

## Detecting evidence for CO<sub>2</sub> fertilization from tree ring studies: The potential role of sampling biases

Roel J. W. Brien<sup>1,2</sup>, Emanuel Gloor<sup>1</sup>, and Pieter A. Zuidema<sup>2,3,4</sup>

Received 14 June 2011; revised 7 December 2011; accepted 26 January 2012; published 17 March 2012.

[1] Tree ring analysis allows reconstructing historical growth rates over long periods. Several studies have reported an increasing trend in ring widths, often attributed to growth stimulation by increasing atmospheric CO<sub>2</sub> concentration. However, these trends may also have been caused by sampling biases. Here we describe two biases and evaluate their magnitude. (1) The *slow-grower survivorship bias* is caused by differences in tree longevity of fast- and slow-growing trees within a population. If fast-growing trees live shorter, they are underrepresented in the ancient portion of the tree ring data set. As a result, reconstructed growth rates in the distant past are biased toward slower growth. (2) The *big-tree selection bias* is caused by sampling only the biggest trees in a population. As a result, slow-growing small trees are underrepresented in recent times as they did not reach the minimum sample diameter. We constructed stochastic models to simulate growth trajectories based on a hypothetical species with lifetime constant growth rates and on observed tree ring data from the tropical tree *Cedrela odorata*. Tree growth rates used as input in our models were kept constant over time. By mimicking a standard tree ring sampling approach and selecting only big living trees, we show that both biases lead to apparent increases in historical growth rates. Increases for the slow-grower survivorship bias were relatively small and depended strongly on assumptions about tree mortality. The big-tree selection bias resulted in strong historical increases, with a doubling in growth rates over recent decades. A literature review suggests that historical growth increases reported in many tree ring studies may have been partially due to the big-tree sampling bias. We call for great caution in the interpretation of historical growth trends from tree ring analyses and recommend that such studies include individuals of all sizes.

**Citation:** Brien, R. J. W., E. Gloor, and P. A. Zuidema (2012), Detecting evidence for CO<sub>2</sub> fertilization from tree ring studies: The potential role of sampling biases, *Global Biogeochem. Cycles*, 26, GB1025, doi:10.1029/2011GB004143.

### 1. Introduction

[2] Forests play a major role in the global carbon cycle as they are large carbon pools and take up and emit enormous amounts of CO<sub>2</sub> annually [Bonan, 2008]. Understanding the responses of forests to atmospheric changes (temperature, precipitation, [CO<sub>2</sub>]) is therefore of great importance to forecast the carbon dynamics in forests and the resulting consequences for atmospheric CO<sub>2</sub> levels. So far, it appears that forests have acted as carbon sinks over the last decades both in the tropics [Phillips *et al.*, 2009] and in temperate zones [Boisvenue and Running, 2006; Spiecker *et al.*, 1996]. An often suggested explanation for this biomass increase is

the fertilizing effect of increased atmospheric CO<sub>2</sub> levels since the onset of the Industrial Revolution caused by fossil fuel burning [Intergovernmental Panel on Climate Change, 2007].

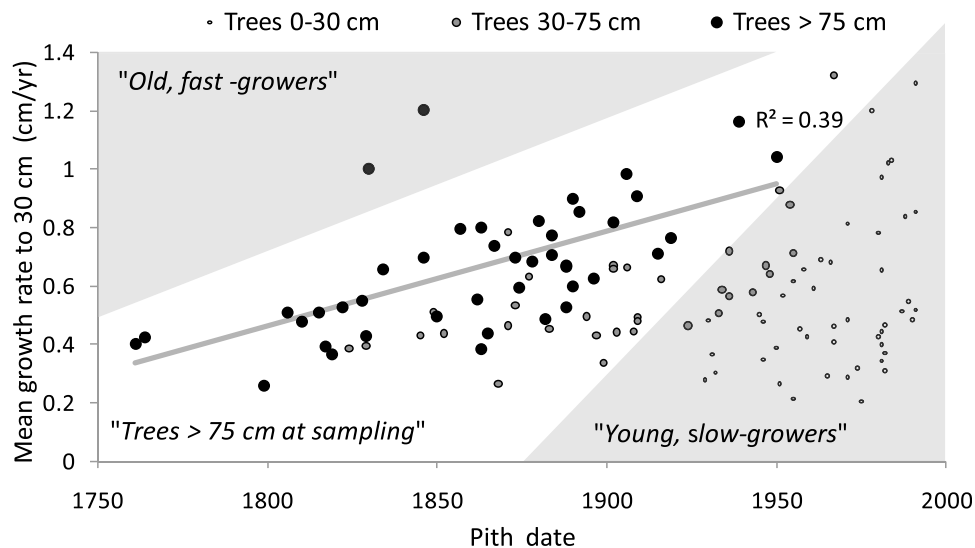
[3] Tree ring analysis is a suitable tool to obtain growth rates over the entire period since the onset of the Industrial Revolution [Huang *et al.*, 2007; Jacoby and D'Arrigo, 1997]. So far, a number of tree ring studies have indeed reported increased growth rates over time for temperate tree species [Gedalof and Berg, 2010, and references therein; Huang *et al.*, 2007; Martinelli, 2004] and tropical tree species [Rozendaal *et al.*, 2010]. The interpretation of an increase in ring width over time as a means to corroborate the CO<sub>2</sub> fertilization hypothesis requires caution as the concurrent increase in tree growth and atmospheric CO<sub>2</sub> levels is correlative, and simultaneous changes in temperature, rainfall, radiation, disturbances and atmospheric deposition may also have affected growth [Boisvenue and Running, 2006; Briffa *et al.*, 2008]. However, there is an additional reason for caution, as the observed increase in ring width may be spurious, brought about by sampling choices and population dynamics. The possible occurrence of biases in the reconstruction of historical growth rates

<sup>1</sup>School of Geography, University of Leeds, Leeds, UK.

<sup>2</sup>Programa de Manejo de Bosques de la Amazonía Boliviana, Riberalta, Bolivia.

<sup>3</sup>Ecology and Biodiversity, Institute of Environmental Biology, Faculty of Science, Utrecht University, Utrecht, Netherlands.

<sup>4</sup>Forest Ecology and Forest Management, Centre for Ecosystem Studies, Wageningen, Netherlands.



**Figure 1.** Observed mean growth rates of *Cedrela odorata* by pith date (calendar year of the innermost ring) for three subsets of trees according to their size at the moment of sampling: diameter >75 cm (large dots), 30–75 cm (intermediate dots), 0–30 cm (small dots). Linear regression slope shown is for trees >75 cm only ( $p < 0.001$ ). A regression for the complete data set did not exhibit a significant slope ( $p = 0.12$ ). Shaded areas indicate trees that are missed by the two sample biases. The “big-tree selection bias” misses young, slow growers over recent times (bottom right corner), and the “slow-grower survivorship bias” misses old, fast-growers over historical times (top left corner). Growth rates and pith dates (calendar date of the innermost ring) were estimated based on ring width analysis using standard dendrochronological techniques [cf. Brien et al., 2006].

has been described recently by Briffa and Melvin [2011] (cf. “modern sample bias”). They noted that “mean ring width plotted by calendar year for a specific sampling diameter will display a steady increase over time independent of any common climate signal as a consequence of different growth rates in contemporaneous trees and because of variations in the longevity of trees allied to common tree sampling practice.” Although these problems in tree rings have only recently attracted attention, in fishery biology the effect of similar biases on reconstruction of growth rates of fishes from annual marks on their scales has been described as early as 1911, and is commonly known as “Lee’s phenomenon” [see also Ricker, 1969].

