Tree growth inference and prediction when the point of measurement changes: modelling around buttresses in tropical forests

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Abstract: Estimation of tree growth is generally based on repeated diameter measurements. A buttress at the height of measurement will lead to overestimates of tree diameter. Because buttresses grow up the trunk through time, it has become common practice to increase the height of measurement, to ensure that measurements remain above the buttress. However, tapering of the trunk means that increasing measurement height will bias estimates of diameter downward by up to 10% per m of height. This bias could affect inference concerning species differences and climate effects on tree demography and on biomass accumulation. Here we introduce a hierarchical state space method that allows formal integration of data on diameter taken at different heights and can include individual variation, temporal effects or other covariates. We illustrate our approach using species from Barro Colorado Island, Panama, and La Selva, Costa Rica. Results include trends that are consistent with some of those previously reported for climate responses and changes over time, but differ in relative magnitude. By including the full data-set and accounting for bias and variation among individuals and over time, our approach allows for quantification of climate responses and the uncertainty associated with measurements and the underlying growth process.

INTRODUCTION

Tree growth underlies population dynamics (Clark & Clark 1999), species interactions (Swetnam & Lynch 1993), carbon sequestration (Caspersen *et al.* 2000) and species responses to climate change (Clark 2002, 2004; Clark *et al.* 2003). Nevertheless, reliable estimates of tree growth are limited, as data are time consuming to collect, and there are challenges associated with inference (Clark *et al.* 2007). Annual growth rates can be stage-dependent (Clark & Clark 1999), temporally correlated (Clark *et al.* 2007), and spatially correlated, primarily through competition (Canham *et al.* 2006, Condit *et al.* 2000, Hubbell *et al.* 1999, 2001; Webster & Lorimer 2005). Tree census data show considerable individual variation in growth, variation inherent in the process of growth, as well as temporal and spatial variation in the covariates affecting growth (Clark & Clark 1999, Clark

et al. 2007, Condit *et al.* 2000, Hubbell *et al.* 1999). Additionally, as with any long-term census, data are often missing and observation errors vary due to changes in protocol.

Clark *et al.* (2007) introduced a hierarchical Bayesian approach to modelling tree growth that accommodates uncertainty in process, data and parameters. The model also allows interpolation of missing data through predictive distributions that reflect uncertainty both in the measurement of growth, and the growth process, with constraints based on known biological information such as the fact that diameter increment growth cannot be negative (Clark *et al.* 2007), growth generally depends on size and growth rate in the previous times step (Wyckoff & Clark 2002), and it may vary from year to year and according to individual effects (Clark *et al.* 2007).

Here, we modify this approach to meet the challenges of tropical tree data sets, particularly the lack of consistency in the height at which trees are measured due to growing buttresses. Growth increments corresponding to years where the height of measurement has changed may

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be simply omitted from analyses (Feeley *et al.* 2007). Alternatively, where at every time-step diameters at several points of measurement are taken on potentially problematic trees, so that no growth increments are lost (Clark *et al.* 2003), suites of measurements within an individual may be from several different heights. Both issues render problematic the inference of individual growth trajectories. However, it is of particular importance to capture these observations, as in two of the major tropical tree data-sets a strong signal of declining growth through time has been detected (Clark 2004, Clark *et al.* 2003, Feeley *et al.* 2007). If there is covariance between time and tree size (Feeley *et al.* 2007), or time and height of measurement, or time and individuals present in the population, there is potential for the perceived decline over time to reflect biases in the estimation techniques that neglect the many levels of variation. Here we develop a method that integrates all sources of information to formally model measurements taken at several heights in the presence of uncertainty in measurements (Clark & Bjornstad 2004). We then show how this framework can be extended to allow inference when long or uneven census intervals are considered, without neglecting the cumulative effects of variance in growth through time that will occur as growth is inherently stochastic.

In the following methods section we first introduce the two methods, then briefly outline the data-sets used for this analysis. The resulting patterns of growth through time are then presented. We conclude by discussing the insights available from our method, and how our results relate to previous work on this topic.

METHODS

Data modelling

Data consist of repeated diameter measures on individuals through time associated with a height of measurement. The model is developed to maximize the support drawn from the full dataset while emphasizing information associated with specific trees and years. Relationships between different model components are specified as conditional distributions, allowing estimation using a Gibbs sampling approach. Specifically, our approach consists of two steps. First, we specify an observation model to convert diameter observed at any height into a 'true' diameter at 1.3 m (allowing for measurement error in our observations). Second, we specify a growth model for diameter growth at 1.3 m to allow direct comparison among individuals and years.

For the first step, for every individual for every year, we model a diameter at a height of 1.3 m as a latent variable denoted $D_{i,1.3,t}$. To infer this value, we use information from observations taken at different heights, and link

them using a tapering model, defined by a parameter α, and a model describing observation error (measurement error). If $D_{i,h,t}^{(o)}$ is the diameter in cm of tree i measured at height $h_{i,h,t}^{(o)}$ in m in year t, we define

$$D_{i,h,t}^{(o)} \sim N\big(D_{i,1.3,t} \exp\big[\alpha\big(h_{i,h,t}^{(o)} - 1.3\big)\big], w\big), \qquad (1)$$

where the (o) superscript indicates an observation, α is the tapering parameter, and variance w captures Gaussian observation error. The concept is illustrated in Figure 1. Since $\exp[\alpha(h_{i,h,t}^{(o)} - 1.3]$ indicates the proportion by which diameter is decreased at increasing heights, the value in brackets will need less than 1, i.e. α will be less than 1. Although proportionate taper (summarized by the constant α, i.e. the tapering parameter) may change during the course of ontogeny, only large trees generally experience shifts in measurement height, so this assumption of a constant exponent will minimally affect results. Trees where several measurements of diameter at different heights are available within the same year will contribute directly to calibrating α. For years where measurements are only available at one height per individual, α will be informed indirectly by all observations.

To complete the observation model, we define priors for each of the parameters, α and w. A parameter's prior is a probability density function that represents prior knowledge about what the parameter's value or range of values should be. For example, if previous analyses indicate that measurement error is of 1 mm then we would centre the probability density function for w narrowly around 1, equivalent to specifying an 'informative prior'. If we have no information, we will use uninformative priors with broad distributions. The forms of the prior distributions used in the full sampling procedure are normal for α and conjugate inverse gamma for w.

