees of certain sizes while protecting others) could differ substantially depending on whether tree mass growth declines or increases with tree size.

In spite of the general dearth of empirical data, forest models necessarily include assumptions about tree growth, and those assumptions influence forecasts of forest change. Models commonly assume that tree mass growth declines as trees approach a predefined maximum size (reviewed by Bugmann 2001) or that mass growth remains roughly constant in large trees (early versions of SORTIE; Pacala *et al.* 1996). Only recently have some models – such as SORTIE-ND (www.sortie-nd.org) – begun to incorporate empirically-derived algorithms that do not rely on untested assumptions about tree growth relative to size (Canham *et al.* 2006, Coates *et al.* 2009).

Why do we lack generalized knowledge of something as fundamental as the relationship between tree size and mass growth? First, most research has focused on mass budgets at the level of forest stands rather than individual trees. Second, the vast silvicultural literature has focused on a handful of economically important species in relatively young, managed stands that generally lack large, old trees. Third, while potential (maximum) *diameter* growth often initially increases but then declines with increasing tree size (e.g., Bragg 2001), there is a lack of recognition that the three-dimensional geometry of tree boles means that tree mass growth might continue to increase even while diameter growth declines (e.g., Enquist *et al.* 1999) (Fig. 1). Finally, and perhaps most important, deeply-ingrained assumptions have kept people from examining alternative hypotheses. For example, a common assumption is that trees senesce the same way vertebrates do (i.e., suffer an inevitable, age-related decline in physiological function, leading to reduced growth), though recent physiological studies contradict this assumption (e.g., Mencuccini *et al.* 2007, Munné-Bosch 2008).

Importantly, results of some growth studies also contradict assumptions about tree senescence, suggesting that both potential and average realized mass growth often increase indefinitely with tree size. For example, studies of a tropical forest (Clark & Clark 1999), temperate angiosperm forests of the eastern U.S. (Johnson & Abrams 2009), and temperate gymnosperm forests of California (Stephenson, *unpublished data*) all showed that, for a majority of species, maximum basal-area increment (a crude surrogate for tree mass growth) increased continuously with tree size. In temperate New Zealand and in several lowland tropical forests of both the New and Old World, tree diameter growth rates (averaged across species) usually either increased indefinitely or leveled off with increasing tree size (Muller-Landau *et al.* 2006, Coomes & Allen 2007, Russo *et al.* 2007). Since tree mass scales as (diameter)^c, and *c* generally falls between 2 and 3 (e.g., Jenkins *et al.* 2004), these latter results imply that average tree mass growth increased with size. Perhaps most interesting is the behavior of some of the world's largest trees. On average, basal area increment continues to increase even for giant sequoias several meters in diameter (Stephenson & Demetry 1995; cf. Fig. 1), and an extraordinary set of growth measurements along entire bole lengths of the largest coast redwoods indicates that their mass growth continues to increase indefinitely with size (Van Pelt & Sillett, *in review*).