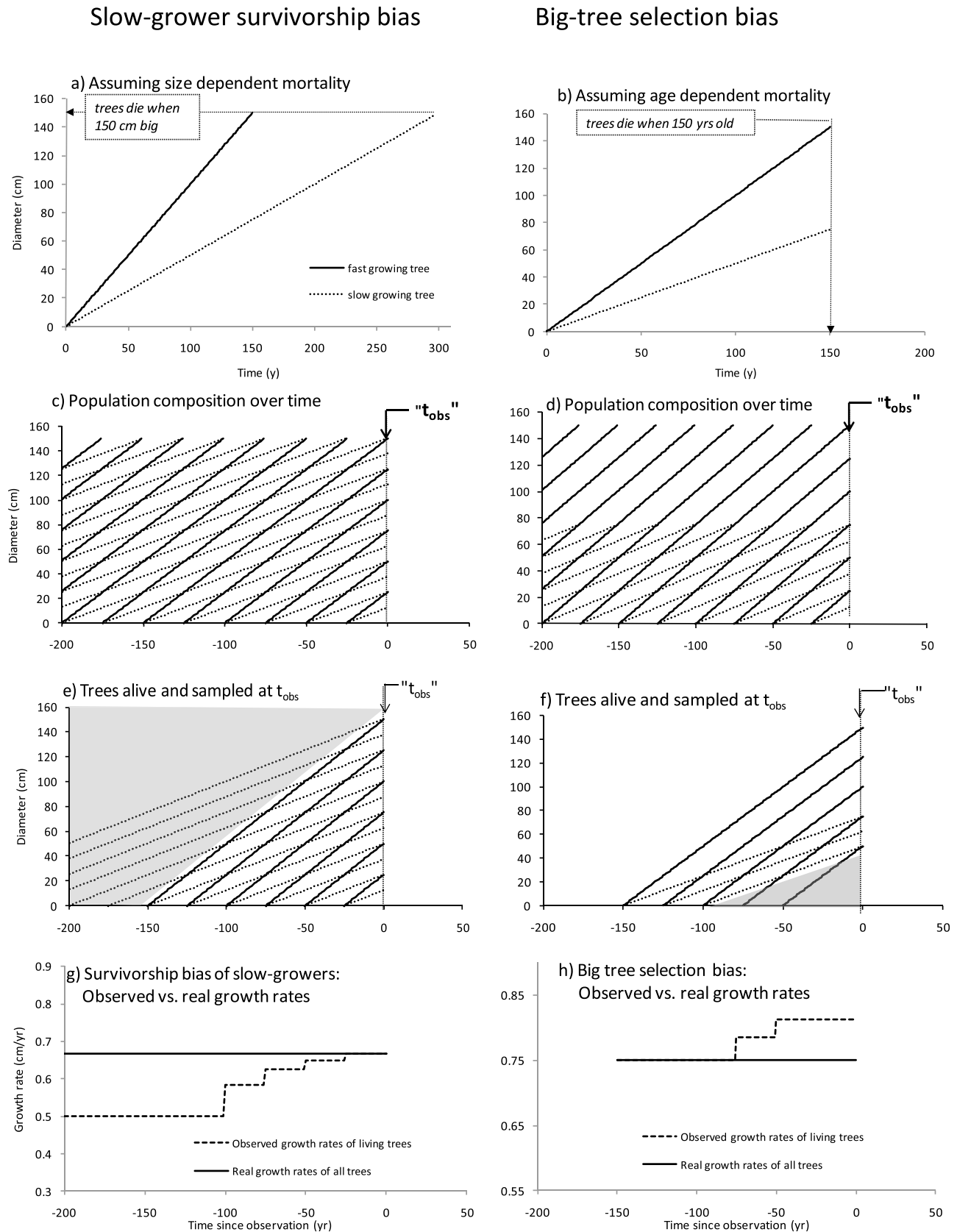
[4] In this study, we use tree ring data from the tropical tree *Cedrela odorata* [Brien et al., 2006] to check whether such a “steady increase” would occur under a “common sampling practice” which includes only measurements from the largest trees in the population. Figure 1 shows the results of this first analysis. When just considering growth rates of alive trees >75 cm diameter, we found a positive growth trend over time (Figure 1,  $R^2 = 0.39$ ). But including also the smaller trees at the moment of sampling (in the shaded triangle to the right, Figure 1), the significant growth increase disappeared. Figure 1 shows that this change is caused by the lower growth rates of these smaller trees in recent years. Excluding small trees is common practice in tree ring sampling, but may lead to apparent increases in growth rates over time: the “big-tree selection bias” (see below). In addition, Figure 1 shows a lack of fast-growing trees in the distant past (other shaded triangle in Figure 1), possibly because fast-growing individuals are shorter-lived, reducing

their representation in the sample. We named this the “slow-grower survivorship bias” (see below).

[5] Although several studies mentioned the existence of these biases [Badeau et al., 1996; Cherubini et al., 1998; Vila et al., 2008; Voelker et al., 2006], or even provided a detailed analysis [Briffa and Melvin, 2011], their magnitude is still unknown. In this study, we quantify the magnitude of these biases using stochastic simulation models for a hypothetical tree species and for *Cedrela odorata*. Specific objectives of this study are i) to quantify the effect and magnitude of the described sample biases for different tree mortality and sample scenarios, ii) to evaluate to what extent these biases may have influenced historical growth increases in published tree ring studies, and iii) to provide recommendations on how tree ring studies can be designed to avoid or reduce sample biases.

## 2. Description of Sampling Biases

[6] The slow-grower survivorship bias is brought about by the fact that trees that survive to be sampled are a small subset of the original juvenile cohort (Figures 2a, 2c, 2e, and 2g). Suppose that individual trees differ in long-term growth rates such that slow-growing trees remain slow growers and vice versa. This results in ‘persistent growth differences’, which have been documented for a number of tree species so far [Brien et al., 2006; Zuidema et al., 2011]. Such a growth pattern is represented schematically in Figure 2a. Suppose furthermore that there is size-dependent mortality, such that – for the special case of strict size-dependent mortality – all trees die at the moment they reach a given



**Figure 2.** Schematic simplified representation of two possible sampling effects in tree ring studies in which changes in historical growth rates are evaluated. See text in Introduction for explanation.

diameter (Figure 2a). For this situation, persistently fast-growing trees will have a shorter lifespan compared to slow growers [Bigler and Veblen, 2009; Black et al., 2008; cf. Schulman, 1954]. Now, when one samples all trees alive at a fixed moment in time ( $t_{\text{obs}}$ ), the group of surviving trees recruited (born) in the distant past consists of a subset of the original cohort. This can readily be appreciated by comparing Figure 2c showing all historical individuals in the population, with Figure 2e showing only those trees still alive at the moment of sampling,  $t_{\text{obs}}$ . While in the recent past (e.g.,  $t_{\text{back}} = 10$  y), the group of sampled trees that were alive at  $t_{\text{obs}}$ , have the same ratio of fast and slow growers compared to the original population (cf. Figure 2e), at more ancient times (e.g.,  $t_{\text{back}} = 75$  y) the group of surviving (sampled) trees contains more slow-growing than fast-growing trees (i.e., 9 slow versus 3 fast growing trees). This ratio of fast and slow growers differs considerably from the ratio of the original population (cf. Figure 2c). Thus -for that time period- it results in lower average growth rates compared to the original population (cf. Figure 2g, broken versus continuous line). The overall effect of this bias is an apparent increase in growth rates in the recent past, even when growth rates did not increase (Figure 1g). Although a very similar bias has been identified for reconstructions of release frequencies [Clark, 1991] and moth outbreaks [Veblen et al., 1991], the consequences for growth rate reconstructions over historical times have not received attention until very recently [Briffa and Melvin, 2011].

[7] The second bias, the big tree selection bias arises when only trees are sampled that have reached a certain diameter threshold (Figure 2f). In tree ring studies such a threshold is usually applied, and often only large trees are included [Cherubini et al., 1998]. In this case, the slow-growing trees that have been recruited in the recent past would not have reached the diameter threshold while the fast ones would (Figure 2f). As a result, tree ring width may overestimate recent growth rates (Figure 2h). Note that – just as for the previous bias – it is assumed that growth rates differ consistently between trees, but in contrast to the slow-grower survival bias, this sample bias is not affected by size-dependency in mortality (Figures 2b, 2d, 2f, and 2h). This bias has been described by Cherubini et al. [1998] and by Briffa and Melvin [2011], but the magnitude of the bias has not yet been quantified.

### 3. Materials and Methods

#### 3.1. Model Construction and Simulations

[8] The purpose of the simulations was to compare historical growth rates reconstructed from tree ring reconstruction, with growth rates that have effectively occurred in the past. As those past growth rates were input in our simulations, we actually know them and we can thus quantify differences between reconstructed and actual growth rates. Such discrepancies are caused by the sample biases. A general description of the model is provided below. The model was developed in Matlab v7.8 (The Mathworks), and codes are available upon request.

[9] The basic model consisted of simulated annual cohorts of trees recruited over a period of 350 years. Each cohort consisted of 50 individuals and for each individual the development in diameter is kept track of for all years until

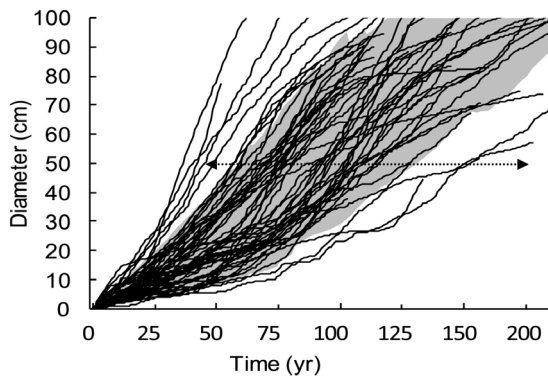
tree death. We simulated the development of a large virtual population of trees over 350 years. We allowed for a period of 200 years during which the population could establish and the full range of sizes and ages would be represented in the population. Next, we used this database of simulated trees to obtain the type of historical growth data that one would typically obtain from tree ring studies, i.e., sampling only alive trees and with a preference for big-diameter trees.

[10] We performed two kinds of growth simulations: (i) for a hypothetical tree species which exhibits growth rates that do not change over the life of the tree, and (ii) based on observed growth rates from tropical Cedar in Bolivia (*Cedrela odorata*, Meliaceae) [Brienen and Zuidema, 2006]. The “hypothetical tree” simulations were used to clearly demonstrate the effects of the two sampling biases for a range of scenarios, while the *Cedrela* simulations were used to obtain realistic estimates and thus quantify the magnitude of the two sampling biases.

[11] For both types of simulations, we started the trajectories with a diameter of 0 cm and an age of 0 years. At every time step, we randomly drew a growth rate from the data set (i.e., constant growth or observed *Cedrela* growth), using a bootstrap approach [cf. Brienen et al., 2006; Lieberman and Lieberman, 1985]. In the case of the hypothetical tree species, we always selected the same growth rate, thus maintaining growth differences between trees throughout their lives. Growth rates for the hypothetical tree species were chosen such that their median value was close to that of *Cedrela* and the degree of variation among growth trajectories was similar to that observed in other species [Brienen et al., 2006]. To this end, we generated growth trajectories with growth rates varying from 0.25 to 1.25 cm yr<sup>-1</sup>, in growth steps of 0.05 cm yr<sup>-1</sup>.