To achieve the second step, we develop a model of growth based on Clark *et al.* (2007) that exploits the information on overall tree growth, with a mean for the full population β_0, random individual effects β_i (how tree i differs from the rest of the population) and fixed year effects β_t (there can be shared year-to-year variation due to, say, climate). We model growth increments at a height of 1.3 m as,

$$X_{i,t} \equiv D_{i,1.3,t+1} - D_{i,1.3,t} = \mu_{i,t} + \varepsilon_{i,t} \qquad (2)$$

where $X_{i,t}$ is the diameter increment added between year t and $t+1$ at a height of 1.3 m. This is a linear equation with deterministic components defined by population mean growth rate β_0, random individual effect β_i, year effect β_t and process error $\varepsilon_{i,t}$,

$$\mu_{i,t} = \beta_0 + \beta_i + \beta_t \qquad (3)$$

$$\beta_i \sim N(0, \tau^2) \qquad (4)$$

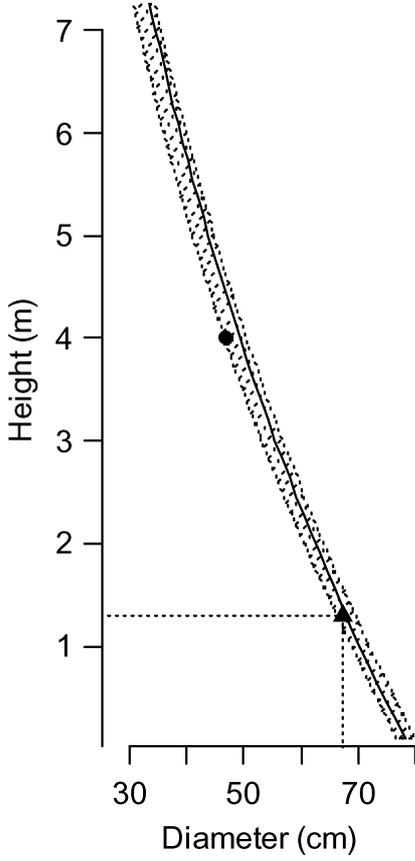$$\varepsilon_{i,t} \sim N(0, \sigma^2). \qquad (5)$$

Figure 1. Illustration of the model for the data observation process (Eqn. 1). Diameter measurements are made at a range of heights. Here one such is shown by the black circle. We wish to identify a relationship between height and diameter like that shown by the cross-hatched area, defined by a tapering parameter α, so that we can obtain an estimate of diameter at the same height of 1.3 m for all trees, shown here by the black triangle and dotted lines. The growth model (Eqn. 2) can then be applied across the data-set to diameter values at a common height of 1.3 m. For a certain number of trees, more than one measurement is available at a particular census (Table 1), so that the tapering relationship can be directly calibrated. For others, the information is borrowed across the entire data set. Results shown here correspond to posteriors for α for *Luehea seemannii* and one individual measurement from that data-set. The cross-hatched area incorporates uncertainty in the tapering parameter, α, and uncertainty around the observed data–point due to observation error, w.

'Process error' $\varepsilon_{i,t}$ is the extent to which main effects (mean, individual and year) fail to describe diameter increment. Prior distributions are conjugate normal and inverse gamma respectively,

$$\beta_0 \sim N(b, v_0),$$
$$\beta_t \sim N(0, v_t), \tag{6}$$
$$\sigma^2 \sim IG(a_1, a_2)$$

For random individual effects, the variance has the prior

$$\tau^2 \sim IG(a_3, a_4). \tag{7}$$

Use of the inverse gamma prior for variances is discussed in Clark (2007) and Clark *et al.* (2007). The beginning of the study is defined as the year when diameter data were first collected for the individual at a particular height, $t_{i,h}$. We define the end of the study $T_{i,h}$ as the time when the most recent diameter data were collected or individual i dies, whichever comes first. For every height, we model the data on a tree-by-tree basis for all years t between $t_{i,h}$ and $T_{i,h}$.

The result of sampling from the full model is that the latent state variable $D_{i,1.3,t}$, corresponding to diameter measured at a height of 1.3 m, is conditionally dependent on observations that might be available for diameter at a range of heights, $D_{i,h,t}^{(o)}$, and on the unknown states $D_{i,1.3,t+1}$ and $D_{i,1.3,t-1}$, which will also be modelled. A full discussion of this structure is contained in Clark *et al.* (2007). Non-independence of data is accommodated by the stochastic treatment of the underlying process. Here is the joint probability for a single tree year (conditioned on the rest of the model):

$$p\big(D_{i,h,t}^{(o)}, D_{i,1.3,t}\big) = p\big(D_{i,h,t}^{(o)}\big|D_{i,1.3,t}\big)p(D_{i,1.3,t})$$
$$= N\big(D_{i,h,t}^{(o)}\big|D_{i,1.3,t}\exp\big[\alpha\big(h_{i,h,t}^{(o)}-1.3\big)\big], w\big)$$
$$\times N(D_{i,1.3,t}-D_{i,1.3,t-1}|\mu_{i,t-1}, \sigma^2)$$
$$\times N(D_{i,1.3,t+1}-D_{i,1.3,t}|\mu_{i,t}, \sigma^2) \tag{8}$$

The densities in the last line are, respectively, the diameter data model, which includes a parameter describing tapering (α) to allow for data from several different heights to enter inference, and the process model for growth from $t-1$ to t and from t to $t+1$. Stochasticity in our process model includes process error and random effects (Eqns 2–5).

We now have specified the full model, including the form of the prior distributions for all parameters, and the conditionals describing how the different components are interrelated. The final step before applying the full model to data is to specify values for parameters of the prior distributions, based on knowledge of the approximate ranges of variability in measurements. Take for example the observation error parameter, w. Re-measurement in the La Selva database yields an average difference between measurements of 0.03 cm, with a maximum of 0.1 cm (Clark & Clark 2006). We could set $w = 0.01$ to reflect a belief that observations are normally distributed around the 'true' value of diameter with a variance of 0.01 (which more or less captures the characteristics above from Clark & Clark 2006). However, we do not know for sure that $w = 0.01$, and wish to infer its value using both information from the data and information based on our prior beliefs (e.g. that it should be 0.01). We therefore define a prior distribution for w, taken as conjugate inverse gamma,

Table 1. Data available for each of the five species. Data from La Selva (species in the first four rows) is much more detailed partly as measurements were taken yearly rather than every 5 y.

	Number of individual trees, n	Number of diameter observations, n_D	Total years of the study, T	Proportion of trees that grow and change height	Number of tree-years with diameters at several heights
Minquartia guianensis	559	7646	18	0.17	188
Lecythis ampla	400	4165	18	0.26	142
Cecropia obtusifolia	208	1114	13	0.14	20
Simarouba amara	415	3311	13	0.14	49
Luehea seemannii	210	1330	23 (6 censuses)	0.27	128

e.g.

$$w \sim IG(a_5, a_6), \tag{9}$$

where the parameters a_5 and a_6 will be chosen so that the mean of this prior distribution is around 0.01, and the variance around this mean reflects how certain we are that measurement error is close to this value vs. how much the data can define it. To weight our belief about the mean value to be a hundred times the weight of the data, we can specify

$$\begin{aligned} a_5 &= 100 n_D \\ a_6 &= 0.01\,(a_5 - 1) \end{aligned} \tag{10}$$

where n_D is the number of diameter observations (Table 1 and Table 2, see Clark *et al.* 2007 for details of weighting). For the BCI database, re-measurement information given in Chave *et al.* (2004) suggests we use a prior mean for observation error variance of 1, and we use the same weighting scheme as in Eqn. 10.

