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TREE GROWTH INFERENCE AND PREDICTION FROM DIAMETER CENSUSES AND RING WIDTHS

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Abstract. Estimation of tree growth is based on sparse observations of tree diameter, ring widths, or increments read from a dendrometer. From annual measurements on a few trees (e.g., increment cores) or sporadic measurements from many trees (e.g., diameter censuses on mapped plots), relationships with resources, tree size, and climate are extrapolated to whole stands. There has been no way to formally integrate different types of data and problems of estimation that result from (1) multiple sources of observation error, which frequently result in impossible estimates of negative growth, (2) the fact that data are typically sparse (a few trees or a few years), whereas inference is needed broadly (many trees over many years), (3) the fact that some unknown fraction of the variance is shared across the population, and (4) the fact that growth rates of trees within competing stands are not independent. We develop a hierarchical Bayes state space model for tree growth that addresses all of these challenges, allowing for formal inference that is consistent with the available data and the assumption that growth is nonnegative. Prediction follows directly, incorporating the full uncertainty from inference with scenarios for "filling the gaps" for past growth rates and for future conditions affecting growth. An example involving multiple species and multiple stands with tree-ring data and up to 14 years of tree census data illustrates how different levels of information at the tree and stand level contribute to inference and prediction.

Key words: Bayesian state space model; data assimilation; forest growth; hierarchical models; observation error; tree rings.

Introduction

Knowledge of tree growth is needed to understand population dynamics (Condit et al. 1993, Fastie 1995, Frelich and Reich 1995, Clark and Clark 1999, Wyckoff and Clark 2002, 2005, Webster and Lorimer 2005), species interactions (Swetnam and Lynch 1993), carbon sequestration (DeLucia et al. 1999, Casperson et al. 2000), forest response to climate change (Cook 1987, Graumlich et al. 1989), and restoration (Pearson and Vitousek 2001). Despite its importance, diameter growth estimates are limited due to the effort required for data collection and problems associated with inference. Estimates derive from any of three methods, diameter measurements, tree rings, and dendrometer bands, each with substantial uncertainty. The most common method involves measuring tree diameters repeatedly and calculating diameter change by subtraction. This approach has the advantages that diameters can be measured rapidly, and it can be used in environments where trees do not produce identifiable annual rings.

There are several disadvantages to diameter measurements. Although measurement is fast, nothing is learned until sufficient time has elapsed between observations to allow for a confident estimate of the increment. If interest focuses on individuals with particular growth characteristics, those individuals may not even be identifiable as such until years have passed. Because intervals between measurements can be long, annual growth rates are unknown. Instead, there is an interpolated average growth rate for the full interval (Biondi 1999). Long intervals may be needed, because diameter measurements have substantial error (Biging and Wensel 1988, Gregoire et al. 1990, Biondi 1999), enough that diameters are frequently observed to decrease (e.g., Clark and Clark 1999). Of course, growth occurs each year (even "missing rings" may not occur over the full circumference), so the apparent decline in diameter results from errors in the measurements themselves (the tape or caliper is not located at precisely the same height and orientation on the tree), from shrink and swell with changing bole moisture storage, or from changes in bark thickness that are unrelated to growth (common in pines and other thick-barked species).

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Various ad hoc remedies (discarding intervals of negative growth, adding to each observation a constant increment to insure that all increments come out positive) introduce bias, even if one simply repeats measurements only on the trees observed to have negative increments (e.g., Clark and Clark 1999). In short, diameter must have increased over the interval, but any estimate of the increment would depend on whatever ad hoc is used to make negative increments come out positive.

Two alternatives to periodic tape measurements are increment cores and dendrometer bands. They share the advantages that annual (or sub-annual) growth can be obtained. For increment cores, this growth rate applies to one radius of the tree, so several increment cores may be taken for each tree and averaged. The true area increment, i.e., integrated over the tree circumference, is not known. Further complications include the fact that trees may not have identifiable growth rings, that cores are time-consuming to obtain and analyze, and that taking multiple cores simultaneously or over time may affect tree health. In temperate environments, growth rings range from being readily identifiable (e.g., many conifers and ring-porous hardwoods) to those having rings that are often missed (e.g., many diffuse porous hardwoods). Like diameter measurements, dendrometer bands provide no information until an increment has accumulated, and the measurements depend on timing of observations, due to shrink and swell of the bole. The effort involved means that increment cores and dendrometer bands are usually obtained for sample individuals, not entire stands. However, without full information on all trees that reside within a known area, calculations of stand biomass increment rely on extrapolation.

As with many ecological analyses, this one involves several types of information (increment cores and diameter measurements). In most cases, there is different information available for each individual, depending on when it was measured, if there is an increment core, and when the increment core was taken. In the data set we describe, some of the increment cores were obtained in 1998, others in 2005 or 2006. Diameter measurements were obtained at irregular intervals. Stands were sampled in different years. Some trees have more than one increment core. If there is no increment core, how do we exploit information that might come from the full sample to make some probability statement about growth for a tree having only a few diameter measurements? If there is an increment core, how do we combine it with diameter measurements, both of which have error?