[12] The procedure for the individual trajectories of *Cedrela* trees was somewhat more complicated, as we wished to produce realistic trajectories such that the simulated growth variation and the simulated age and size distributions were comparable with those observed from tree ring data [Brienen et al., 2006]. As input data for these simulations we used diameter growth measurements from a tree ring study of *Cedrela odorata*, a relatively light demanding species with annual rings, from undisturbed tropical moist forest in northern Bolivia (11°24'S, 68°43'W; more details are given by Brienen and Zuidema [2006]). For large trees (>60 cm in diameter), we collected discs from stumps of felled trees (n = 68), while for small trees we took 2–3 increment cores per tree (n = 56). We selected these smaller trees such that they were evenly distributed over diameter categories between 5 and 60 cm (i.e., 5–10 cm, 10–20 cm, 20–30 cm, etc). Wood preparation and ring measurement procedures are described by Brienen and Zuidema [2006].

[13] For the *Cedrela* simulations, the growth rate for the first simulation year was randomly drawn from the observed growth rates for trees of age 1 and added to the starting diameter. During the next and further time steps, growth rates were randomly drawn from trees of comparable size, and trees with a comparable previous growth rate. Specifically, at each time  $t$  a growth rate ( $G_{\text{sim},t}$ ) was drawn from trees of a diameter that could be up to  $0.5 \cdot dD$  above or below diameter of the simulated tree ( $D_{\text{sim}}$ ), where  $dD$  is the diameter window (see below). At the same time, the growth



**Figure 3.** Observed growth trajectories for *Cedrela odorata* (lines,  $n = 56$ ) from a population from northern Bolivia, and the interval in which 95% of the simulated growth trajectories are found (shaded area). Parameters used for this growth simulation are  $dD = 0.5 \text{ cm yr}^{-1}$ ,  $dD = 5 \text{ cm}$ ,  $D_{mort} = 100$  and  $a = 0.001$ . The arrow indicates the simulated variation (min-max ages) for the hypothetical tree species with constant-growth trajectories (see methods).

rate was also drawn from a growth-rate window ( $dG$ ), i.e., in the range of  $0.5 \cdot dG - G_{sim,t-1}$  to  $0.5 \cdot dG + G_{sim,t-1}$ , where  $G_{sim,t-1}$  is the simulated growth rate at  $t-1$ . Changes in  $dD$  and  $dG$  influence the degree of growth autocorrelation [cf. Brien et al., 2006] and the possibility of sudden changes in diameter growth. A narrow growth-rate window limits temporal variation in the growth of an individual tree and leads to persistent growth differences among simulated trees. The reverse is true for a wide  $dD$  window as this allows for more temporal variation in the growth of individual trees. In the simulations, we set  $dD$  to 5 cm, and  $dG$  to  $0.5 \text{ cm yr}^{-1}$ , as these resulted in simulated growth trajectories that resembled the observed patterns most (Figure 3). The mean and standard deviation of ages of simulated trees of 60 cm diameter were almost equal to observed values (mean<sub>obs</sub> = 94.5 yr, mean<sub>sim</sub> = 96.5 yr; STD<sub>obs</sub> = 27.0 versus STD<sub>sim</sub> = 26.8; cf. Figure S2 in the auxiliary material).<sup>1</sup>

[14] The diameter development of every simulated tree was continued until tree death. Trees had a uniform probability of dying ( $m_0$ ) of 1.5%. To evaluate the magnitude of the slow-grower survivorship bias, we raised mortality risk ( $m$ ) once its diameter exceeded a threshold diameter ( $D_{mort}$ ), after which it increased linearly proportionally to the difference between the actual tree diameter ( $D_{sim}$ ) and the threshold diameter ( $D_{mort}$ );

$$m = m_0 + a \cdot (D_{sim} - D_{mort}). \quad (1)$$

We varied  $D_{mort}$  and the mortality increase factor,  $a$ .

[15] We also performed a validation of the simulation output for all 350 cohorts. To this end, we compared the population size structure of simulated trees at year 350 of the simulations with the observed structure in the Purissima forest in Bolivia, and we compared the age and growth rate distributions of simulated trees of 60 cm diameter or bigger at year 350. We used these comparisons to assess the degree

of realism of the growth simulations and mortality parameters.

### 3.2. Magnitude of Sampling Biases

[16] The magnitude of the *slow-grower survivorship bias* estimated by mimicking a tree ring study in which all trees that are still alive were sampled. The magnitude of the *big-tree selection bias* was estimated by mimicking a study that only included trees bigger than a minimum sampling diameter ( $D_{saml}$ ). We then compared the historical growth rates of this subset of individuals with that of the entire historical population, thus including all trees that were alive during the year for which the growth rate was evaluated (but did not necessarily survive to the sampling date). So, for instance, we compared the mean growth rates from the tree ring-based data for trees 50 years before tree ring sampling with that of all trees alive at the time of sampling. To obtain insight into the shape of sampling biases over time, we performed these comparisons for the last 150 years. As growth rates of *Cedrela* show strong size-dependent growth trends due to ontogeny and changing light conditions during growth to the canopy [Brien et al., 2006], we performed separate comparisons for 10-cm wide diameter classes. Results of both the hypothetical tree and *Cedrela* are shown for three diameter classes: 0–10, 20–30, and 40–50 cm.

[17] To assess the impact of size-dependent mortality on the slow-grower survivorship bias, we conducted simulations using different assumptions on mortality. For the hypothetical trajectories, we varied the size threshold at which mortality starts to increase ( $D_{mort} = 50, 75, 100 \text{ cm}$ ) while keeping “ $a$ ” constant ( $a = 0.005$ ), and we varied the mortality increase factor ( $a = 0.01, 0.005, 0.001$ ) while keeping “ $D_{mort}$ ” constant ( $D_{mort} = 75 \text{ cm}$ ). For *Cedrela*, we show results of three mortality scenarios, which varied in the degree of resemblance with observed size, age and growth rates (cf. Figures S1–S3).

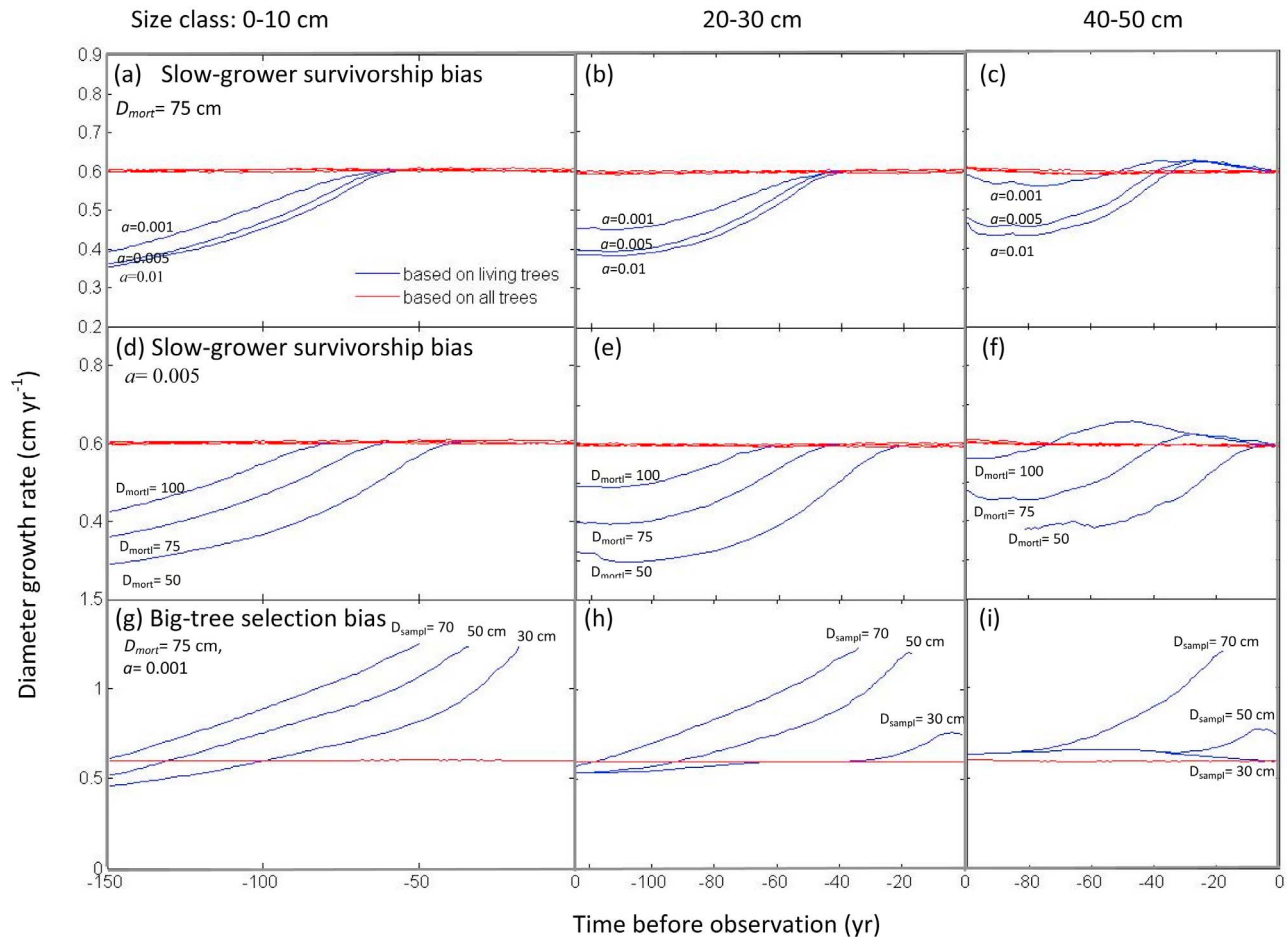
[18] To assess the effect of different field sampling designs on the magnitude of the big-tree selection bias, we used the most realistic mortality scenario as a base-line simulation. This is the scenario with a relatively moderate increase in mortality with size (i.e., a mortality increase factor,  $a$  of 0.001, cf. equation (1)) for trees reaching diameters larger than 100 cm (cf. Figures S1–S3). We quantified the effect of three minimum sampling diameters,  $D_{saml} = 30, 50$ , and  $70 \text{ cm}$ , and of a sampling scenario in which an equal number of trees is sampled from all size classes.