For process error σ^2, we use a prior mean of 0.5, and weight it to be twice the number of tree years and heights, $n_T = \sum_{i,h}(T_{i,h} - t_{i,h})$. This is equivalent to restricting possible values of σ^2 to be quite close to 0.5, so that the process error will generally be large, to avoid excessive smoothing,

$$\begin{aligned} a_1 &= 2 n_T \\ a_2 &= 0.5(a_1 - 1) \end{aligned} \tag{11}$$

Other priors are non-informative, e.g. we do not introduce prior beliefs into their modelling. The prior distribution for mean growth rate is normally distributed with mean $b = 0.8$, i.e. a prior mean growth rate of 0.80 cm y^{-1}; and $v_0 = 500$ where this large variance reflects our lack of prior certainty. Inference about this parameter will consequently be chiefly determined by the data. The prior on the tapering parameter α has mean $\alpha_0 = -0.1$ and variance $v_\alpha = 100$, which is likewise weak, so that data will dominate. The prior for the variance of random effects τ^2 has mean set to 1, and weighted roughly 0.01 of the data. This is accomplished with $a_3 = n/100$, where n is the number of trees (Table 1 and Table 2). Year effects β_t have prior mean zero and $v_t = 1$.

Analysis of the model is accomplished by Gibbs sampling (Gelfand & Smith 1990), implementation of which is discussed in the Appendix 1. The model output will be a sample from the posterior distributions of all parameters and of latent diameters for every individual at every time-step. Posterior distributions are density functions defined by the product of the prior distributions and conditional distributions defining the observation and the process model. Posterior distributions were not influenced by the mean values selected for β_0, τ^2 and β_t because priors were weak. Increments are sampled from truncated normal distributions to ensure that they remain positive.

Extension for uneven sampling intervals

For some data-sets, measurements are taken at intervals longer than a year, in which case, there is no information for growth in individual years. Furthermore, intervals may be uneven, further complicating estimation of yearly growth increments. To model data in this case, we can explicitly model the differing time lags. We define the multi-year increments as $\Delta X_{i,t}$, and Δt as the number of years separating consecutive censuses, such that

$$\Delta X_{i,t} \equiv D_{i,1.3,t+\Delta i,t} - D_{i,1.3,t}, \tag{12}$$

Assuming that variation accumulates as white noise (variance scales linearly with Δt), using the same notation as above for $\mu_{i,t}$ (i.e. growth increment in one time-step) and σ^2 (process error for one time-step) this is distributed as

$$\Delta X_{i,t} \sim N(\Delta_{i,t}\mu_{i,t}, \Delta_{i,t}\sigma^2), \tag{13}$$

which can be sampled directly. This formulation captures the fact that variance will increase with time elapsed. The joint probability for a single tree becomes

$$\begin{aligned} p\big(D^{(o)}_{i,h,t+\Delta i,t}, D_{i,1.3,t+\Delta i,t}\big) &= p\big(D^{(o)}_{i,h,t+\Delta i,t} \big| D_{i,1.3,t+\Delta i,t}\big) \\ &\quad \times p\big(D_{i,1.3,t+\Delta i,t}\big) \\ &= N\big(D^{(o)}_{i,h,t+\Delta i,t} \big| D_{i,1.3,t+\Delta i,t} \exp[\alpha(h^{(o)}_{i,h,t+\Delta i,t} - 1.3)], w\big) \\ &\quad \times N\big(D_{i,1.3,t} - D_{i,1.3,t-\Delta i,t-1} \big| \Delta_{i,t-1}\mu_{i,t-1}, \Delta_{i,t-1}\sigma^2\big) \\ &\quad \times N\big(D_{i,1.3,t+\Delta i,t} - D_{i,1.3,t} \big| \Delta_{i,t}\mu_{i,t}, \Delta_{i,t}\sigma^2\big). \end{aligned}$$

Table 2. Prior parameters (calculated using the text and Table 1) and the posterior means, Bayesian standard errors, and credible intervals for the mean growth increment, μ (cm), the tapering parameter, α, the process error, the individual standard deviation τ, and the observation error standard deviation $\sqrt{w}$.

	Prior parameter values	Posterior mean	Bayesian SE	Credible interval: 2.5%	Credible interval: 97.5%
Minquartia guianensis					
b_0	$b = e^{-0.22}$, $v_b = 500$	0.1722	0.000088	0.1476	0.1965
α	$\alpha_0 = -0.01$, $v_\alpha = 100$	−0.0194	0.000001	−0.0195	−0.0192
σ	$a_1 = 20124$, $a_2 = 10061$	0.6594	0.000015	0.6552	0.6637
τ	$a_3 = 5.59$, $a_4 = 4.59$	0.2080	0.000057	0.1929	0.2245
$\sqrt{w}$	$a_5 = 1394600$, $a_6 = 13945$	0.1007	0.000000	0.1006	0.1008
Lecythis ampla					
b_0	$b = e^{-0.22}$, $v_b = 500$	0.2808	0.000151	0.2391	0.3227
α	$\alpha_0 = -0.01$, $v_\alpha = 100$	−0.0247	0.000001	−0.0250	−0.0244
σ	$a_1 = 20124$, $a_2 = 10061$	0.6712	0.000019	0.6660	0.6764
τ	$a_3 = 5.59$, $a_4 = 4.59$	0.3131	0.000123	0.2795	0.3480
$\sqrt{w}$	$a_5 = 13956$, $a_6 = 13.9$	0.1027	0.000001	0.1026	0.1028
Cecropia obtusifolia					
b_0	$b = e^{-0.22}$, $v_b = 500$	0.4895	0.000257	0.4161	0.5602
α	$\alpha_0 = -0.01$, $v_\alpha = 100$	−0.0149	0.000011	−0.0178	−0.0122
σ	$a_1 = 20124$, $a_2 = 10061$	0.6881	0.000032	0.6794	0.6971
τ	$a_3 = 5.59$, $a_4 = 4.59$	0.2992	0.000187	0.2505	0.3537
$\sqrt{w}$	$a_5 = 13956$, $a_6 = 13.9$	0.1000	0.000001	0.0998	0.1002
Simarouba amara					
b_0	$b = e^{-0.22}$, $v_b = 500$	0.4761	0.000189	0.4227	0.5271
α	$\alpha_0 = -0.01$, $v_\alpha = 100$	−0.0272	0.000013	−0.0289	−0.0220
σ	$a_1 = 20124$, $a_2 = 10061$	0.6743	0.000022	0.6682	0.6804
τ	$a_3 = 5.59$, $a_4 = 4.59$	0.4230	0.000137	0.3869	0.4623
$\sqrt{w}$	$a_5 = 13956$, $a_6 = 13.9$	0.1000	0.000001	0.0999	0.1002
Luehea seemannii					
b_0	$b = -1$, $v_b = 500$	0.3070	0.000243	0.2386	0.3743
α	$\alpha_0 = -0.5$, $v_\alpha = 100$	−0.1190	0.000005	−0.1203	−0.1178
σ	$a_1 = 2520$, $a_2 = 1259.5$	0.7871	0.000056	0.7718	0.8027
τ	$a_3 = 2.1$, $a_4 = 1.1$	0.5529	0.000242	0.4906	0.6241
$\sqrt{w}$	$a_5 = 175400$, $a_6 = 175399$	1.0253	0.000009	1.0229	1.0277

We can model $\mu_{i,t}$ essentially as above; see Appendix 2 for further details. As above, there are truncated normal priors on sampled increments, to ensure positive increments for all years. Unlike the model described above, we model only observed diameters, and not unobserved diameters for years where data is not taken. Below we illustrate these two procedures with two data-sets.