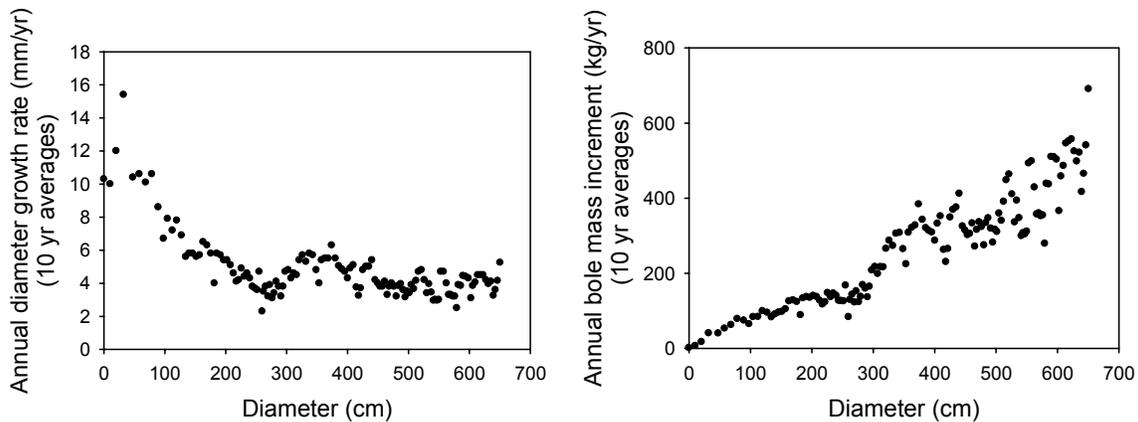


Figure 1. Growth of giant sequoia #263, from tree ring measurements (data from Stephenson & Demetry 1995). The tree was 1347 years old when cut. *Left:* Diameter growth rate initially declined, but then leveled off and remained nearly constant until the tree was cut at 6.5 m in diameter. *Right:* The tree's mass growth rate, calculated using a species-specific allometric equation (Means *et al.* 1994), increased throughout the tree's lifespan, even during the period of diameter growth decline (because sequoia mass scales as a power function of diameter, with an exponent of 2.40).

We will conduct the first global-scale characterization of the relationship between tree mass growth rate and tree size. Our study will analyze millions of trees and more than 1,000 species representing most major global forest types. We will interpret our results in light of existing theories of drivers of tree mass growth: metabolic and scaling theory, physiological and hydrological limitations, competition, and tree senescence. We will place particular emphasis on interpreting implications for understanding and modeling forest carbon balances.

Proposed Activities

General approach:

Tree masses will be estimated from taxon-specific allometric equations based on tree diameter (e.g., Jenkins *et al.* 2004). The raw data driving our analyses will be changes in tree diameter through time, which will be determined from repeated diameter measurements. We will not use growth determined from tree-ring chronologies because (1) virtually no tree-ring data are available from the tropics, and (2) with few exceptions, most available ring-width series (e.g., in the International Tree-Ring Data Bank) fail to record crucial information (such as tree diameters and spatial locations of competing trees) and usually are from a strongly biased subset of trees – those growing on marginal sites that make them particularly sensitive to climate.

We will analyze both potential mass growth rate (because it is a critical input to forest models) and average realized mass growth rate (because of its implications for forest management). Both metrics will help us interpret our results in light of existing theory.

Data:

Our analytical approaches are data-intensive. However, members of our workgroup are stewards of, or have access to, many of the world's largest forest monitoring datasets (Table 1). We will limit our analyses to species represented by at least 300 trees spanning a full range of sizes. This leaves us with more than 1,000 species and 8,000,000 trees (Table 1).

Table 1. Forest types and regions that we will analyze, with approximate numbers of species and trees. We may add additional data sources.

Forest type, region	Descriptive reference(s)	Approx. # of species with >300 trees	Approx. number of trees
Temperate coniferous, western North America	van Mantgem <i>et al.</i> 2009; http://frames.nbii.gov/ffi/	20	54,000
Temperate deciduous, eastern North America	http://fia.fs.fed.us/	75	6,000,000
Temperate deciduous, Europe		28	82,000
Tropical, Americas (Panama, Colombia, Puerto Rico)	Losos & Leigh 2004	200	400,000
Tropical, Africa (Cameroon, Congo)	Losos & Leigh 2004	170	613,000
Tropical, Asia (China, Malaysia, Singapore, Sri Lanka, Taiwan, Thailand)	Losos & Leigh 2004	750	1,130,000
Southern temperate, New Zealand	Coomes <i>et al.</i> 2003	60	300,000
Southern subtropical, Argentina	Easdale <i>et al.</i> 2007	5	7,000
TOTALS	--	1,308	8,586,000

Analytical Approach:

In all analyses described below, models will be parameterized using maximum likelihood methods, and best models will be selected using an information theoretic approach (Burnham and Anderson 1998).

Realized growth

We will use simple but flexible functions to characterize the relationship between average realized mass growth rates and tree size. Average realized growth will also be a byproduct of our approaches to characterizing potential growth (below).