The uncertainty associated with data suggests need for inference, i.e., estimates of diameter and growth with confidence envelopes. Available methods do not apply to this problem. For diameter measurements, we can expect to have no observations for most individuals and years, and errors are unknown. For increment measurements, a fraction of trees and years may be represented. Growth rates vary among individuals, and this variation can be important (Lieberman and Lieberman 1985, Clark et al. 2003*b*). Sparse observations means that we would like to borrow information across all or part of the population as basis for "filling" the gaps. This need to share information is evident in regressions used for approximating a mean growth rate schedule for a population (Condit et al. 1993, Terborgh et al. 1997, Baker 2003). Regression methods that have been applied to this problem do not exploit the full data set (by fitting separate models for different classes of individuals) and they do not accommodate variability contributed by population heterogeneity (by not estimating tree-to-tree differences). Moreover, previous regression approaches ignore the nonindependence of observations and the time series character of data (where multiple observations accumulate for the same individuals over time), of the process (diameter-age estimation based on static assumptions concerning canopy position), or of both.

The challenges of inference carry through to prediction, which requires estimates of uncertainty in both diameter and growth rate. Due to the errors summarized above, the estimated confidence envelope for diameter in year t would overlap with that for year $t + 1$. A naïve Monte Carlo simulation of tree growth based on such estimates (drawing at random from diameter sequences) would predict negative growth in many years. The need to avoid this unrealistic outcome has spawned various ad hoc methods (e.g., Lieberman and Lieberman 1985) that involve resampling data with constraints that do not yield a predictive interval, because they are not based on a consistent probability model for the process and data.

In summary, methods are needed for combining information in a way that is consistent with knowledge that (1) growth is not negative, (2) some variation in growth is shared among years and across individuals, and (3) there are different types of observation errors associated with each data type. Moreover, given estimates of past growth, we need to know the uncertainty associated with potential for future growth. Often, the principle objective of growth estimation is the perspective it can provide on how stands may develop in the future. In light of the information available, to what extent can we predict growth trends?

In this paper, we describe a general method for estimating tree growth where multiple, but incomplete, sources of information are available and for projecting that growth forward. We develop a Bayesian state space model of growth (Carlin et al. 1992, Calder et al. 2003, Clark and Bjørnstad 2004), conditioned on the fact that actual (and unknown) growth is nonnegative, that the rate of growth is potentially informed by observations of increment width and diameter measurements, and that observations will be sparse, both within individual sequences and across the stand. The Bayesian framework allows exploitation of prior information on measurement errors and "borrowing strength" across the full data set(s), while responding to the amount, type, and observation errors associated with them. We

TABLE 1. Number of *Quercus* trees and sample sizes for each of the stands included in this analysis.

Stand	C1	C2	C3	C4	C5	CL	CU	D1	D2	Total
Beginning year	1992	1992	1992	1992	1992	2000	2000	2000	1999	
Increment observed	379	282	294	346	80	300	255	938	0	2874†
Diameter observed	874	204	571	789	112	1219	1081	1267	460	6577‡
Tree-years	3472	800	2016	2784	384	2992	2392	3344	1656	19 840§
Q. alba	12	0	0	0	1	0	0	229	65	307
Q. coccinea	25	7	1	14	0	41	44	0	0	132
Q. falcata	0	0	0	0	0	0	0	19	7	26
Q. marilandica	10	0	0	0	0	0	0	20	0	30
Q. phellos	0	0	0	0	0	0	1	18	71	90
Q. montana	88	32	99	101	0	176	173	0	0	669
Q. rubra	38	5	19	56	23	132	49	60	2	384
Q. stellata	0	0	0	0	0	0	0	41	39	80
Q. velutina	44	6	7	3	0	8	14	29	0	111
Species uncertain	0	0	0	0	0	17	18	2	0	37
Total trees	217	50	126	174	24	374	299	418	184	1866¶

Notes: Sample sizes are for each of nine stands included in this analysis of *Quercus*. Stands are located at the Coweeta Hydrologic Lab (C in stand name) or the Duke Forest (D in stand name). Beginning year is the year in which diameter measurements began; increment observed is the number of growth increments measured from increment cores; diameter observed is the number of diameters measured using a tape; tree-years is the total number of diameter estimates; and total trees is the total number of trees, not tree years.

† Total = n_I.
‡ Total = n_D.
§ Total = n.
¶ Total = n_T.

simultaneously provide estimates for every individual every year in the stand together with the stand, on average.

DATA SETS

Growth data come from nine mapped stands in the southern Appalachians and Piedmont of North Carolina (Table 1), established since 1991 for purposes of monitoring and experimental analysis of forest dynamics (Clark et al. 1998, Beckage et al. 2000, Hille Ris Lambers et al. 2005, Ibáñez et al. 2007). Multiple diameter measurements are available for all trees, obtained at intervals of one to four years. The measurements are made at breast height marked by a nail that holds a tag indicating the identifying tree number. Increment cores were obtained on a subset of trees in 1998 (Wyckoff and Clark 2002) and in 2005 (M. Wolosin, J. S. Clark, and M. Dietze, *unpublished manuscript*). The increment cores were oriented with a compass, and several cores were taken from some trees. Orientation of cores was done only for future reference in the event that a core is taken again from the same tree. Cores were mounted on a solid frame, finely sanded, and measured with a sliding stage micrometer. For purposes of demonstration we use data on six species of *Quercus* (Table 1). A full analysis of all species is reported separately (M. Wolosin, J. S. Clark, and M. Dietze, *unpublished manuscript*).

DATA MODELING

Model fitting

Due to the fact that data will typically be sparse, the model is developed to maximize the support that can be drawn across the full data set(s), while emphasizing the information for specific trees and years, when available. The level of uncertainty, as represented by a confidence envelope, reflects the combined information available for all individuals and years. Information from the full set of trees and years enters through the log mean growth rate β_0. Each individual is unique, with individual differences supported by a term for random individual effects β_{ij}, which draw on the fact that there can be multiple diameter and growth observations for specific individuals. There can be shared year-to-year variation due to climate, for example, which supports an estimate of fixed year effects β_t. By modeling each of these effects, we strike a balance between the data that can enter in one or more ways for each tree-year and the support that comes from the fact that some of the variation may be shared across the population and over time. Variation is not smoothed away: the degree of smoothing depends on the extent to which variation is shared across the data set, the size of the data set(s), and the weighting of data sets. We discuss weighting after introducing the model.