Data

For the first method, we use the large, long-term dataset gathered on tree growth and survival in an old-growth tropical wet forest in La Selva, Costa Rica, provided in Clark & Clark (2006). These data contain measurements of tropical forest tree species that exhibit distinct life-history strategies. Complex and variable diameter growth patterns (Clark & Clark 1999) as well as strong year effects related to climatic conditions (Clark *et al.* 2003) have all been reported. The data are unusually detailed, with measurements of diameter taken every year for a total of 3382 individual trees from 10 species from 1983 to 2006, including *Minquartia guianensis* Aubl., *Lecythis ampla* Miers, *Cecropia obtusifolia* Bertol. and *Simarouba amara* Aubl. which we use to illustrate the method here. Diameter was measured using callipers or tape measures. In some years, when on some individuals the upwards-growth of buttresses or other irregularities was judged to be approaching the current point of measurement (POM), double measurements were made – one at the current POM and a second at a new POM established at least 50 cm above the irregularity (Clark & Clark 2006). In years where the point of measurement changed, diameters at both the new and old height are not directly provided (Clark & Clark 2006). However, the value at the lower height at the later time is indirectly available through the variable DGRO, which indicates the increment growth for each year from the last year to the lower point of measurement. We used this to obtain two observed heights and diameters for every individual

in every year where the point of measurement changed. For the remaining years, a single diameter and height were available. We set the maximum yearly diameter increment to 4.5 cm y^{-1} and the minimum to 0.002 cm y^{-1}.

For the second method, geared to inferring growth in the presence of long uneven census intervals, we used the diameter data available from the Center for Tropical Science plot on Barro Colorado Island, in the Panama Canal, initiated in 1981/1982 and re-censused in 1985, 1990, 1995, 2000 and 2005. In the 1982 and 1985 censuses, diameters were rounded to the lower 5 mm for trees with diameters of less than 5 cm. From 1985, diameter was measured at a point chosen to be representative of the diameter of the trunk, i.e. above buttresses and roots. If buttresses later encroached on this height, workers increased the height of measurement, recording both the old and new heights and diameters. In the last two or three censuses, a height well above the maximum range of buttresses was set as the new height. For this analysis, we focused on a single species, *Luehea seemannii*, a tall species with a large trunk and irregular buttresses, found abundantly in secondary growth or gaps. Modelling this species is also of interest, as it has a very irregular bole surface and is likely to represent an extreme case of trunk deformation across tropical tree data-sets. We set the maximum yearly diameter increment to 4.5 cm y^{-1} and the minimum to 0.002 cm y^{-1}, the latter being an arbitrarily low value consistent with the possibility that growth may not occur in some years. These values could be altered for application to species with different characteristics. Efforts were made to measure individuals during the first 10 mo of each year; however, some individuals were measured very early in 1991 and 1996. These trees generally correspond to individuals whose measurements are identified as potentially erroneous during the course of data-screening, and are subsequently re-measured. Variation in timing of measurement over the course of the year could have influenced estimates of individual and period effects. We therefore used the time between measurements in days to define $\Delta_{i,t}$, obtaining fractional yearly intervals (e.g. we could obtain $\Delta_{i,t} = 4.55$).

RESULTS

In the analysis presented here, all parameters are well identified as indicated by narrow credible intervals (Table 2). The credible intervals for mean growth β_0 of shade-tolerant species *Lecythis ampla* and *Minquartia guianensis* are lower than the credible intervals of the three other light-demanding species we analysed. For all La Selva species, the posterior of the tapering parameter is considerably smaller than the non-informative prior (Table 2, α posterior means); but *Simarouba amara* has the greatest taper of the four, around double that of the others, in accordance with species descriptions. Across species, *Luehea seemannii* shows the largest levels of taper; individuals measured 7 meters off the ground would see their diameter reduced to ∼54% of the diameter at 1.3 m (Table 2).

Error parameter estimates are influenced by informative priors. The informative priors ensure that posterior estimates of σ^2 are cantered on 0.5. Large weights on w ensure that it dominates for individuals and years where observations are available (Table 2). For all species, the posterior of individual variance is distinct from the deliberately non-informative prior. In the La Selva database, individual variation is highest for *Simarouba amara* (Table 2, posterior mean for τ in all La Selva species), a species with potentially varied life trajectories as it is described as both light-responsive and shade tolerant. The two shade-tolerant species *Lecythis ampla* and *Minquartia guianensis* show similar degrees of variation across individuals (Table 2, posterior mean for τ for these two species).

The model predicts the data well (Figure 2, 3), and diagnostics indicate good agreement between predicted and observed distributions. In the simple model presented here, higher growth of trees with large diameters is captured through process error, i.e. for the same tree, imputed values of $X_{i,t}$ can be larger for larger $D_{i,1.3,t}$, even though the underlying linear predictor $\mu_{i,t}$ is the same. For *Minquartia*, the mean value of $X_{i,t}$ inferred for time steps where the height had changed was 0.146, vs. 0.144 where the height had not changed, indicating no systematic bias in the method.

Following Eqn 1, the height at which measurement occurs can substantially affect the diameter increment recorded. For example, in *Luehea seemannii* individual 2 from Figure 3 was measured initially at 1.3 m, but in 1990, the height of measurement was moved to 4 m. The observed diameter increments at this measurement height were 5.4, 6.4 and 6.9 cm (in 1990–1995, 1995–2000 and 2000–2005 respectively). Using the posterior for α to convert the diameter at a height of 4 m into the diameter at a height of 1.3 m, we can calculate that the increments observed at 1.3 m would have been of 7.2, 8.6, 9.2 cm respectively, i.e. considerably larger in each period.