## 4. Results

### 4.1. Magnitude of Sampling Biases for a Hypothetical Tree Species

[19] The simulations for the hypothetical tree species (uniform growth trajectories) showed that both sample biases affected the reconstruction of historical growth rates, and resulted in apparent growth rate increases over time (Figure 4). The form and magnitude of the observed growth increases differed between biases (cf. Figures 4a–4f and 4g–4i). The slow-grower survivorship bias led to observed growth rates over more ancient time periods that were lower than the actual growth rates (including trees that died before  $t_{obs}$ ), while the big-tree selection bias led to higher observed

<sup>1</sup>Auxiliary materials are available in the HTML. doi:10.1029/2011GB004143.



**Figure 4.** Effects of two sampling biases on historical growth reconstruction for a hypothetical tree species. The magnitude of the sampling bias corresponds to the differences between the red line (actual historical rate) and blue line (reconstructed growth rate). Trajectories are shown for three diameter classes: (a, d, and g) 0–10 cm, (b, e, and h) 20–30 cm and (c, f, and i) 40–50 cm. Shown are the effects of the strength of the mortality increase factor,  $a$ , on the *slow-grower survivorship bias* (Figures 4a–4c), and the effect of size thresholds for mortality increase,  $D_{mort}$ , on the *slow-grower survivorship bias* (Figures 4d–4f). Figures 4g–4i show the effect of the *big-tree selection bias* when limiting sampling to trees bigger than 30, 50 or 70 cm in diameter (i.e., varying  $D_{samp}$ ).

growth rates over more recent times. The big-tree selection bias resulted in the steepest growth increases, with a doubling of growth rates over the last decades in some sampling scenarios.

[20] The strength and form of the slow-grower survivorship bias was sensitive to assumptions on the mortality increase factor ( $a$ ), and the size at which mortality started increasing ( $D_{mort}$ ). Higher  $a$ , or smaller  $D_{mort}$  resulted in larger sample biases. Variation in the mortality increase factor affected the strength of the increase in growth rates, while the choice of  $D_{mort}$  basically affected only the “start time” of the deviation, not its strength. For the big-tree sampling bias, the minimum sampling size ( $D_{samp}$ ) had a similar effect on the timing of the deviation. In this case, the timing of the onset of the deviation depended on both  $D_{samp}$  and the size class. The biases of the largest size classes were only evident over the last decades prior to sampling, while biases in observed growth rates in the smallest size classes started much earlier, in some cases more than 100 years

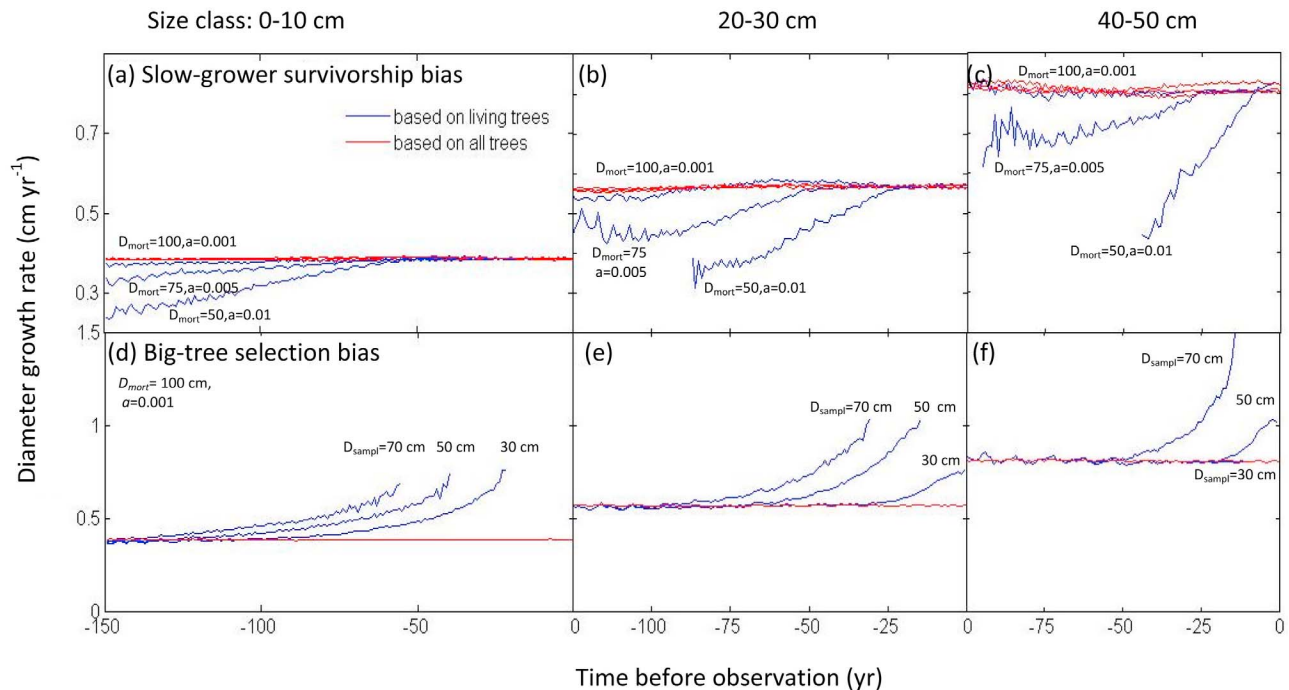
before  $t_{obs}$ . No biases were observed for the evaluation of growth rates within size classes bigger than  $D_{samp}$  (cf.  $D_{samp}$  30 in size class 40–50 cm, Figure 4i).

[21] We noted that in size class of 40–50 cm at intermediate time periods observed growth rates are slightly higher compared to actual growth rates (Figures 4c and 4f). This difference is caused by the lower survival chance of slow growers to reach a given size. Hence, in addition to a higher longevity, slow growers also have a lower chance to reach the same size as they accumulate a higher mortality risk before reaching a given size compared to fast growers.

#### 4.2. Sampling Biases in *Cedrela*

[22] The magnitude and effects of the two sample biases based on the *Cedrela* growth data were very similar to those for the hypothetical tree species (Figure 5). The effect of the slow-grower survivorship bias on growth rate reconstruction was in general weaker than the bias observed in the hypothetical tree species. This is probably due to the somewhat





**Figure 5.** Effects of two sampling biases on historical growth reconstruction for *Cedrela odorata*. The magnitude of the sampling bias corresponds to the differences between the red line (actual historical rate) and blue line (reconstructed growth rate). Trajectories are shown for three diameter classes: (a and d) 0–10 cm, (b and e) 20–30 cm and (c and f) 40–50 cm. Figures 5a–5c show the effect of the *slow-grower survivorship bias* for three mortality scenarios. Figures 5d–5f show the effect of the *big-tree selection bias* when limiting sampling to trees bigger than 30, 50 or 70 cm in diameter (i.e., varying  $D_{\text{sample}}$ ).

lower variation among the simulated *Cedrela* trajectories compared to the hypothetical, uniform trajectories (cf. Figure 3). Note that the actual, observed trajectories had a magnitude of variation more close to the hypothetical trajectories than the simulated *Cedrela* trajectories.

[23] The strength of the slow-grower survivorship bias depended strongly on the set of parameters used for  $a$  and  $D_{\text{mort}}$ . For the combination of  $a$  and  $D_{\text{mort}}$ , that most closely matched the distributions for age, size and growth rates of the observed data (i.e.,  $a = 0.001$ ,  $D_{\text{mort}} = 100$ , cf. Figures S1–S3), we do not find a noteworthy deviation for observed growth rates for the slow-grower survivorship bias (Figures 5a–5c). Simulations with lower  $D_{\text{mort}}$  and higher  $a$  values did show relatively large deviations between observed and actual growth rates (cf. Figures 5a–5c,  $a = 0.01$ ,  $D_{\text{mort}} = 50$  cm).

[24] Simulations of the big-tree selection bias showed that the effect of this sample bias is much larger and resulted in strong increases in observed growth rates (Figures 5d and 5f). Over recent time periods, growth rates increased to levels that were almost double the actual growth rates.