Potential Growth

Potential growth rate is the rate at which a tree would grow at a given site in the absence of modifying factors such as competition. Ideally, potential growth is estimated from trees that are completely open-grown (e.g., Moore 1989). However, open-grown trees are rare in forest settings, and estimates of potential growth rates therefore require approaches that extract the estimates from large forest monitoring data sets (e.g., Bragg 2001, Canham et al. 2004, Coates et al. 2009). We will compare results from at least two different approaches, with modifications as needed:

Growth rate distributions. The first approach is to estimate the distribution of growth rates in populations of individuals and how it varies with diameter, site, or species. Growth rates are often log-normal or gamma-distributed, and the variance increases with diameter. Fitting models via maximum likelihood allows the parameters fitting these distributions to be estimated, and these in turn produce rigorous estimates of maximum and any quantile of growth (e.g., the fastest-growing 10%) as a function of whatever independent variables are chosen. This approach effectively identifies the fastest growing individuals of particular species and size classes, and assumes they best represent potential growth rate (cf. Teck & Hilt 1991, Bragg 2001).

Competition models. The second approach to modeling potential growth is based on the assumption that realized tree growth can be described as:

$$\text{Realized growth} = \text{Potential growth} * \text{Modifier}$$

Assuming that potential growth is itself a function of tree size, the modifier typically represents competitive effects and perhaps a site effect (Canham *et al.* 2006, Coomes & Allen 2007, Coates *et al.* 2009). The potential growth function and modifier function are fit simultaneously. This approach allows the use of the full data set, but unlike the growth-rate distributions method (above), it explicitly factors out competitive effects to estimate potential growth. The potential growth function will be specified as for the growth-rate distributions procedure, and the modifier function will include competitive effects and, where possible, site effects (see Canham *et al.* 2004, Canham *et al.* 2006).

Participants

We have assembled an international team that includes world-renowned scientists with extensive experience analyzing (and setting analytical standards for) large forest data sets, and with strong publication records in some of the world's top journals (follow the web links in Table 2, below). To help us keep our budget within the Powell Center's \$30,000 limit, the Smithsonian Tropical Research Institute's Center for Tropical Forest Science (CTFS; <http://www.ctfs.si.edu>) has agreed to fund travel for several of its members (*personal communication* from Stuart Davies, CTFS Director). See our Budget for further details.

Table 2. Workgroup members.

Participant

- * **Nathan Stephenson**, U.S. Geological Survey, California, USA
<http://www.werc.usgs.gov/products/personinfo.asp?PerPK=29>
- *† **Adrian Das**, U.S. Geological Survey, California, USA
<http://www.werc.usgs.gov/products/personinfo.asp?PerPK=2131>
- * **Phillip van Mantgem**, U.S. Geological Survey, California, USA
<http://www.werc.usgs.gov/products/personinfo.asp?PerPK=1663>
- * **Charles Canham**, Cary Institute of Ecosystem Studies, New York, USA
http://www.ecostudies.org/people_sci_canham.html

- * **Richard Condit**, Smithsonian Tropical Research Inst., Rep. of Panama
http://www.stri.org/english/scientific_staff/staff_scientist/scientist.php?id=5
- * **David Coomes (prof.) & Emily Lines (graduate student)**, University of Cambridge, U.K. <http://www.plantsci.cam.ac.uk/research/davidcoomes.html>
- * **Sabrina Russo**, University of Nebraska, Lincoln, USA
<http://www.unl.edu/srusso/index.html>
- * **Mark Harmon & Thomas Spies**, Oregon State University, Corvallis, USA <http://eco-informatics.engr.oregonstate.edu/harmonsrc.html> ;
<http://www.forestry.oregonstate.edu/cof/fs/people/faculty/spies.php>
- * **Ricardo Grau (prof.) & Agustina Malizia (postdoc)**, Instituto de Ecología Regional, Universidad Nacional de Tucumán, Argentina
<http://www.icologia.com.ar/integrantes/integrantesdetalle.asp?id=28>
- * **Álvaro Duque**, Universidad Nacional de Colombia, Medellín, Colombia
<http://www.corfor.com/>
- ** **Stuart Davies & graduate student**, Harvard University, Mass., USA
<http://www.huh.harvard.edu/ctfs/ctfs/davies.htm>
- ** **Maria Uriarte (prof.) & Liza Comita (postdoc)**, Columbia University, New York, USA. <http://www.columbia.edu/~mu2126/> ;
<http://www.columbia.edu/~mu2126/liza.htm>
- ** **Patrick Baker & graduate student**, Monash Univ., Australia
<http://www.biolsci.monash.edu.au/staff/baker/index.html>
- ** **Yu-Yun Chen**, National Tsing Hua University, Taiwan
- *** **Jerry Franklin**, University of Washington, Seattle, USA
- *** **Keping Ma**, Institute of Botany, Chinese Academy of Sciences, Beijing, China
- *** **I Fang Sun**, Tunghai University, Taiwan
- *** **Bunyavejchewin Sarayudh**, Royal Forestry Dept., Thailand
- *** **Abdul Rahmann**, Forest Research Institute of Malaysia
- *** **Sylvester Tan**, Center for Tropical Forest Science, Malaysia
- *** **Jean-Remy Makana**, Wildlife Conservation Society, Congo
- *** **Duncan Thomas**, Oregon State University, USA
- *** **David Kenfack**, University of Michigan, USA