There is substantial shared variation represented by year effects (Figure 4); which shows similar patterns across the species within the La Selva database. Year effects for the La Selva data-base also show a temporal trend compatible with previous results from this area. For the BCI database the temporal trend is also observed (Figure 5). For both data-sets there is considerable
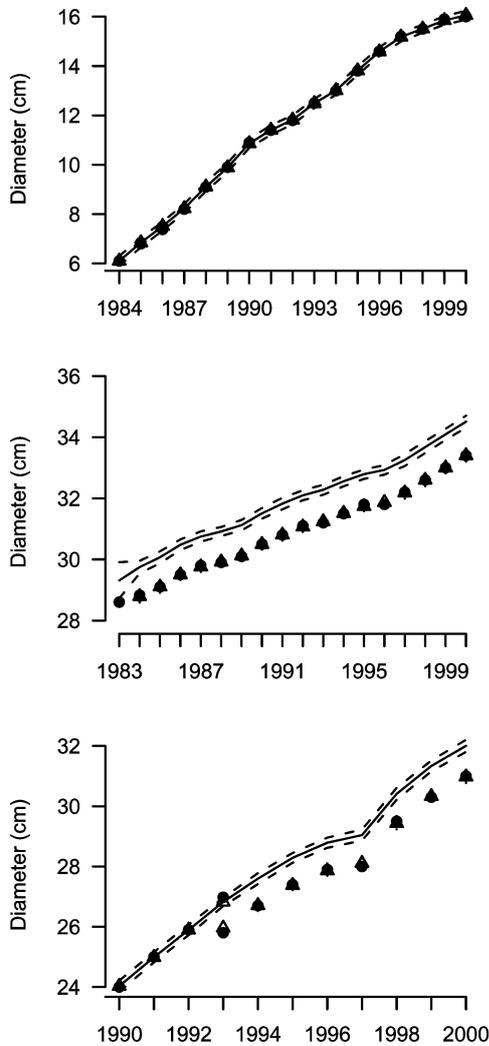
Figure 2. Diameter trajectories of three *Minquartia guianensis* individuals over the course of the census. Solid black points are diameter measurements. Solid lines are the predicted posterior mean trajectory of diameter for each individual at a height of 1.3 m; dashed lines are the corresponding 95% predictive intervals. The triangles are the predicted diameters for measurements taken at the same height as the data (i.e. the black points). The associated vertical dashed lines are the corresponding predictive intervals, including uncertainty in estimation of the tapering parameter, α (which is slight for these examples). The first individual was measured at a height of 1.3 m throughout the course of the census; the second individual was measured at a height greater than 1.3 m throughout the course of the census. For the third individual, measurement height changed over the course of the census. Overall, the observed values are accommodated by the predicted mean values at that height, and their predictive intervals.

overlap between credible intervals of year effect posterior distributions.

DISCUSSION

In recent years, much of the key inference on tree growth in tropical forests has been based on the two datasets
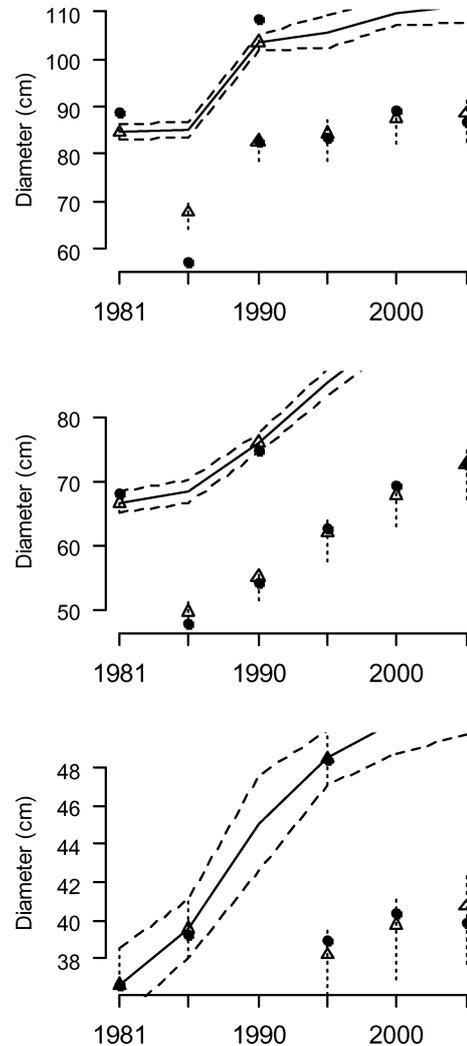
Figure 3. As in Figure 1 for *Luehea seemannii*, for the model including varying census intervals, since observations are taken approximately only every 5 y. The degree of taper for this species is considerable. Diameter measurements taken at ~7 m will be only ~50% of those taken at 1.3 m. Note that for the first individual shown, the second observed diameter implies shrinkage of more than 30 cm. Even allowing for a change in height of measurement of ~1 m, this is unlikely, and the observed diameter is therefore outside the predicted confidence intervals, and will be encompassed through measurement error (not shown).

analysed here. For example, they have been used to infer the effect of global warming on forests (Clark *et al.* 2003), to track directional changes in growth (Feeley *et al.* 2007), to test the relationship between diversity and degree of demographic variance within and across species (Condit *et al.* 2006), to test for trade-offs between growth and survival (Gilbert *et al.* 2006), and even to test for empirical evidence for the metabolic theory (Muller-Landau *et al.* 2006). However, changing heights of measurement is a ubiquitous feature of these tropical tree datasets. Analyses to date where diameters from several points of measurement are not available (Clark
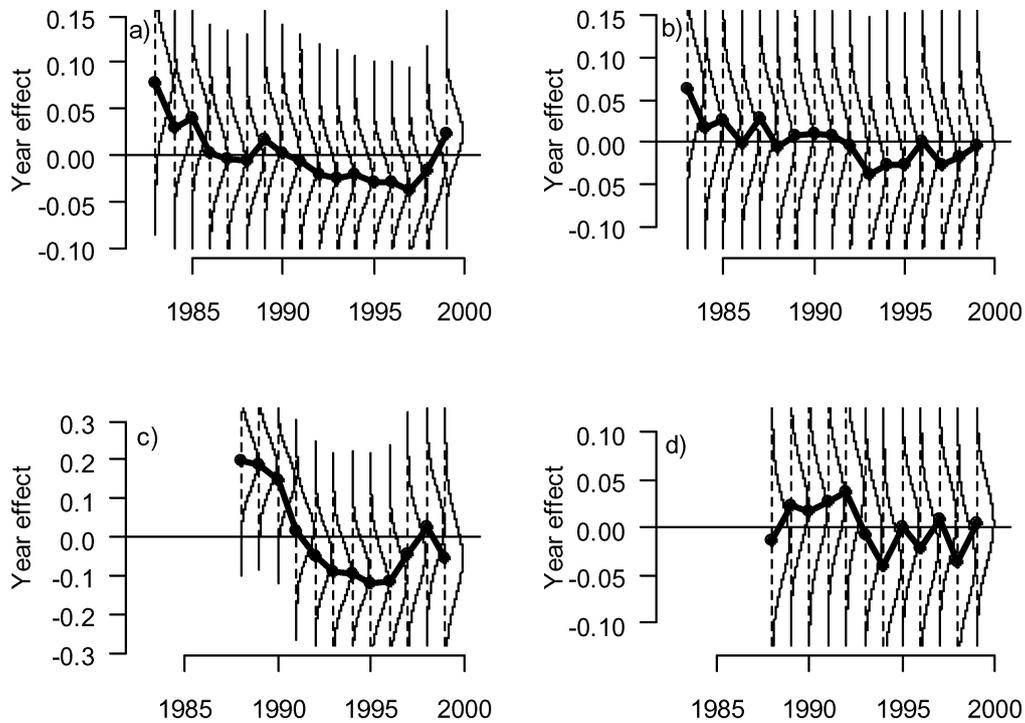
Figure 4. The posterior densities for year effects in the growth model (one solid curve for each year), with posterior means (dots, connected by solid lines) for four species from the La Selva database; the area bounded by each curve and the vertical dashed line for each year integrates to one. *Minquartia guianensis* (a) and *Lecythis ampla* (b) show a similar temporal trend to those estimated by Clark *et al.* (2003). Later years, which correspond to higher minimum night-time temperatures, have more negative effects on growth. However, our results differ from Clark *et al.* (2003) in the magnitude of year effects, and the details of patterns. For example, the last year shows an increase in year effects for *Minquartia guianensis*, and for *Lecythis ampla* the increment from 1995 to 1996 is larger than that from 1994 to 1995 whereas in Clark *et al.* (2003) the opposite pattern is recorded. For *Lecythis ampla*, the trend through time is particularly weak when credible intervals are taken into account, in agreement with Clark *et al.* (2003), who found the negative trend to be non-significant for this species. *Cecropia obtusifolia* (c) and *Simarouba amara* (d) were not considered in previous analyses.

et al. 2003) have either discarded such measurements (Condit *et al.* 2006), or set them to a chosen value such as the mean value for trees of the appropriate size whose measurement point did not change (Feeley *et al.* 2007). Errors are not limited to the years in which the measurement height changes. Trees measured at greater heights can appear to be growing more slowly, simply due to the taper. A key way to strengthen the inference obtained from these important data is to have a coherent approach that includes all measurements, accounts for all sources of variation including changes in the height of measurement, and does not neglect potential sources of bias. Our approach is founded on a consistent probability model for both data and process.