Let $D_{ij,t}$ be the diameter in centimeters of tree i in stand j in year t, and $X_{ij,t}$ be the diameter increment added between year t and $t+1$. We develop a model of growth (Fig. 1) that exploits the information on overall tree growth, with log mean for the full population β_0, random individual effects β_{ij} (how tree ij 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). Because growth must be positive, we model log increments,

$$\ln(X_{ij,t}) \equiv \ln(D_{ij,t+1} - D_{ij,t}) = \mu_{ij,t} + \varepsilon_{ij,t} \qquad (1)$$

as a linear equation with population log mean growth rate β_0, random individual effect β_{ij}, year effect β_t, and

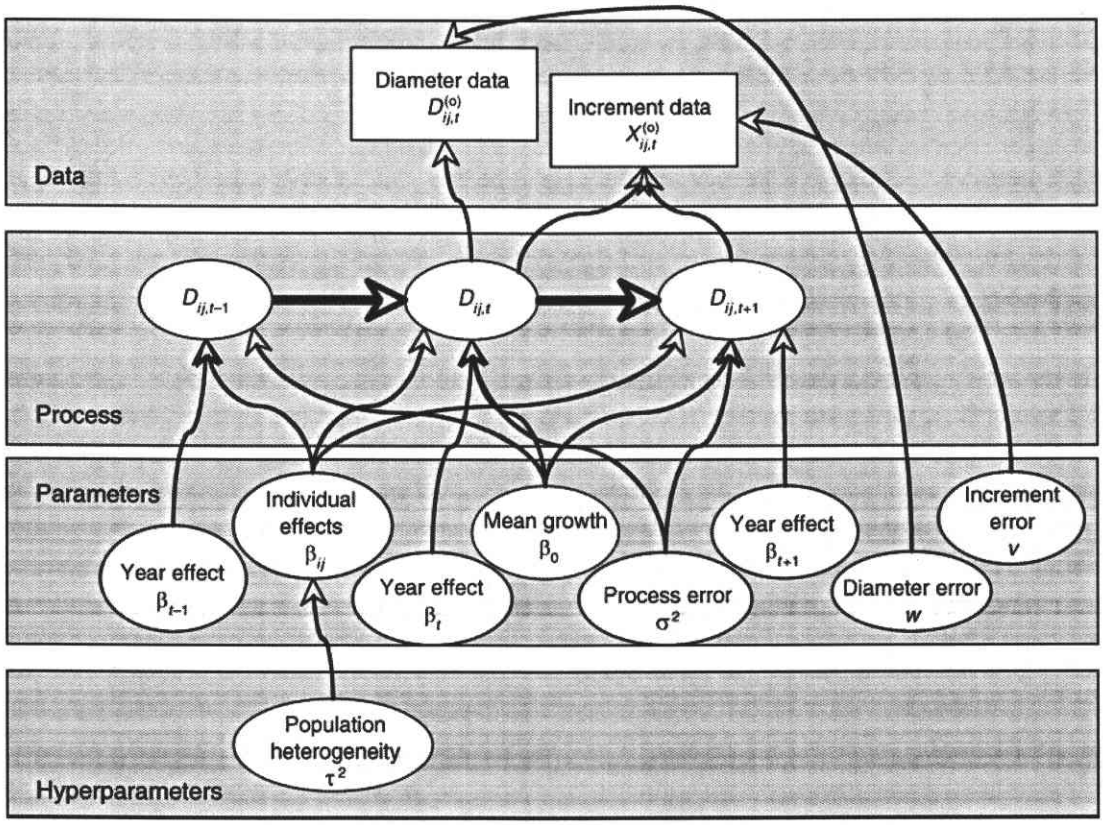

FIG. 1. Graphical representation of the model. The main process to be modeled is represented by the change in diameter ("Process" box). For each tree and year there may be diameter data, increment data, or both ("Data" box). Diameter growth depends not only on data, but also on parameters ("Parameters" box), allowing for population heterogeneity ("Hyperparameters" box).

process error $\varepsilon_{ij,t}$:

$$\mu_{ij,t} = \beta_0 + \beta_{ij} + \beta_t \tag{2}$$

$$\beta_{ij} \sim \mathcal{N}(0, \tau^2) \tag{3}$$

$$\varepsilon_{ij,t} \sim \mathcal{N}(0, \sigma^2). \tag{4}$$

"Process error" $\varepsilon_{ij,t}$ 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:

$$\begin{aligned} \beta_0 &\sim \mathcal{N}(b, v_0) \\ \beta_t &\sim \mathcal{N}(0, v_t) \\ \sigma^2 &\sim \mathrm{IG}(a_1, a_2). \end{aligned} \tag{5}$$

Random individual effects add an additional stage with variance having the prior

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

Use of the inverse gamma prior for variances is discussed in Clark (2007).

The beginning of the study is defined as the year when diameter data were first collected for the individual, t_{ij}. We define the end of the study T_{ij} as the time when the most recent diameter data were collected (2006) or individual i in plot j dies, whichever comes first. We model the data on a tree-by-tree basis for all years t between t_{ij} and T_{ij}. Prediction beyond year T_{ij} is discussed in the next section.