#### 4.3. Alternative Sampling Strategies

[25] We evaluated whether sampling equal numbers of trees from all size classes would avoid the big-tree selection bias. As shown in Figure 6, a strategy of sampling 30 individuals from each size class reduces the magnitude of sample biases considerably compared to scenarios that sample only big trees (cf. Figure 5). However, over ancient time

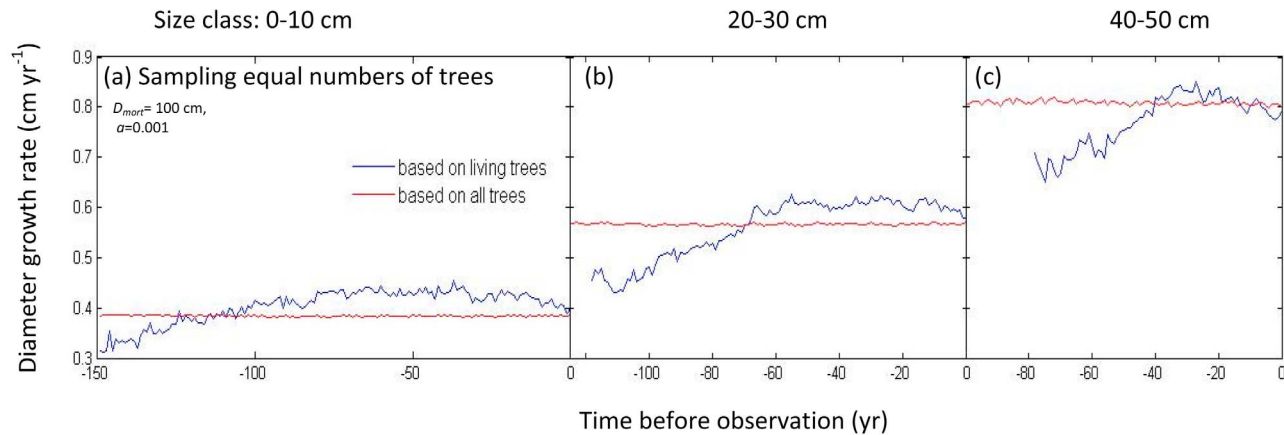
periods there is still a considerable bias in growth rates, leading to a long-term trend of increasing growth rates.

## 5. Discussion

### 5.1. Magnitude of Sampling Biases

[26] The simulations clearly showed that both sample biases lead to spurious increases in historical growth rates. The common practice in tree ring studies to sample only large trees and only those individuals that are alive, leads to increased observed growth rates in recent time even though actual contemporaneous growth rates may not have changed. There are distinct differences in the magnitude and temporal pattern of historical growth increases between the two biases. In terms of overall magnitude the big-tree selection bias results in the strongest growth increases, while effects of the slow-grower survivorship bias are comparatively weak and depend strongly on the assumptions for mortality. Another important difference between the biases is that the big-tree selection bias leads to growth increases over the most recent time periods, while the slow-grower survivorship bias results in growth increases over earlier, historical time periods.

[27] The strongly increasing growth rates over recent times for the big tree selection bias (cf. Figures 4g–4i and 5d–5f) look deceptively similar to the expected response of growth to (nonlinear) increases in atmospheric [CO<sub>2</sub>], or temperature, and could thus easily be misinterpreted. This bias was also clearly present in the actual observed tree ring data (cf. Figure 1), as the selection of the biggest trees



**Figure 6.** The effect of sampling equal numbers of trees across different size classes on the *big-tree* selection bias for *Cedrela odorata*. In this sampling scenario 30 trees were selected from 10 different size classes (0–10 cm, 10–20 cm, etc.). The mortality scenario was  $a = 0.001$  and  $D_{mort} = 100$  cm.

(>75 cm) resulted in a 50% growth increase compared to growth reconstructions based on all trees. Together, these findings show that reconstructions of historical growth rates using only the biggest trees in a natural uneven-aged population will lead to positively biased growth rates over recent decades [cf. Briffa and Melvin, 2011]. Our simulation approach allowed us to quantitatively assess the magnitude of this bias, and showed that this bias may actually be substantially higher (i.e., a doubling of growth rates within a few decades) than the 20% increase in ring index estimated by Briffa and Melvin [2011].

[28] With respect to different tree sampling strategies, our simulations showed that historical growth increases, specifically the timing of the onset of such increases, were sensitive to differences in the minimum diameter criteria (cf. Figures 4g–4i and 5d–5f). Adopting a low minimum diameter threshold for sampling trees seems an effective way of avoiding sample biases, at least for reconstruction growth rates over those diameter trajectories that are bigger than the minimum size criterion applied. The reconstruction of growth rates for trees of sizes smaller than those included in the sample remains risky because of large biases, however (cf. Figures 4g–4i and 5d–5f).

[29] A simple strategy that was hypothesized to avoid sample biases is the sampling of (equal numbers of) trees from all size classes [cf. Rozendaal et al., 2010]. Our simulation of such a sampling strategy shows that it does indeed reduce the sample bias over recent times, but still results in observations of increasing growth trends over ancient times.

## 5.2. The Crucial Role of Long-Term Growth Differences and Mortality Rates

[30] The strength of the sample biases depends on two important assumptions. First, for both biases to occur at all, growth rates need to differ persistently over time between trees resulting in differences in ages of similar sized trees [Briffa and Melvin, 2011]. Such persistent growth differences have been observed widely in temperate [Bigler and Veblen, 2009; Grubb et al., 2002; Voelker et al., 2006] and tropical forest trees [Brienen et al., 2006; Zuidema et al., 2011]. Differences in growth rates arise due to genetic

[Cole et al., 2010] or environmental effects on individual tree performance. Some examples of environmental effects that may result in long-term differences in growth rates are differences in resource or water availability [Baker et al., 2003; Brienen et al., 2010], asymmetric competition between trees [Weiner, 1990], or liana infestation [Ingwell et al., 2010].

[31] A second assumption, controlling the magnitude of the slow-grower survivorship bias, is that mortality rates indeed increase after reaching a certain size, resulting in a trade-off between growth rates and tree longevity. In this regard it is important to distinguish between extrinsic and intrinsic causes of mortality, as they affect trees at different life-stages. During earlier and middle life stages mortality is mostly related to external events, of which some increase in frequency with tree size. For example, large trees are more susceptible to wind blow [Canham et al., 2001] and more vulnerable to drought [Phillips et al., 2010] probably related to increased hydraulic limitations for large trees [Ryan et al., 2006]. For trees in their latest life stages, intrinsic mortality due to senescence becomes more important. This type of mortality is often thought to increase with increasing tree age. However, Mencuccini et al. [2005] show that tree vigor (i.e., growth rates and photosynthesis) decreases with tree size and not with age per se. This strongly suggests that natural senescence is probably also more closely related to tree size than age. Note that we have made an explicit distinction between extrinsic and intrinsic mortality causes for the sake of clarity, although the two causes cannot be separated unambiguously. For instance, mortality seems nearly always triggered by external causes, but their effect is higher in trees with decreased performance due to intrinsic decreases in photosynthesis and stomatal conductance [McDowell, 2011]. More direct lines of evidence for a trade-off between growth and longevity are found in tree ring studies. Bigler and Veblen [2009] showed that tree longevity correlated negatively with growth rates (over the first 50 yrs) for three different tree species, and Briffa and Melvin [2011] show a clear tendency for slow growers to live longer compared to fast growers, using a subfossil tree ring data set from Grubb et al. [2002]. For the tropics, a tree



ring study by *Schöngart et al.* [2005] found a strong negative relationship between growth rate and tree age mediated by differences in site conditions. Finally, some tree ring studies find patterns that are consistent with a growth–longevity trade-off [cf. *Black et al.*, 2008; *Johnson and Abrams*, 2009], but as the sampled trees were still alive and not taken randomly, but from the biggest individuals, these patterns may also have been resulting from the big-tree selection bias. Together, these lines of evidence strongly support the idea of a trade-off between fast growth and longevity, and that the slow-grower survivorship bias may indeed affect historical growth rate reconstructions. However, determining the magnitude of this bias remains impossible until specific data on the (strength of the) trade-off between growth rate and tree longevity, or size-dependent mortality are available for more species and sites.

[32] Related to this, there is an additional mortality effect that affects historical growth rate reconstructions. Several studies find positive relationships between growth rates prior to tree death and short-term survival probabilities [*Bigler and Bugmann*, 2003; *Das et al.*, 2007; *Wyckoff and Clark*, 2002]. As a result, ring widths over recent times, which include individuals that are dying and have lower growth rates, may be lower than those in the distant past. This phenomenon has been observed in ring studies in temperate and tropical trees, leading to apparent growth decreases over recent time periods [*Landis and Peart*, 2005; *Rozendaal et al.*, 2010]. The magnitude of this effect depends –at least partially on the shade-tolerance of species, with stronger effects in shade-intolerant species as these are more likely to die from suppressions [*Kobe et al.*, 1995]. The effect is also likely to occur most strongly in juvenile trees that have not yet reached a position in the canopy and may remain suppressed for extended time periods [cf. *Landis and Peart*, 2005; *Brienen and Zuidema*, 2006]. The length of these periods of reduced growth varies from several years [*Wyckoff and Clark*, 2002] to several decades [*Pedersen*, 1998]. For uncompromised analysis of trends in tree rings, those tree ring series showing recent growth declines indicative of increased mortality risks [cf. *Bigler and Bugmann*, 2003; *Pedersen*, 1998] should be excluded from analysis. However, great care should be taken that this does not unintentionally lead to additional biases. We deliberately did not treat this effect in our simulations, as our objective was to demonstrate the uncompromised magnitude of the two main biases on historical growth increases.

### 5.3. A Review of Possible Sampling Biases in Published Studies

[33] Since the earliest suggestions of CO<sub>2</sub> fertilization effects on ring width patterns by *Lamarche et al.* [1984], over a dozen studies have reported increasing growth rates over recent decades (cf. Table 1) [*Huang et al.*, 2007]. We evaluate a number of these studies to determine whether and to what extent sample biases may have played a role in shaping these findings. Note that this evaluation excludes studies that reported growth decreases [e.g., *Nock et al.*, 2011; *Silva et al.*, 2010], or those using flexible detrending procedures [e.g., *Gedalof and Berg*, 2010; *Graumlich*, 1991; *Knapp et al.*, 2001; *Koutavas*, 2008; *Peñuelas et al.*, 2011],

as these are not affected by the sample biases described here (see next section).