It has been shown that for all La Selva species, growth varies in a complex fashion across diameter (Clark & Clark 1999). Here, we did not explicitly model an effect of diameter on growth, although process error in the model should capture such patterns, e.g. $\varepsilon_{i,t}$ will increase with tree diameter because the deviation between the mean predicted from the linear predictor, $\mu_{i,t}$ and the observed data will be larger for large trees. However, we have estimates of all latent diameter states, a unique aspect of

our method, which provides a strong basis for inference on biomass change. Furthermore, the regression at the core of the model is flexible to a wide range of assumptions, and can be extended to include, for example, diameter, age, or other covariates such as crown class observations (Clark & Clark 2006) or minimum nocturnal temperature (Clark *et al.* 2003). Diverse sources of information beyond repeated diameter measurements, such as increment core data can also be built onto the model to inform inference in a straightforward manner (Clark *et al.* 2007). Explicit models of measurement error that vary through time and at specific sizes could be imposed to absorb the rounding differences that occur during the course of collection of the BCI data. (Less than 7% of measurements are affected in the BCI species used for illustration here, so we did not feel it was warranted in this case.)

For large mapped plots where thousands of trees are measured at each census, e.g. Condit *et al.* (2006), it is almost inevitable that not all trees can be measured in all years. It is also likely that census intervals can be staggered over years, as it takes more than a single year to measure all individuals and verify unlikely measurements (this occurs for example in the BCI dataset in 1995). This will
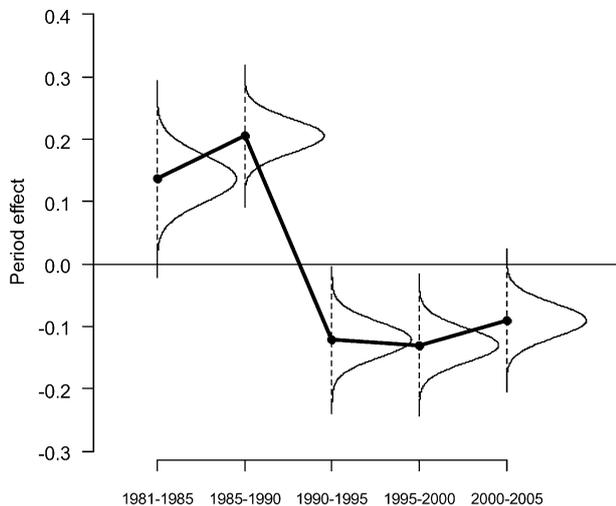
Figure 5. Period effects for *Luehea seemannii*; the first period starts between 1981 and 1983; see description of data for details. This result is similar to that obtained in Feeley *et al.* (2007), with particularly poor growth during the 1990–1995 period, credible intervals before and after overlap substantially. This result may be partly an artefact linked to having the same BCI census supervisors from 1995 on, probably leading to a more constant (if not rigorous) methodology since then (R. Pérez pers. comm.).

mean that growth intervals for different individuals will be of different lengths. Growth is a stochastic process, and variance in growth will accumulate through time, so that diameter measurements separated by longer intervals will be more unalike than they would be if growth were deterministic. Consequently, estimating growth rate by simply taking the average growth increment and dividing it by the time interval could be misleading (Clark & Clark 1999). If census intervals are not too long, our approach allows straightforward inference on missing diameters (Clark *et al.* 2007). Where census intervals are long, the second method we introduce allows inference on observed diameters based on a process model that includes measurement error, process error, and period effects based around yearly growth increments. The yearly time step facilitates comparison across data-sets with different census periods; and explicit modelling of increasing variance with increasing time increments prevents this aspect from biasing resulting inference.

In both models, all components are estimated in a single framework, so credible intervals on year and period parameters represent the integrated knowledge obtained from all other components of the model. In terms of inference about broad-scale climatic patterns, our analysis supports the overall results presented in Clark *et al.* (2003). Yearly increments for *Lecythis ampla* and *Minquartia guianensis* obtained here are similar to those presented in Figure 1 in Clark *et al.* (2003). In both analyses, growth in years 1994–1997 is particularly

poor. However, the details of patterns differ between our analyses and that of Clark *et al.* (2003) (Figure 4). Additionally, our results also allow exact quantification of the yearly growth effects. In the best year (1983), the posterior median indicates that *Minquartia guianensis* grows ∼2 mm more than average, and in the worst year (1997), ∼2 mm less than average. By contrast, *Lecythis ampla*, a deciduous, and therefore perhaps more resilient species, shows little yearly trend, and the magnitude of yearly deviations for this species is smaller. Our results also indicate a sharp decline with growth rate in later years for *Cecropia obtusifolia* (not analysed by Clark *et al.* 2003), likely to also be related to increased nocturnal temperatures. The magnitude of this effect is around twice that observed in *Minquartia guianensis*, suggesting that this pioneer species exploits good years through fast growth, but suffers proportionally more in bad years. By contrast, *Simarouba amara* shows very little yearly trend. Although light-responsive and with a high average growth rate, this species is described as shade-tolerant, so its life-history may lead to more averaging of the environment, similar to *Minquartia guianensis*. Species differences in magnitude of yearly effects coupled with data on their relative abundances will provide another key to understanding the positive feedback of tree growth declines to on-going atmospheric CO_2 accumulation (Clark *et al.* 2003).

For the BCI data-set, in agreement with Feeley *et al.* (2007), year effects isolated by our analysis show a negative trend, through a sharp decline in growth between 1990 and 1995, followed by slow growth thereafter; the magnitude of yearly variation is similar to that found for *Cecropia obtusifolia*. However, using simple ANCOVA approaches, this distinct feature of continued slow growth after the 1990–1995 period is only clearly captured if diameter increments associated with change in the height of measurement are included (Figure 6). The increment measurements made unavailable by a change in height at measurement may be key to revealing years of particularly poor growth, particularly where census intervals are long. Our method provides a way of explicitly modelling these increments and long census intervals. Incorporating all data into a single framework increases our power to detect whether patterns are global, and whether the magnitude of growth varies between years or periods. Given the key role these tropical tree data-sets have had in a range of aspects of ecological inference, the benefits of raising analysis to the next level is likely to be high.