Assimilation of multiple data types, combined with the constraint that growth is nonnegative is accomplished with Gaussian observation error on log diameter measurements $D^{(o)}_{ij,t}$,

$$\ln\left[D^{(o)}_{ij,t}\right] \sim \mathcal{N}\left(\ln(D_{ij,t}), w\right) \tag{6}$$

and on growth increment,

$$\ln\left[X^{(o)}_{ij,t}\right] \sim \mathcal{N}\left(\ln(X_{ij,t}), v\right). \tag{7}$$

(In cases where shrinkage of cores due to moisture loss introduces bias, a parameter can be added to accommodate it in the model for increment core data; see Appendix.) Thus, the latent state variable $D_{ij,t}$ is conditionally dependent on observations that might be available for diameter $D^{(o)}_{ij,t}$, for the growth increment $X^{(o)}_{ij,t}$, or both, and on the unknown states $D_{ij,t-1}$ and $D_{ij,t+1}$, which will also be modeled. A full discussion of this structure is contained in Clark (2007).

Nonindependence of data is accommodated by the stochastic treatment of the underlying process. We are jointly modeling growth of interacting plants. It has long been known that growth rates of competing plants cannot be treated as independent observations (e.g., Mitchell-Olds 1987). A simple analysis of multiple interacting trees would violate this most fundamental assumption about the distribution of data. Our hierarchical approach accommodates correlations among observations (both within and among trees), because those relationships are taken up at the process stage. Consider a single tree-year for which there are both increment and diameter data. Here is their joint probability (conditioned on the rest of the model):

$$\begin{aligned} p[D^{(o)}_{ij,t}, X^{(o)}_{ij,t}, D_{ij,t}] &= p[D^{(o)}_{ij,t}, X^{(o)}_{ij,t}|D_{ij,t}]p(D_{ij,t}) \\ &= p[D^{(o)}_{ij,t}|D_{ij,t}]p[X^{(o)}_{ij,t}|D_{ij,t}]p(D_{ij,t}) \\ &= \mathcal{N}\left(\ln[D^{(o)}_{ij,t}]|\ln(D_{ij,t}), w\right) \\ &\quad \times \mathcal{N}\left(\ln[X^{(o)}_{ij,t}]|\ln(D_{ij,t+1} - D_{ij,t}), v\right) \\ &\quad \times \mathcal{N}\left(\ln(D_{ij,t+1} - D_{ij,t})|\mu_{ij,t}, \sigma^2\right). \end{aligned}$$

The densities in the last line are, respectively, diameter data model, increment data model, and process model. The two data models are connected by way of their relationship to the process model. If $D_{ij,t}$ is not stochastic, we cannot claim that the two data types bring new information. Each is just a deterministic transform of the other. Placing independent data models on each would be inconsistent. This incorrect assumption is implicit if we replace the third factor (a density) with a constant value. Once we admit uncertainty in $D_{ij,t}$ we allow for the possibility of conditional independence between data types: both data types might have errors that are independent (conditional on $D_{ij,t}$), because errors in measuring tree rings are unrelated to errors in measurements of tree diameter.

Stochasticity in our process model includes process error and random effects (Eqs. 1–4). The random effects could be spatial, involving inter-tree distances. If such an effect were evident, we could have included part of this interdependence as a fixed effect, using a competitive index involving size and distance. Had we included such a fixed effect, we would still want to explore additional random effects that are not accommodated by such indices. We did not include such effects in this model, because there are no trends in diameter increments in our data that are correlated with distances among trees or locations within stands. Clark (2007) provides an example showing how the spatial random effect can be modeled with Bayesian kriging. Although there is no spatial pattern in random effects for these data, variation among individuals cannot be ignored. Here, the variation is large, albeit not well described by simple spatial relationships. The fact that random effects are nonspatial (no evidence of a crowding effect on growth) is not surprising. With few exceptions, all trees in this analysis are crowded. Had we analyzed a data set with a range of crowing levels we would expect to see a spatial trend in random effects.

Prior parameter values allow for a weighting of the multiple data types, and they admit knowledge of the approximate ranges of variability in measurements to be expected. Priors for observation errors are conjugate inverse gamma:

$$v \sim \mathrm{IG}(a_5, a_6) \tag{8a}$$

$$w \sim \mathrm{IG}(a_7, a_8). \tag{8b}$$

There is a natural weighting that comes from measurement errors. To see this, consider the conditional posterior for a growth increment $X_{ij,t} = D_{ij,t+1} - D_{ij,t}$, for which there exist an increment measurement and diameter measurements for year t and $t + 1$:

$$\begin{aligned} p(X_{ij,t} \cdots) \propto\ & \mathcal{N}\left(\ln(X_{ij,t})|\mu_{ij,t}, \sigma^2\right)\mathcal{N}\left(\ln[X^{(o)}_{ij,t}]|\ln(X_{ij,t}), v\right) \\ & \times \mathcal{N}\left(D^{(o)}_{ij,t}|D_{ij,t}, w\right)\mathcal{N}\left(D^{(o)}_{ij,t+1}|D_{ij,t+1}, w\right). \end{aligned} \tag{9a}$$

By contrast, the conditional posterior for a growth year with no observations is

$$p(X_{ij,t} \cdots) = \mathcal{N}\left(\ln(X_{ij,t})|\mu_{ij,t}, \sigma^2\right). \tag{9b}$$