Expertise

- Forest population ecology and dynamics; climate change
- Statistical and analytical approaches; forest dynamics
- Forest dynamics; statistical models of forest change
- Statistical modeling; tree population dynamics, and models of forest dynamics
- Population biology and modeling; quantitative ecology
- Forest dynamics, scaling of demographics with tree size
- Demographic trade-offs, forest populations & communities
- Forest carbon dynamics and modeling; forest structure, dynamics, and ecology
- Forest dynamics in relation to climate, land use change, and disturbances
- Forest population and community ecology
- Tropical forest dynamics; Malaysian forest plots
- Tropical forest dynamics, statistical and analytical approaches
- Forest dynamics; Thailand forest plots
- Taiwan forest plot network
- PNW forest plot network
- Chinese forest plot network

- Taiwan forest plot network
- Thailand forest plots
- Malaysian forest plot
- Malaysian forest plot
- Congo forest plot
- Cameroon forest plot
- Cameroon forest plot

* Confirmed participant.

** Data contributor and potential participant (has expressed interest, but has not yet formally committed to attending the workshops).

*** Data contributor and collaborator, but probably will not attend the workshops.

† Das will serve as technical liaison to the Powell Center and will be responsible for ensuring compliance with the Powell Center's Data and Information Policy.

Timetable of Activities

Our collective experience is that in massive and potentially complex analyses such as ours, the devil is in the details (e.g., agreeing upon details of analytical methods and appropriate comparisons among them; how best to analyze error and error propagation; identifying and overcoming problems with individual data sets; classifying taxa according to life-history traits). While many details will be worked out by email exchanges and conference calls, there is no reliable substitute for meeting face-to-face for several days of focused effort. Additionally, we expect our meetings to be fertile grounds for spirited exchanges leading to new insights that otherwise might be overlooked.

- Jan. – May 2010: Email exchanges and conference calls: Refine project goals, analytical approaches, and data sets to be used. Establish common data formats. Secure *pro forma* permissions to use the New Zealand and European data sets. Conduct some preliminary analyses. Finalize CTFS-funded participants.
- June 2010: First meeting, three days (+2 travel days): Compare results of preliminary analyses, and adjust analytical approaches accordingly. Conduct additional analyses and begin collective interpretation of results. Assign manuscript writing tasks.
- July – Dec. 2010: Continuing analyses, and sharing and interpretation of results, with email exchanges and conference calls as needed. Write first drafts of manuscripts.
- Jan. 2011: Second meeting, three days (+2 travel days): Hammer out final problems and analyses as needed. Critique draft manuscripts, and begin revisions.
- Feb. – Dec. 2011: Complete manuscripts and internal reviews. Submit manuscripts for publication.

Anticipated Results and Benefits

We anticipate at least four papers:

- (1) An overview of our findings and their implications, aimed at *Nature*, *Science*, or *PNAS*. As described in our Problem Statement, we will produce the world's first global-scale assessment of individual tree mass growth, with potentially profound implications both for theory and for understanding and forecasting the role of forests in the global carbon cycle.
- (2) A more in-depth analysis of implications for metabolic and scaling theory, focusing on taxon-related differences in growth.
- (3) A more in-depth analysis of implications for understanding and modeling forest carbon dynamics.
- (4) An analysis of latitudinal trends in neighbor effects on tree growth, and implications for theory (Janzen-Connell hypothesis, Grime hypothesis, etc.).

Data and software products will include summary data needed for others to reproduce our results, plus the scripts we used for our analyses. Proposed public release date of these products is February 2011.

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