To conclude, if buttresses or other features of trees lead to a requirement that the height of measurement be changed during the course of the study, either across individuals or within individuals through time, estimation of growth effects will be biased if changing height is not taken into account. Our results indicate
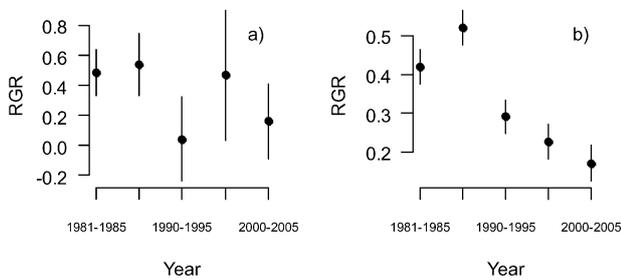
Figure 6. Fitted period effects with confidence intervals for *Luehea seemannii* where different amounts of information were included based on height of measurement. Fitting an ANCOVA to only data where diameter pairs were measured at the same height with as response variable $y = [D^{(o)}_{i,t+\Delta} - D^{(o)}_{i,t}]/\Delta$, captures the substantial decrease during 1990–1995 found in Figure 4 but not the continuing low growth after 1995, (a). Performing a similar analysis using $y = [D^{(p)}_{i,t+\Delta} - D^{(p)}_{i,t}]/\Delta$ where the p superscript indicates that diameters are predicted according to Eqn. 1 using the posterior mean of α from Table 2 produces a pattern that better captures the continuation of low growth (b), as much more of the data can be included. Fitting individual effects did not substantially change the estimated coefficients. Note that both very large and very small increments were set to the minimum or maximum diameter increment deemed possible as there is no way to formally eliminate measurement error in this setting.

that if and when height of measurement is changed, continued measurement at the old height will greatly improve calibration of taper effects, and thus precision of estimates of overall growth.

ACKNOWLEDGEMENTS

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Appendix 1

Gibbs sampling is a Markov chain Monte Carlo (MCMC) technique that involves alternate sampling from each of the full conditional distributions of all unknowns in the model, including parameters and latent variables (Clark 2007, Gelfand & Smith 1990). Here we provide conditional distributions, together with algorithms used to sample from them. For the first model, the conditional distribution of diameters for individual i is

$$p\left(\{D_{i,1.3,t}\}\Big|\{D^{(o)}_{i,h,t}\}, \beta, \alpha, \sigma^2, w\right)$$

$$\times \propto \prod_{t=t_i}^{T_i} N(D_{i,1.3,t}|D_{i,1.3,t-1} + X_{i,t}, \sigma^2)$$

$$\times \prod_{t=t_{i,h}}^{T_{i,h}} N\left(D^{(o)}_{i,h,t}\Big|D_{i,1.3,t}\exp\left[\alpha\left(h^{(o)}_{i,h,t} - 1.3\right)\right], w\right)$$

The density for $D^{(o)}_{i,h,t}$ is included only for years and heights in with diameter measurements are available, the second probability density is taken over all heights available at all times. A Metropolis sample from this distribution begins with a proposal for the first diameter value from a normal density that is centred on the first observation. Then all diameter increments are proposed from a truncated normal distribution (to ensure that they are positive) for the years in which individuals were alive and included in the study. Proposals are accepted on a tree-by-tree basis. In other words, blocking is by tree, but there are no loops over trees or years. The conditional distribution of growth increments for individual i is

$$p\left(\{X_i\}\Big|\{D^{(o)}_{i,h}\}, \beta, \alpha, \sigma^2, w\right) \propto \prod_{t=t_{i,h}}^{T_{i,h}} N\left(X_{i,t}\Big|V_{i,t}v_{i,t}, V_{i,t}\right)$$

$$\times \prod_{t=t_i}^{T_i} N\left(D^{(o)}_{i,h,t}\Big|(D_{i,1.3,t-1} + X_{i,t})\exp[\alpha(h_{i,t} - 1.3)], w\right)$$

$$\times I(0.002 < X_{i,t} < 7.5)$$

where I is the indicator function, and defined to insure that growth increments are contained between a chosen lower bound 0.002 cm y^{-1}; and an upper bound of 7.5 cm y^{-1}, and

$$V^{-1}_{i,t} = 1/\sigma^2$$
$$v_{i,t} = \mu_{i,t}/\sigma^2$$

The solutions for these conditional distributions are provided in Clark (2007). Parameters involved in Eqns 1 and 2 are all sampled directly from conditional Gaussian densities. For the overall mean growth rate, the conditional posterior, integrated over random effects, is

$$\beta_0 \sim N(Vv, V)$$

$$V^{-1} = \frac{1}{\sigma^2 + \tau^2}\sum_{i=1}^{n}(T_i - t_i - 1) + \frac{1}{v_0}$$

$$v = \frac{1}{\sigma^2 + \tau^2}\sum_{i=1}^{n}\sum_{t=t_i}^{T_i - 1}(X_{i,t} - \beta_t) + \frac{b}{v_0}$$

where n is the number of trees and t_i and T_i are the first and last measurements for individual i. Random individual effects are sampled from

$$\beta_i \sim N(V_i v_i, V_i)$$

$$V^{-1}_i = \frac{T_i - t_i - 1}{\sigma^2} + \frac{1}{\tau^2}$$

$$v_i = \frac{1}{\sigma^2}\sum_{t=t_i}^{T_i - 1}(X_{i,t} - \beta_0 - \beta_t)$$

Year effects are sampled from

$$\beta_t \sim N(V_t v_t, V_t)$$

$$V^{-1}_t = \frac{n_t}{\sigma^2} + \frac{1}{v_\kappa}$$

$$v_t = \frac{1}{\sigma^2}\sum_{i=1}^{n}(X_{i,t} - \beta_0 - \beta_i)$$

$$n_t = \sum_{i=1}^{n_j} I(\text{individual } i \text{ alive at } t)$$

where $I(A)$ is the indicator variable equal to one, when event A is true, and zero, otherwise. All year effects are updated simultaneously, and we impose a sum-to-zero constraint on the year effects by subtracting the mean at each Gibbs step. The tapering parameter is sampled indirectly using a Metropolis–Hastings step, from

$$p(\alpha) \propto \sum_{i=1}^{n}\sum_{t=t_{i,h}}^{T_{i,h}} N\left(\alpha\Big|D^{(o)}_{i,h,t} - D_{i,1.3,t}\right.$$

$$\times \left.\exp\left[\alpha\left(h^{(0)}_{i,t} - 1.3\right)\right], w\right) N(\alpha|\alpha_0, v_\alpha).$$

Variance parameters are all directly sampled from inverse gamma distributions. These are

$$\sigma^2 \sim IG(s_1, s_2)$$

$$s_1 = a_1 + \frac{1}{2}\sum_{i=1}^{n}(T_i - t_i - 1)$$

$$s_2 = a_2 + \frac{1}{2}\sum_{i=1}^{n}\sum_{t=t_i}^{T_i - 1}(X_{i,t} - \beta_0 - \beta_i - \beta_t)^2$$

$$\tau^2 \sim IG(s_1, s_2)$$

$$s_1 = a_3 + \frac{1}{2}n$$

$$s_2 = a_4 + \frac{1}{2}\sum_{i=1}^{n}\beta_i^2$$

Observation errors on diameter are sampled from

$$w \sim IG(s_1, s_2)$$

$$s_1 = a_7 + \frac{n_D}{2}$$

$$s_2 = a_8 + \frac{1}{2} \sum_{i=1}^{n} \sum_{t \in \{T_i^D\}} \left(D_{i,h,t}^{(o)} - D_{i,1.3,t} \exp\left[\alpha \left(h_{i,t}^{(0)} - 1.3\right)\right] \right)^2$$

where $\{T_i^D\}$ is the set of diameter observations on tree i.