For a tree increment with both types of observations (Eq. 9a), (1) diameter measurements $D^{(o)}_{ij,t}$ will have large impact if their variance w is small (Eq. 6), (2) increment measurements $X^{(o)}_{ij,t}$ will have large impact if their variance v is small (Eq. 7), and (3) the degree to which the estimate will be influenced by the full data set will increase with decreasing variance σ^2 (Eqs. 1 and 2). Prior information not only informs these estimates, but it also weights their contributions. We select priors that bring in what is known about the measurement errors w and v, but weight both to insure that measurements dominate over the population model (Eqs. 1 and 2). In other words, we want the relationship between w and v to reflect what is known about errors in both observations, while insuring that both carry much more weight than σ^2. This is a subjective decision to emphasize blending of data, rather than smoothing over variability. With this approach the process model has most impact for tree years having no data. From multiple measurements of trees and increment cores (e.g., Wyckoff and Clark 2005; M. Wolosin, J. S. Clark, and M. Dietze, *unpublished manuscript*) we know standard deviations are approximately 1 cm and 0.01 cm, respectively. Variances are on a log scale in the model, reflecting the fact that errors proportionately increase with tree diameter and decrease with increment

width (values $\ll 1$). Diameter measurements with an error variance of 1 cm have a variance on log error from 0.0004 (50 cm diameter trees) to 0.01 (10 cm diameter trees). Increment measurements with an error variance of 0.0001 (standard deviation of 0.01 cm) have a variance on log increment from 0.001 (0.3 cm increment) to 0.01 (0.1 cm increment). Thus, informative priors can be centered on 0.001 to 0.01 for both types of data. We used priors for these variances with mean values of 0.01 (v) and 0.001 (w). Posteriors are insensitive to the precise values of these priors. We then weight these variances such that each is 10 times the number of observations:

$$a_5 = 10n_{\mathrm{I}}$$
$$a_6 = 0.01(a_5 - 1)$$
$$a_7 = 10n_{\mathrm{D}}$$
$$a_8 = 0.001(a_7 - 1)$$

where n_{I} and n_{D} are the number of increment and diameter observations, respectively (Table 1). This weighting is based on moment matching (Clark 2007). By contrast, we use a large prior mean on σ^2 of 1, and weight it to be 100 times less than the number of tree years:

$$n = \sum_{ij}(T_{ij} - t_{ij}) = 19\,840$$
$$a_1 = n/100$$
$$a_2 = a_1 - 1.$$

Because n is large, we effectively downweight the population model (Eqs. 1 and 2) to insure minimal smoothing. This will dominant for tree years for which there are no observations (Eq. 9b).

Other priors are proper, but noninformative. The prior on log mean growth rate has mean and variance $b = -2$ (i.e., a prior mean growth rate of $e^{-2} = 0.13$ cm/yr) and $v_0 = 1 \times 10^7/n$. This prior is 1×10^7 times weaker than the sample size (total number of tree years). The prior mean for the variance of random effects τ^2 was set to an arbitrary value of 1, and weighted roughly 0.01 of the data. This is accomplished with $a_3 = n_{\mathrm{T}}/100$, where n_{T} is the number of trees (Table 1). Year effects β_t have prior mean zero and $v_t = 1$. Posterior distributions were not influenced by the mean values selected for β_0, τ^2, and β_t, because priors were weak.

Analysis of the model is accomplished by Gibbs sampling (Gelfand and Smith 1990), implementation of which is discussed in the Appendix.

Prediction

We use a Bayesian prediction framework to forecast growth several years ahead. The predictive density for diameter one year ahead is represented by the integral

$$p\left(D_{ij,T_{ij}+1} \middle| \left\{D^{(\mathrm{o})}_{ij,t}\right\}, \left\{X^{(\mathrm{o})}_{ij,t}\right\}, \beta^*\right) = \iint p\left(D_{ij,T_{ij}+1} \middle| \left\{D^{(\mathrm{o})}_{ij,t}\right\}, \left\{X^{(\mathrm{o})}_{ij,t}\right\}, \beta^*_{T_{ij}+1}, \theta\right) \times p\left(\theta \middle| \left\{D^{(\mathrm{o})}_{ij,t}\right\}, \left\{X^{(\mathrm{o})}_{ij,t}\right\}\right) p(\beta^*_{T_{ij}+1} | \beta^*) d\theta d\beta^*_{T_{ij}+1} \quad (10)$$

where

$$\theta \equiv [\{D_{ij,t}\}, \{\mu_{ij,t}\}, \beta_0, \{\beta_{ij}\}, \{\beta_t\}, \sigma^2, \tau^2, w, v]$$

is the set of parameters and latent variables estimated from the model, and $p(\theta \mid \{D^{(\mathrm{o})}_{ij,t}\}, \{X^{(\mathrm{o})}_{ij,t}\})$ is the joint posterior, conditioned on all diameter and increment data. To simplify notation, we have omitted the prior parameter values from the left hand side of Eq. 10. This predictive distribution mixes over the uncertainty in parameter estimates (the inner integral is taken over the posterior), and over the uncertainty in the scenario for the year $T_{ij} + 1$. The scenario is expressed in terms of the effect for the upcoming year, $\beta^*_{ij,T_{ij}+1}$, the uncertainty of which is described by density $p(\beta^*_{ij,T_{ij}+1} \mid \beta^*)$ and written conditionally to remind us that the prediction will depend on whatever assumptions β^* went into the construction of this scenario. The outer integral incorporates this scenario uncertainty (Draper et al. 1999, Clark 2007). The scenario could involve assumptions about growth conditions in future years, expressed in terms of the density $p(\beta^*_{ij,T_{ij}+1} \mid \beta^*)$. In fact, we do not actually solve this integral, but rather use Monte Carlo simulation. Using the same approach, we can predict further ahead, expecting the uncertainty to increase as we consider years further into the future. This uncertainty magnifies if we allow that the uncertainty in growing conditions (the scenario $\beta^*_{ij,T_{ij}+k}$, where k is taken in years) might likewise increase. Because we expect predictive capacity to decline, we limit predictions to a lead time of $k = 10$ yr.