[34] Our review shows that all studies, except for *Briffa et al.* [1998] are potentially affected by the slow-grower survivorship bias, as they relied entirely on living, contemporaneous trees (Table 1). However, the effect of this bias is probably small. In addition, at least half of the revised studies are affected by the big-tree selection bias, as they focused entirely on dominant, mature or big trees. As the observed historical growth increases of these studies are within the magnitude observed in our simulations for the big-tree selection bias, the general conclusion of these studies that these trends represent a “true” increase in growth rates of the population seems not justified.

[35] There are a few exceptions to the common sampling scenario of choosing only the biggest trees. Most notably, *Martínez-Vilalta et al.* [2008] and *Rozendaal et al.* [2010] sampled from across a range of size classes. *Martínez-Vilalta et al.* [2008] sampled proportional to the size distribution which should in principle not lead to biases. However, in the analysis they include only trees bigger than 10 cm which may lead to biases for trajectories smaller than that. *Rozendaal et al.* [2010] choose a fixed number of trees per size class which may still partially be affected by the big-tree selection bias (cf. Figure 6). A set of studies on growth trends in French forests [*Becker*, 1989; *Becker et al.*, 1994; *Bert*, 1992; *Lebourgeois and Becker*, 1996; *Picard*, 1995] adopted a different approach by sampling dominant trees from mostly even-aged stands. Although it is difficult to assess possible biases, such a sampling design should not be affected by the big-tree selection bias. However, many of these sites have also been subjected to silvicultural management in the past which may potentially influence historical growth rate reconstructions (see *Badeau et al.* [1996] for further details).

[36] Some of the reviewed studies discuss the potential effect of sample biases [*Badeau et al.*, 1996; *Vila et al.*, 2008; *Voelker et al.*, 2006]. Specifically, *Voelker et al.* [2006] take great care in their evaluation of observed growth increases. They argue that a bias due to focusing on larger dominant trees (cf. big-tree selection bias) is most likely to occur only in longer-lived species with great shade tolerance, and thus not in their focus species. We showed that the big-tree selection bias will occur in any stand where persistent growth differences between trees exist. As the size variation among trees of similar ages in *Voelker*’s study (Figure 2a) is equally large as what we simulated, we expect that historical growth rate biases may be of similar magnitude. *Voelker et al.* [2006] also checked whether samples from older trees may come from inherently slower growing trees (cf. slow-grower survivorship bias), and indeed found that samples from older, dead stumps grew slightly faster over the same historical time period as trees that are currently alive [cf. *Voelker et al.*, 2006, Figure 7]. This is consistent with our predictions of the slow-grower sampling bias, but its effect seems indeed small relative to the reconstructed growth increase. Nonetheless, our results show that the magnitude of the big-tree selection bias alone may be large enough to explain the historical growth increases. Therefore, the conclusion of *Voelker et al.* [2006] that observed trends were not the result of sampling biases does not seem justified.

**Table 1.** Overview of Tree Ring Studies Detecting Increasing Growth Trends, and Assessment of the Potential Presence (Plus Sign) or Absence (Minus Sign) of Sampling Biases in the Evaluated Studies

Country, Site	Species	Growth Trend <sup>a</sup>	Increase (%decade <sup>-1</sup> )	Standardization <sup>b</sup>	Size of Sampled Trees	Sampling Bias?			Attributed Cause <sup>c</sup>	Observations	Authors
						Big-Tree Selection	Slow-Grower Survivorship	Attributed Cause <sup>c</sup>			
Spain, NE	<i>Pinus sylvestris</i>	+	8.4%	Raw	>10 cm: proportional to size distribution. >5 cm: even number per size class.	–	+	CO <sub>2</sub>			Martinez-Vilalta et al. [2008]
Bolivia, S	<i>Cedrela odorata</i>	+	n.a.	Size classes		–	+	CO <sub>2</sub>			Rozendaal et al. [2010]
France, NE and S	<i>Cedrelinga catenaeformis</i>	–									
	<i>Claristia racemosa</i>	+									
	<i>Peltogyne heterophylla</i>	+									
	<i>Pseudotsuga laevis</i>	+									
	<i>Picea abies</i>	+	11%	RCS	Dominant trees, age range	–	+	Mixed			in Badeau et al. [1996]
	<i>Pinus uncinatum</i>	+	3%			–	+				
France, NE	<i>Abies alba</i>	+	7%	RCS	Dominant trees, age range	–	+	Mixed		Even-aged stands	Becker [1989]
France, NE	<i>Fagus sylvatica</i>	+	5%	RCS	Dominant trees, age range	–	+	Mixed		Even-aged stands	Picard [1995]
France, NW	<i>Pinus nigra</i>	+	8%	RCS	Dominant trees, age range	–	+	Mixed		Even-aged stands	Lebourgeois and Becker [1996]
France, NE	<i>Quercus petraea</i>	+	6.4%	RCS	Dominant trees, age range	–	+	Mixed		Even-aged stands	Becker et al. [1994] and in Badeau et al. [1996]
France, S	<i>Quercus robur</i>	+	4%								
	<i>Fagus sylvatica</i>	+	9%								
	<i>Abies alba</i>	+	10%	RCS	Dominant trees, age range	+	+	CO <sub>2</sub>			cited by Badeau et al. [1996] and Bert [1992]
USA, NE	<i>Abies balsamea</i>	–	–	BAI	(co-)dominant trees	+	+	n.a.			Hornbeck et al. [1988]
France, S Vietnam	<i>Acer rubrum</i>	0	–								
	<i>Acer saccharum</i>	+	10%								
	<i>Betula alleghaniensis</i>	+	7%								
	<i>Fagus grandifolia</i>	+	7%								
	<i>Fraxinus americana</i>	+	18%								
	<i>Picea rubens</i>	–	–								
	<i>Picea strobus</i>	+	11%								
	<i>Quercus rubra</i>	0	–								
	<i>Tsuga canadensis</i>	+	6%								
	<i>Quercus humilis</i>	+	10%	RCS	Oldest trees	+	+	CO <sub>2</sub>			Rathgeber et al. [1999]
	<i>Annamocarya sinensis</i>	–	n.a.	Size classes	Big trees	+	+	CO <sub>2</sub>			Zuidema et al. [2011]
	<i>Calocedrus macrolepis</i>	–									
USA, Wisconsin France, SE	<i>Dacrydium elatum</i>	–	–								
	<i>Pinus kwangtungensis</i>	–/+									
	<i>Populus tremuloides</i>	+	10%	RCS	Big trees	+	+	CO <sub>2</sub>			Cole et al. [2010]
	<i>Pinus sylvestris</i>	–/+	5%	RCS	Dominant trees	+	+	Mixed			Vila et al. [2008]
USA, Missouri	<i>Pinus halepensis</i>	+	15%								
	<i>Quercus velutina</i>	+	10%	RCS	Big trees	+	+	CO <sub>2</sub>			Voelker et al. [2006]
	<i>Quercus coccinea</i>	+	10%								
	<i>Pinus echinata</i>	+	10%								
France, Alps	<i>Picea abies</i>	+	10%	Age classes	Dominant trees	+	+	Mixed			Rolland et al. [1998]
	<i>Larix decidua</i>	+	2.5%								
	<i>Pinus cembra</i>	+	4%								
	<i>Pinus uncinata</i>	+	3%								
Austria, Alps USA, Georgia	<i>Pinus cembra</i>	+	1.5%	RCS	Mature, dominant trees	+	+	CO <sub>2</sub>			Nicolussi et al. [1995]
	<i>Pinus palustris</i>	+	1.7%	RCS	Big trees (>40 cm)	+	+	CO <sub>2</sub>			West et al. [1993]
		+	10%								

Table 1. (continued)

Country, Site	Species	Growth Trend <sup>a</sup> (%decade <sup>-1</sup> )	Standardization <sup>b</sup>	Size of Sampled Trees	Sampling Bias?			Attributed Cause <sup>c</sup>	Observations	Authors
					Big-Tree Selection	Slow-Grower Survivorship				
Switzerland, USA, Cyprus	<i>Picea</i> (4 species)	-/+	n.a.	Big trees (30–60 cm)	+	+		Mixed	Growth increases at 8 sites (24%)	Kienast and Luxmoore [1988]
	<i>Pinus</i> (4 species)									
	<i>Pseudotsuga menziesii</i>									
	<i>Abies alba</i>									
USA, California	<i>Cedrus brevifolia</i>	+	7%	Not reported <sup>d</sup>	+	+		Mixed		Lamarche et al. [1984]
	<i>Pinus longaeva</i>									
N- Hemisphere	<i>Pinus</i>	+	<3%	Not reported <sup>d</sup>	+	+		Mixed	includes subfossil trees	Briffa et al. [1998]
	<i>Picea</i>	+								
	<i>Larix</i>	+								

<sup>a</sup>Plus sign indicates increases, minus sign indicates decreases, and 0 indicates no observed trend.

<sup>b</sup>RCS, Region Curve Standardization; BAI, Basal Area Increment; Raw, use of unstandardized ring widths.

<sup>c</sup>CO<sub>2</sub>, CO<sub>2</sub>-fertilization effect; Mixed, multiple possible causes including climate N-deposition, CO<sub>2</sub>, etc.