We do not prove convergence, but extensive simulation indicates that the algorithm does converge to appropriate estimates. The latent diameter states were initialized by interpolation, subject to the constraint that there can be no decreasing diameters. The latent growth rates are initialized as the differenced initial diameter series.

For the Metropolis steps in the Gibbs sampler (e.g. updating latent diameters for the first time step, $D_{i,1}$, latent diameter increment values, $X_{i,t}$, and updating the tapering parameter, α) we generated candidates as random normal deviates around current parameter values, or time-series estimates, and accepted or rejected based on the Metropolis–Hastings ratios. We chose variances for these sampling distributions to obtain acceptance rates of between 0.1 and 0.4. The Gibbs sampler was run 500 000 iterations to insure convergence and then run an additional 500 000 iterations to obtain posterior estimates. Because of the large number of estimates for most species, we did not retain all estimates each for diameter and growth. Rather, we retained the sums and the sums of the squared diameter and log growth estimates from every twentieth Gibbs step. Because both variables were approximately Gaussian, 95% credible intervals were calculated as ± 1.96 standard deviations, which came, in turn, from first and second moments. These are the intervals shown in Figures 1 and 2. For all other parameters credible intervals are obtained as percentiles of the Gibbs output (Table 2).

Appendix 2

For the second model, which includes varying time increments, the full conditional distribution is

$$p\left(\left\{\ln D_{i,1.3,t+\Delta it}\right\} \left| \left\{D_{i,h,t+\Delta it}^{(o)}\right\}, \beta, \alpha, \sigma^2, w\right)\right.$$

$$\propto \prod_{t=t_i}^{T_i} N\left(D_{i,1.3,t+\Delta it} \left| D_{i,1.3,t} + X_{i,t}, \Delta_{i,t}\sigma^2\right)\right.$$

$$\times \prod_{h=1}^{m_i} \prod_{t=t_{i,h}}^{T_{i,h}} N\left(D_{i,h,t+\Delta it}^{(o)} \left| D_{i,1.3,t+\Delta it} \exp\left[\alpha\left(h_{i,h,t+\Delta it}^{(o)} - 1.3\right)\right], w\right)\right.$$

As above, a Metropolis sample from this distribution begins with a proposal for the first diameter value from a lognormal density that is centred on the first observation. Then all diameter increments are proposed from a truncated normal distribution (to ensure that they are positive) for the years in which individuals were alive and included in the study. Proposals are accepted on a tree-by-tree basis using the likelihood above. The conditional distribution of average growth increments in one time step X_i for individual i is

$$p\left(\{\Delta X_i\} \left| \left\{D_{i,h}^{(o)}\right\}, \beta, \alpha, \sigma^2, w\right) \propto \prod_{t=t_{i,h}}^{T_{i,h}} N\left(\Delta X_{i,t} \left| V_{i,t}v_{i,t}, V_{i,t}\right)\right.$$

$$\times \prod_{t=t_i}^{T_i} N\left(D_{i,h,t+\Delta it}^{(o)} \left| (D_{i,1.3,t} + \Delta X_{i,t}) \exp[\alpha(h_{i,t} - 1.3)], w\right)\right.$$

$$\times I(0.002\Delta_{i,t}, \Delta X_{i,t}, 7.5\Delta_{i,t})$$

where I is the indicator function, and insures that growth increments are contained between a chosen lower bound 0.002 cm y^{-1}; and an upper bound of 7.5 cm y^{-1}, and

$$V_{i,t}^{-1} = 1/(\Delta_{i,t}\sigma^2)$$
$$v_{i,t} = \mu_{i,t}/\sigma^2. \tag{13}$$

The solutions for these conditional distributions are provided in Clark (2007). For the overall mean growth rate, the conditional posterior (for simplicity not integrated over random effects), is

$$\beta_0 \sim N(Vv, V)$$

$$V^{-1} = \sum_{i=1}^{n} \sum_{t_i}^{T_i-1} \frac{\Delta_{i,t}}{\sigma^2} + \frac{1}{v_0}$$

$$v = \sum_{i=1}^{n} \sum_{t=t_i}^{T_i-1} \left(\frac{\Delta X_{i,t} - \beta_t \Delta_{i,t} - \beta_i \Delta_{i,t}}{\sigma^2}\right) + \frac{b}{v_0}$$

where n is the number of trees and t_i and T_i are the first and last measurements for individual i, and $\Delta X_{i,t}$ denotes the modelled increment obtained from Δ time steps, as above. Random individual effects are sampled from

$$\beta_i \sim N(V_i v_i, V_i)$$

$$V_i^{-1} = \sum_{t=t_i}^{T_i-1} \frac{\Delta_{i,t}}{\sigma^2} + \frac{1}{\tau^2}$$

$$v_i = \sum_{t=t_i}^{T_i-1} \left(\frac{\Delta X_{i,t} - \beta_0 \Delta_{i,t} - \beta_i \Delta_{i,t}}{\sigma^2}\right)$$

As year effects are modelled above, here we can model equivalent period effects. As there is overlap with the census intervals considered, these period effects are not confounded with the census intervals, and are identifiable. They can be sampled from

$$\beta_t \sim N(V_t v_t, V_t)$$

$$V_t^{-1} = \sum_{i \in n_i} \frac{\Delta_{i,t}}{\sigma^2} + \frac{1}{v_\kappa}$$

$$v_t = \sum_{i=1}^{n} \left(\frac{\Delta X_{i,t} - \beta_0 \Delta_{i,t} - \beta_i \Delta_{i,t}}{\sigma^2}\right)$$

We impose a sum-to-zero constraint on the period effects by subtracting the mean at each Gibbs step.

The tapering parameter, and observation error variance is sampled as above. Variance parameters are all directly sampled from inverse gamma distributions. These are

$$\sigma^2 \sim IG(s_1, s_2)$$

$$s_1 = a_1 + \frac{1}{2} \sum_{i=1}^{n} (T_i - t_i - 1)$$

$$s_2 = a_2 + \frac{1}{2} \sum_{i=1}^{n} \sum_{t=t_i}^{T_i-1} \frac{\left(\Delta X_{i,t} - \beta_0 \Delta_{i,t} - \beta_i \Delta_{i,t} - \beta_t \Delta_{i,t}\right)^2}{\Delta_{i,t}}$$

$$\tau^2 \sim IG(s_1, s_2)$$

$$s_1 = a_3 + \frac{1}{2}n$$

The Gibbs sampler was run as is detailed above.