Results

Several parameters describe a population-wide pattern in the data. In this analysis of 10 *Quercus* species (Table 1), all parameters are well identified, as indicated by narrow credible intervals (Table 2). Error parameter estimates reflect priors. The informative prior insures that the posterior estimate of σ^2 is centered at the large value of 1. Large weights on w and v insure that they dominate for individuals and years with observations. The standard deviation for random individual effects τ had a posterior mean of 0.536, substantially lower than the prior mean value, and selected to be non-informative.

There is substantial shared variation represented by year effects (Fig. 2). The range of these estimates (−0.2 to 0.2) is roughly the magnitude of random individual effects. Posterior estimates indicate trends across years. Such clear evidence of temporal coherence suggests covariates (e.g., climate), which can be readily included in the regression part of the model (M. Wolosin, J. S.

TABLE 2. Parameter estimates for the model of data sets in Table 1.

Parameter	Prior parameter values	Posterior mean	Bayesian SE	Credible interval 2.5%	Credible interval 97.5%
β_0	$b = -2$, $v_0 = 504$	−2.10	0.0139	−2.13	−2.07
σ	$a_1 = 198.4$, $a_2 = 197.4$	0.945	0.00297	0.939	0.950
τ	$a_3 = 18.7$, $a_4 = 17.7$	0.536	0.0134	0.511	0.563
$\sqrt{w}$	$a_7 = 65\,770$, $a_8 = 6.58$	0.0316	0.00000617	0.0316	0.0316
$\sqrt{v}$	$a_5 = 24\,780$, $a_6 = 247.8$	0.224	0.000649	0.222	0.225

Clark, and M. Dietze, *unpublished manuscript*). To determine whether this trend came from incorporating data sets spanning different intervals, we analyzed stands spanning just the full 14 years and found that the trend persisted.

Because our goal focuses on predicting missing and future values for growth, we do not include covariates in Eqs. 1 and 2 (we do so in J. S. Clark, M. Dietze, I. Ibáñez, S. LaDeau, and M. Wolosin, *unpublished manuscript*). With more complex models, we can entertain model selection, which is typically done using an index that incorporates goodness of fit and penalty for model complexity. There are no generally accepted model selection techniques, and there are reasons to minimize the role of formal model selection (Clark 2005, Clark and Gelfand 2006). We include one technique here, predictive loss (Gelfand and Ghosh 1998), which is discussed for ecological applications by Clark (2007) and for state-space models in particular by Clark and Bjørnstad (2004). The index is described in the Appendix.

It is no surprise that the model predicts the data well (Fig. 3), because data are highly weighted (*Data Modeling*). The slight tendency for the data cloud to have a shallower slope than 1:1 in Fig. 3 is the familiar "regression to the mean" effect, whereby there is at least some smoothing brought in by Eqs. 1 and 2 tending to smooth over extreme high and low values. It is important to emphasize again, that this is simply an effect of the weighting in the model: we could fit the data even more closely by applying still more weight to data over Eqs. 1 and 2. There is a limit to how "good" the fit can be, determined by the level of disagreement between the two data types. If there were only one data type, we could fit the data precisely. Again, the goal is to predict missing data and not to necessarily find a simple model that fits every observation. For model selection, one might consider the criterion D_m for this model vs. one with, say covariates. Because there are multiple data sets (two, in this case), there can be multiple D_m values to consider (Fig. 3).

The ways in which multiple data sets inform the analysis is best illustrated with concrete examples. In Fig. 4, we present estimates of both diameter and growth rate for example trees having different levels of information and agreement. Trees differ in terms of estimated growth rate as indicated by the slopes of diameter estimates at left and the different rates shown at right. Tight credible intervals indicate confident estimates for trees where there is substantial data of both types, and these data tend to "agree" on the rate of growth of that individual. All possibilities are illustrated in Fig. 4. A *Q. rubra* tree (Fig. 4a) has especially tight credible intervals on diameter, because there are no increment data to contradict diameter data, and the tree is growing at a rate close to the overall population. A different *Q. rubra* tree (Fig. 4b) shows tight predictive intervals on growth rate until the growth increment data end in 1998, at which point predictive intervals widen. A *Q. alba* tree (Fig. 4c) has only two diameter measurements, meaning that estimates rely heavily on the full population, which has large uncertainty. Fig. 4d, e

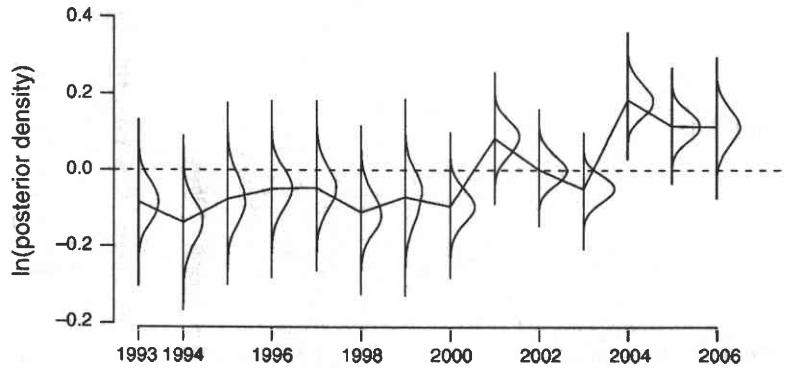

FIG. 2. Posterior densities for each year effect, with a solid line connecting the posterior means, show a trend from negative to positive over the course of the study, 1993–2006. With the exception of drought years in the early 2000s, recent growth rates tend to be higher than during the 1990s. The log-transformed year effect was originally measured in cm.