<sup>d</sup>Exact sampling strategy not reported. Assumed standard tree ring strategies focusing on biggest trees.

[37] In all, our evaluation shows that observed increases for at least half of the studies, may also be explained by the big-tree selection bias. This raises doubts about the validity of growth rate increase trends in a large amount of studies available to us. The true reason why so many studies seem unsuitable to evaluate mean long-term trends in growth is that tree ring data were often primarily collected for the purpose of palaeoclimatic reconstructions (thus selecting only the biggest trees), and were then used without restraint for testing long-term trends over time. Unfortunately, this is still common practice even in recent literature [cf. *Gedalof and Berg*, 2010; *Huang et al.*, 2007; *Peñuelas et al.*, 2011].

#### 5.4. Implications and Recommendations for Future Studies

[38] The larger of the two biases, the big-tree selection bias, can be avoided by a field sampling strategy with low minimum size criteria. Even then, only historical growth rates within size classes bigger than the minimum sampled size are valid for an unbiased evaluation of historical growth trends. The best strategy would be to sample all individuals of a population. However, this is often not possible due to the large number of (especially small) trees that would need to be sampled. Alternative strategies would be to sample proportional to the size distribution [cf. *Martinez-Vilalta et al.*, 2008] by selecting trees entirely randomly, or sampling all trees from a small fixed area. Other sampling strategies, like selecting a fixed number of trees per size class [cf. *Rozendaal et al.*, 2010], may still result in observations of increasing growth trends over ancient times (cf. Figure 6). Useful indications on the probability of biases in sets of tree ring data may be obtained by separating the collected data into subsets of trees according to their size at the moment of sampling, as we did in Figure 1. The recommendation to focus tree ring sampling on trees from all size classes was made by *Cherubini et al.* [1998] already more than a decade ago, but has still not been adopted widely. We hope that the insights from our study will help change this.

[39] The slow-grower survivorship bias seems to have a much smaller effect on historical growth rate reconstructions, but it is also more difficult to account for. One powerful approach to evaluate whether the bias has affected historical growth rates is to check whether growth rates differed between contemporaneous dead and living trees [cf. *Badeau et al.*, 1996; *Briffa and Melvin*, 2011; *Voelker et al.*, 2006]. However, this is not possible for (tropical) areas where decomposition occurs at a high rate.

[40] Most tree ring studies aim at extracting climate information or long-term growth trend. One of the most fundamental tasks for such studies is the removal of “residual” variation in growth rates due to the age or size of trees, or differences in site conditions. Many detrending and standardization techniques have been developed for this purpose. Those approaches that eliminate persistent growth differences between individual trees (e.g., flexible curve standardization procedures [Cook and Peters, 1997]) are not affected by the sample biases described here, while alternative approaches like the Regional Curve Standardization (RCS) [Briffa et al., 1998; Esper et al., 2002] which maintain growth differences between trees are still affected strongly by the biases described here. RCS was specifically

designed to maintain long-term variation in tree ring data, but the downside is that it is susceptible to sample biases [cf. *Briffa and Melvin*, 2011]. Some improvements were made to remove biases in RCS techniques by applying individual or multiple RCS curves according to trees' individual growth rates [cf. *Melvin*, 2004; *Nicault et al.*, 2010], but these approaches are also less powerful in maintaining long-term variation. One of the largest challenges for historical growth rates reconstructions is the preservation of long-term, low-frequency variation, while minimizing the effect of sample biases [Briffa and Melvin, 2011]. A wider awareness of the existence of biases and their potentially large effect, as shown here and by *Briffa and Melvin* [2011], will hopefully further stimulate developments toward producing methods for unbiased growth rate reconstructions.

## 6. Conclusions

[41] We showed that common tree ring sampling practices, which select the largest, living trees from a natural, uneven-aged population, leads to biases in growth rate reconstructions. The magnitude of these biases is relatively large, even leading to a doubling of growth rates over the last decades, and may explain observed growth increases in a substantial number of published tree ring studies. To avoid such biases, we recommend that future sampling strategies include trees from smaller size classes. However, even then great care should be taken in the interpretation of historical growth rate patterns based on trees rings, as the living trees in a population are only a subset of the original population. The potential magnitude of sample biases in tree ring studies may have been underestimated so far, and this phenomenon deserves much wider attention.

[42] **Acknowledgments.** RJWB was supported by the Betty and Gordon Moore foundation, EG was supported by the UK-NERC funded grant to AMAZONICA, and PAZ was supported by ERC grant 242955.

## References

- Badeau, V., et al. (1996), Long-term growth trends of trees: Ten years of dendrochronological studies in France, in *Growth Trends in European Forests*, edited by H. Spiecker et al., pp. 167–181, Springer, Berlin, doi:10.1007/978-3-642-61178-0\_14.
- Baker, T. R., et al. (2003), Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest, *J. Trop. Ecol.*, **19**, 109–125.
- Becker, M. (1989), The role of climate on present and past vitality of silver fir in forest in the Vosges mountains of northeastern France, *Can. J. For. Res.*, **19**, 1110–1117, doi:10.1139/x89-168.
- Becker, M., et al. (1994), Short-term variations and long-term changes in oak productivity in northeastern France. The role of climate and atmospheric CO<sub>2</sub>, *Ann. Sci. For.*, **51**, 477–492, doi:10.1051/forest:19940504.
- Bert, D. (1992), Influence du climat, des facteurs stationnels et de la pollution sur la croissance et l'état sanitaire de Sapin pectiné (*Abies alba* Mill.) dans le Jura. Etude phytocologique et dendrochronologique, PhD thesis, 200 pp., Nancy I Univ., Nancy, France.
- Bigler, C., and H. Bugmann (2003), Growth-dependent tree mortality models based on tree rings, *Can. J. For. Res.*, **33**, 210–221, doi:10.1139/x02-180.
- Bigler, C., and T. T. Veblen (2009), Increased early growth rates decrease longevities of conifers in subalpine forests, *Oikos*, **118**, 1130–1138, doi:10.1111/j.1600-0706.2009.17592.x.
- Black, B. A., et al. (2008), Relationships between radial growth rates and lifespan within North American tree species, *Ecoscience*, **15**, 349–357, doi:10.2980/15-3-3149.
- Boisvenue, C., and S. W. Running (2006), Impacts of climate change on natural forest productivity—Evidence since the middle of the 20th century, *Global Change Biol.*, **12**, 862–882, doi:10.1111/j.1365-2486.2006.01134.x.
- Bonan, G. B. (2008), Forests and climate change: Forcings, feedbacks, and the climate benefits of forests, *Science*, **320**, 1444–1449, doi:10.1126/science.1155121.
- Brienen, R. J. W., and P. A. Zuidema (2006), Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis, *J. Ecol.*, **94**, 481–493, doi:10.1111/j.1365-2745.2005.01080.x.
- Brienen, R. J. W., et al. (2006), Autocorrelated growth of tropical forest trees: Unraveling patterns and quantifying consequences, *For. Ecol. Manage.*, **237**, 179–190, doi:10.1016/j.foreco.2006.09.042.
- Brienen, R. J. W., et al. (2010), Attaining the canopy in dry and moist tropical forests: Strong differences in tree growth trajectories reflect variation in growing conditions, *Oecologia*, **163**, 485–496, doi:10.1007/s00442-009-1540-5.
- Briffa, K., and T. M. Melvin (2011), A closer look at regional curve standardization of tree-ring records: Justification of the need, a warning of some pitfalls, and suggested improvements in its application, in *Dendroclimatology: Progress and Prospects*, edited by M. K. Hughes et al., pp. 113–146, Springer, Dordrecht, Netherlands.
- Briffa, K. R., et al. (1998), Trees tell of past climates: But are they speaking less clearly today?, *Philos. Trans. R. Soc. London, Ser. B*, **353**, 65–73, doi:10.1098/rstb.1998.0191.
- Briffa, K. R., et al. (2008), Trends in recent temperature and radial tree growth spanning 2000 years across northwest Eurasia, *Philos. Trans. R. Soc. B*, **363**, 2269–2282, doi:10.1098/rstb.2007.2199.
- Canham, C. D., et al. (2001), Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species, *Can. J. For. Res.*, **31**, 1–10, doi:10.1139/x00-124.
- Cherubini, P., et al. (1998), Potential sampling bias in long-term forest growth trends reconstructed from tree rings: A case study from the Italian Alps, *For. Ecol. Manage.*, **109**, 103–118, doi:10.1016/S0378-1127(98)00242-4.
- Clark, J. S. (1991), Forest-tree growth rates and probability of gap origin: A comment, *Ecology*, **72**, 1166–1169, doi:10.2307/1940616.
- Cole, C. T., et al. (2010), Rising concentrations of atmospheric CO<sub>2</sub> have increased growth in natural stands of quaking aspen (*Populus tremuloides*), *Global Change Biol.*, **16**, 2186–2197, doi:10.1111/j.1365-2486.2009.02103.x.
- Cook, E. R., and K. Peters (1997), Calculating unbiased tree-ring indices for the study of climatic and environmental change, *Holocene*, **7**, 361–370, doi:10.1177/095968369700700314.
- Das, A. J., et al. (2007), The relationship between tree growth patterns and likelihood of mortality: A study of two tree species in the Sierra Nevada, *Can. J. For. Res.*, **37**, 580–597, doi:10.1139/X06-262.
- Esper, J., et al. (2002), Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability, *Science*, **295**, 2250–2253, doi:10.1126/science.1066208.
- Gedalof, Z., and A. A. Berg (2010), Tree ring evidence for limited direct CO<sub>2</sub> fertilization of forests over the 20th century, *Global Biogeochem. Cycles*, **24**, GB3027, doi:10.1029/2009GB003699.
- Graumlich, L. J. (1991), Sub-alpine tree growth, climate, and increasing CO<sub>2</sub>—An assessment of recent growth trends, *Ecology*, **72**, 1–11, doi:10.2307/1938895.
- Grudd, H., et al. (2002), A 7400-year tree-ring chronology in northern Swedish Lapland: Natural climatic variability expressed on annual to millennial timescales, *Holocene*, **12**, 657–665, doi:10.1191/0959683602hl578rp.
- Hornbeck, J. W., et al. (1988), Growth trends in 10 species of trees in New England, 1950–1980, *Can. J. For. Res.*, **18**, 1337–1340, doi:10.1139/x88-206.
- Huang, J. G., et al. (2007), Response of forest trees to increased atmospheric CO<sub>2</sub>, *Crit. Rev. Plant Sci.*, **26**, 265–283, doi:10.1080/07352680701626978.
- Ingwell, L. L., et al. (2010), The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama, *J. Ecol.*, **98**, 879–887, doi:10.1111/j.1365-2745.2010.01676.x.
- Intergovernmental Panel on Climate Change (2007), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, 996 pp., Cambridge Univ. Press, Cambridge, U. K.
- Jacoby, G. C., and R. D. D'Arrigo (1997), Tree rings, carbon dioxide, and climatic change, *Proc. Natl. Acad. Sci. U. S. A.*, **94**, 8350–8353, doi:10.1073/pnas.94.16.8350.
- Johnson, S. E., and M. D. Abrams (2009), Age class, longevity and growth rate relationships: Protracted growth increases in old trees in the eastern United States, *Tree Physiol.*, **29**, 1317–1328, doi:10.1093/treephys/tpp068.
- Kienast, F., and R. J. Luxmoore (1988), Tree-ring analysis and conifer growth-responses to increased atmospheric CO<sub>2</sub> levels, *Oecologia*, **76**, 487–495.