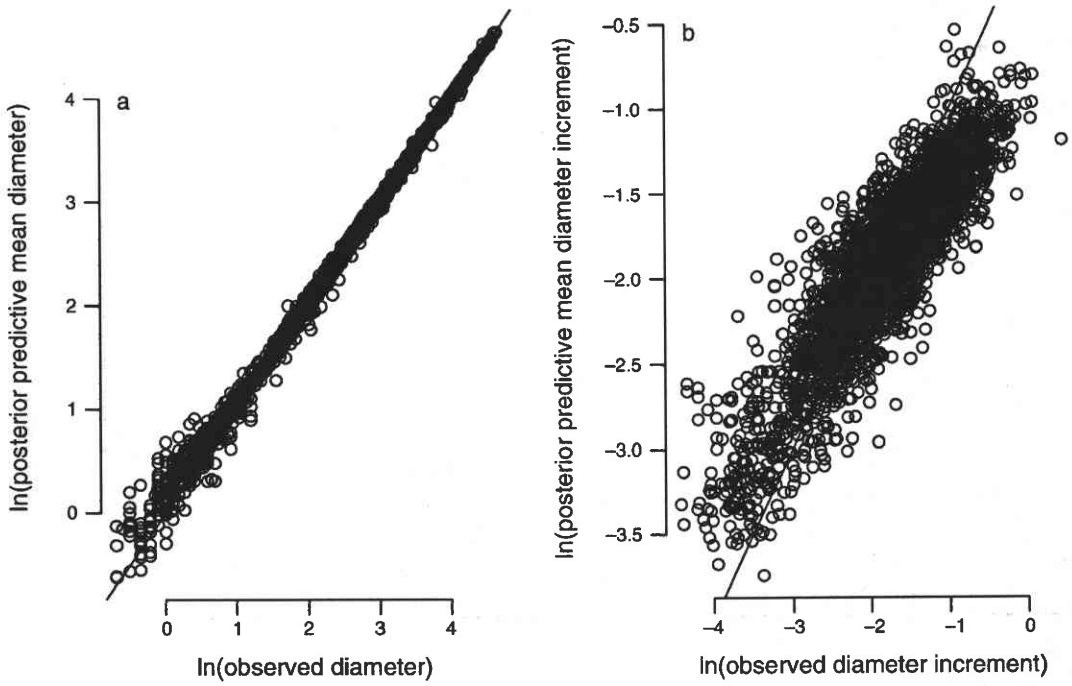

FIG. 3. Observations and predictive means for all tree-years in which at least one observation was available. (a) The predictive loss values for diameter data are $G_m = 25.8$, $P_m = 30.5$, and $D_m = 56.1$; and (b) for diameter increment data are $G_m = 489$, $P_m = 2786$, and $D_m = 3275$. Log-transformed diameter and diameter increment were originally measured in cm. Definitions of variables: D_m, predictive loss; G_m, predictive mean; P_m, predictive variance.

contrasts situations where there is substantial data of both types, one where they agree (Fig. 4d) and one where diameter data imply faster growth than increment data (Fig. 4e). Fig. 4f shows an example where diameter data decline over all measurements, and growth rates are predicted to be low, but positive.

Due to relatively small error terms, predictive intervals for further growth do not expand much beyond the credible intervals for the fitted data set (Fig. 5). We used two scenarios for predictions, both assuming that year effects continue with the same mean, one with the standard deviation remaining constant

$$\beta^*_{ij,T_{ij+k}} \sim \mathcal{N}\left(0, \mathrm{var}(\beta_t)\right) \tag{11a}$$

and another with the standard deviation increasing linearly with lead time k

$$\beta^*_{ij,T_{ij+k}} \sim \mathcal{N}\left(0, \mathrm{var}(k\beta_t)\right) = \mathcal{N}\left(0, k^2\mathrm{var}(\beta_t)\right) \tag{11b}$$

where the variance in year effects is taken over the posterior estimates all years. The variances in Eqs. 11a, b simply use the variance among estimates of β_t from the analysis, i.e., var[β_t]. Because year effects were relatively small in this data set, the two scenarios did not show much difference and only that for Eq. 11a is presented. Of course, there are many scenarios that could be examined; this example is for demonstration.

Parameter error makes an inconsequential contribution to both credible and predictive intervals. This result implies that collecting more data, in an effort to sharpen estimates of parameters in Table 2, would not improve predictive capacity, as has been previously demonstrated for dispersal (Clark et al. 2003*a*) and demographic rates (Clark 2003). However, it would improve estimates of diameter and growth rate for the individual trees (Fig. 4), providing observations for tree years that do not currently have them. In other words, the principle value of collecting more data would be to fill gaps in past growth rates, rather than improving parameter estimates.

The variation among individuals is large indicating the importance of allowing for individual level variation in the model (Fig. 6). This means that much of the variability is structured among individuals. In other words, population variability exceeds variation in time, a result that can contrast with fecundity, where the opposite can be the case (Clark et al. 2004).