- Knapp, P. A., et al. (2001), Detecting potential regional effects of increased atmospheric CO<sub>2</sub> on growth rates of western juniper, *Global Change Biol.*, 7, 903–917, doi:10.1046/j.1365-2486.2001.00452.x.
- Kobe, R. K., et al. (1995), Juvenile tree survivorship as a component of shade tolerance, *Ecol. Appl.*, 5, 517–532, doi:10.2307/1942040.
- Koutavas, A. (2008), Late 20th century growth acceleration in greek firs (*Abies cephalonica*) from Cephalonia Island, Greece: A CO<sub>2</sub> fertilization effect?, *Dendrochronologia*, 26, 13–19, doi:10.1016/j.dendro.2007.06.001.
- Lamarche, V. C., et al. (1984), Increasing atmospheric carbon-dioxide—Tree-ring evidence for growth enhancement in natural vegetation, *Science*, 225, 1019–1021, doi:10.1126/science.225.4666.1019.
- Landis, R. M., and D. R. Peart (2005), Early performance predicts canopy attainment across life histories in subalpine forest trees, *Ecology*, 86, 63–72, doi:10.1890/03-0848.
- Lebourgeois, F., and M. Becker (1996), Dendroecological study of Corsican pine in western France. Growth potential evolution during the last decades, *Ann. Sci. For.*, 53, 931–946, doi:10.1051/forest:19960502.
- Lieberman, M., and D. Lieberman (1985), Simulation of growth curves from periodic increment data, *Ecology*, 66, 632–635, doi:10.2307/1940415.
- Martinelli, N. (2004), Climate from dendrochronology: Latest developments and results, *Global Planet. Change*, 40, 129–139.
- Martínez-Vilalta, J., et al. (2008), Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions, *Global Change Biol.*, 14, 2868–2881, doi:10.1111/j.1365-2486.2008.01685.x.
- McDowell, N. G. (2011), Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality, *Plant Physiol.*, 155, 1051–1059.
- Melvin, T. M. (2004), Historical growth rates and changing climatic sensitivity of boreal conifers, PhD thesis, 271 pp., Univ. of East Anglia, Norwich, U. K.
- Mencuccini, M., et al. (2005), Size-mediated ageing reduces vigour in trees, *Ecol. Lett.*, 8, 1183–1190, doi:10.1111/j.1461-0248.2005.00819.x.
- Nicault, A., et al. (2010), Preserving long-term fluctuations in standardisation of tree-ring series by the adaptive regional growth curve (ARGC), *Dendrochronologia*, 28, 1–12, doi:10.1016/j.dendro.2008.02.003.
- Nicolussi, K., et al. (1995), Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO<sub>2</sub>-related, *Trees Struct. Funct.*, 9, 181–189, doi:10.1007/BF00195270.
- Nock, C. A., et al. (2011), Long-term increases in intrinsic water-use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand, *Global Change Biol.*, 17, 1049–1063, doi:10.1111/j.1365-2486.2010.02222.x.
- Pedersen, B. S. (1998), The role of stress in the mortality of midwestern oaks as indicated by growth prior to death, *Ecology*, 79, 79–93, doi:10.1890/0012-9658(1998)079[0079:TROSIT]2.0.CO;2.
- Peñuelas, J., et al. (2011), Increased water-use efficiency during the 20th century did not translate into enhanced tree growth, *Glob. Ecol. Biogeogr.*, 20, 597–608, doi:10.1111/j.1466-8238.2010.00608.x.
- Phillips, O. L., et al. (2009), Drought sensitivity of the Amazon rainforest, *Science*, 323, 1344–1347, doi:10.1126/science.1164033.
- Phillips, O. L., et al. (2010), Drought-mortality relationships for tropical forests, *New Phytol.*, 187, 631–646, doi:10.1111/j.1469-8137.2010.03359.x.
- Picard, J. F. (1995), Évolution de la croissance radiale du hêtre (*Fagus sylvatica* L) dans les Vosges. Premiers résultats sur le versant lorrain, *Ann. For. Sci.*, 52, 11–21, doi:10.1051/forest:19950102.
- Rathgeber, C., et al. (1999), Augmentation de productivité du chêne pubescent en région méditerranéenne française, *Ann. For. Sci.*, 56, 211–219, doi:10.1051/forest:19990303.
- Ricker, W. E. (1969), Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield, *J. Fish. Res. Board Can.*, 26, 479–541.
- Rolland, C., et al. (1998), Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750, *Trees Struct. Funct.*, 13, 40–53, doi:10.1007/PL00009736.
- Rozendaal, D. M. A., et al. (2010), Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time, *New Phytol.*, 185, 759–769, doi:10.1111/j.1469-8137.2009.03109.x.
- Ryan, M. G., et al. (2006), The hydraulic limitation hypothesis revisited, *Plant Cell Environ.*, 29, 367–381, doi:10.1111/j.1365-3040.2005.01478.x.
- Schöngart, J., et al. (2005), Wood growth patterns of *Macarobium acaciifolium* (Benth.) Benth. (*Fabaceae*) in Amazonian black-water and white-water floodplain forests, *Oecologia*, 145, 454–461, doi:10.1007/s00442-005-0147-8.
- Schulman, E. (1954), Longevity under adversity in conifers, *Science*, 119, 396–399, doi:10.1126/science.119.3091.396.
- Silva, L. C. R., et al. (2010), Recent widespread tree growth decline despite increasing atmospheric CO<sub>2</sub>, *PLoS ONE*, 5(7), e11543, doi:10.1371/journal.pone.0011543.
- Spiecker, H., et al. (Eds.) (1996), *Growth Trends in European Forests*, 372 pp., Springer, Berlin, doi:10.1007/978-3-642-61178-0.
- Veblen, T. T., et al. (1991), Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests, *Can. J. For. Res.*, 21, 242–254, doi:10.1139/x91-030.
- Vila, B., et al. (2008), Has global change induced divergent trends in radial growth of *Pinus sylvestris* and *Pinus halepensis* at their bioclimatic limit? The example of the Sainte-Baume forest (south-east France), *Ann. For. Sci.*, 65(7), 709, doi:10.1051/forest:2008048.
- Voelker, S. L., et al. (2006), Historical CO<sub>2</sub> growth enhancement declines with age in *Quercus* and *Pinus*, *Ecol. Monogr.*, 76, 549–564, doi:10.1890/0012-9615(2006)076[0549:HCGEDW]2.0.CO;2.
- Weiner, J. (1990), Asymmetric competition in plant populations, *Trends Ecol. Evol.*, 5, 360–364, doi:10.1016/0169-5347(90)90095-U.
- West, D. C., et al. (1993), Recent growth increases in old-growth longleaf pine, *Can. J. For. Res.*, 23, 846–853, doi:10.1139/x93-110.
- Wyckoff, P. H., and J. S. Clark (2002), The relation between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains, *J. Ecol.*, 90, 604–615, doi:10.1046/j.1365-2745.2002.00691.x.
- Zuidema, P. A., et al. (2011), Ages and long-term growth patterns of four threatened Vietnamese tree species, *Trees*, 25, 29–38, doi:10.1007/s00468-010-0473-2.

R. J. W. Brien and E. Gloor, School of Geography, University of Leeds, Woodhouse Lane, Leeds LS2 9JT, UK. (r.brien@leeds.ac.uk)  
 P. A. Zuidema, Programa de Manejo de Bosques de la Amazonía Boliviana, PO Box 107, Riberalta, Bolivia.