DISCUSSION

Tree growth represents an important archive of environmental variation, population dynamics, and species interactions. The portioning of growth variation within and among individuals, and its relationship to local crowding and resources and to regional climate fluctuation, can only be understood with models that accommodate variability in the underlying growth process. Models must also allow proper treatment of the ways in which different data types relate to growth. There is general agreement that valuable growth information can come from multiple sources. Tree ring

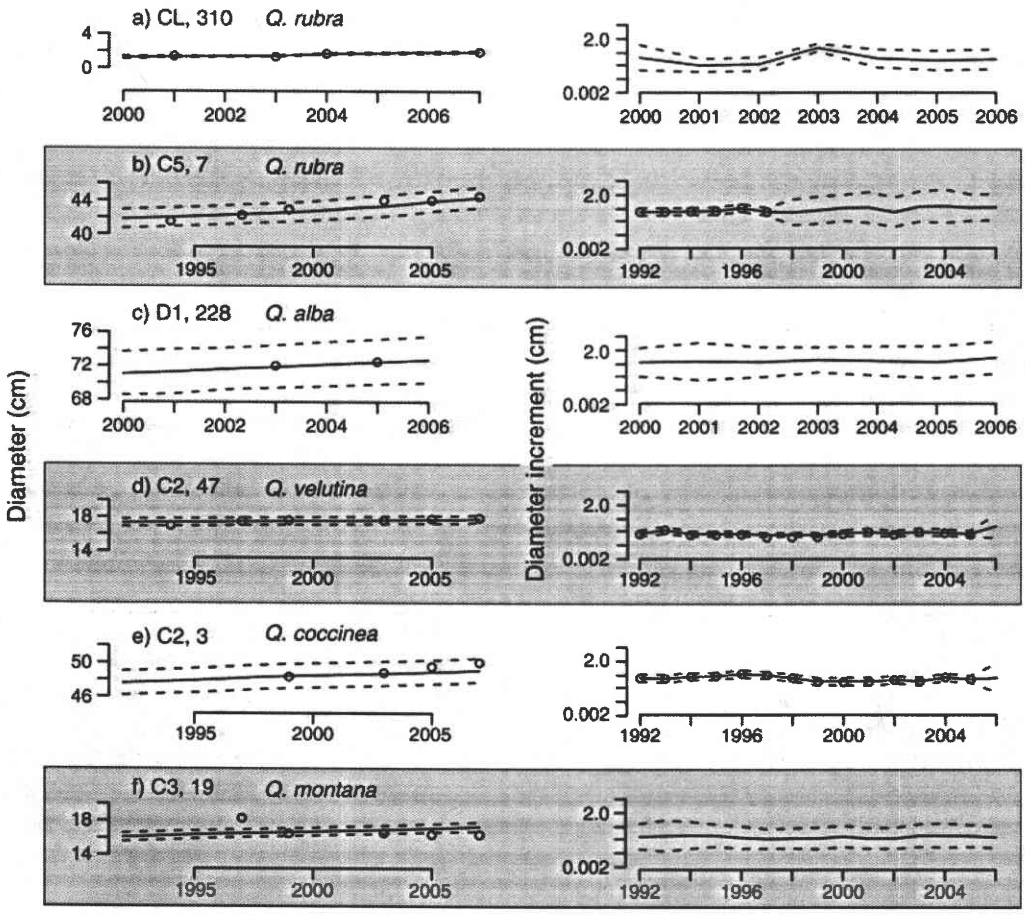

FIG. 4. Diameter and growth rates (diameter increment) for example trees having different amounts and combinations of observations (open circles) over sample years. Predictive intervals of diameter (left) and growth rate (right) are indicated by the predictive median (solid lines) and 95% predictive intervals (dashed lines). Diameter increments are on a log scale. The label for each panel consists of the stand designation from Table 1 followed by the nominal tree number.

data should not be analyzed in isolation of diameter measurement data. There has been no consistent method to combine these sources that allows for their different types of errors and for realistic assumptions about the growth process, such as growth must be positive, some variation is shared among individuals across years (e.g., climate variation), other variation is associated with specific individuals (e.g., genotype and local microsites), and there will be residual "process error."

Advantages of the approach

The modeling strategy developed here allows for full assimilation of increment and diameter information as basis for inference and prediction of tree growth. The approach works for either data type alone, or they can be combined in a manner that is consistent with how tree growth occurs and with how observations are obtained, a goal that has previously only been addressed informally (e.g., Biondi 1999). Credible and predictive intervals provide intuitive interpretations for how much is known about each individual and year (Fig. 4). This is especially important in light of the fact that tree growth data will typically be sparse. Even the large mapped tree plots involving tens of thousands of individuals (e.g., Condit et al. 1993) have observations only for a subset of years. The flexible method described here admits distributional assumptions that are transparent and tailored to the specific relationships. The "negative growth" that is commonly observed (e.g., Fig. 4f), especially when diameter observations at taken at frequent intervals (e.g., Clark and Clark 1999), is fully accommodated by the model, which allows that growth must be nonnegative, and both process and observations are uncertain. Our only assumption is that diameter in year t lies somewhere between that of years $t-1$ and $t+1$. Within that interval, growth conditionally depends on both types of observations (if available), population, individual, year effects, and uncertainty. It provides inference (Fig. 4) and prediction (Figs. 4 and 5) at both the individual (Lieberman and Lieberman 1985, Baker 2003) and the stand scale (Condit et al. 1993, Terborgh et al. 1997) by integrating over the full uncertainty associated with observation errors and growth rates of all trees in all stands. Predictions follow in a consistent fashion from data (Fig. 5).

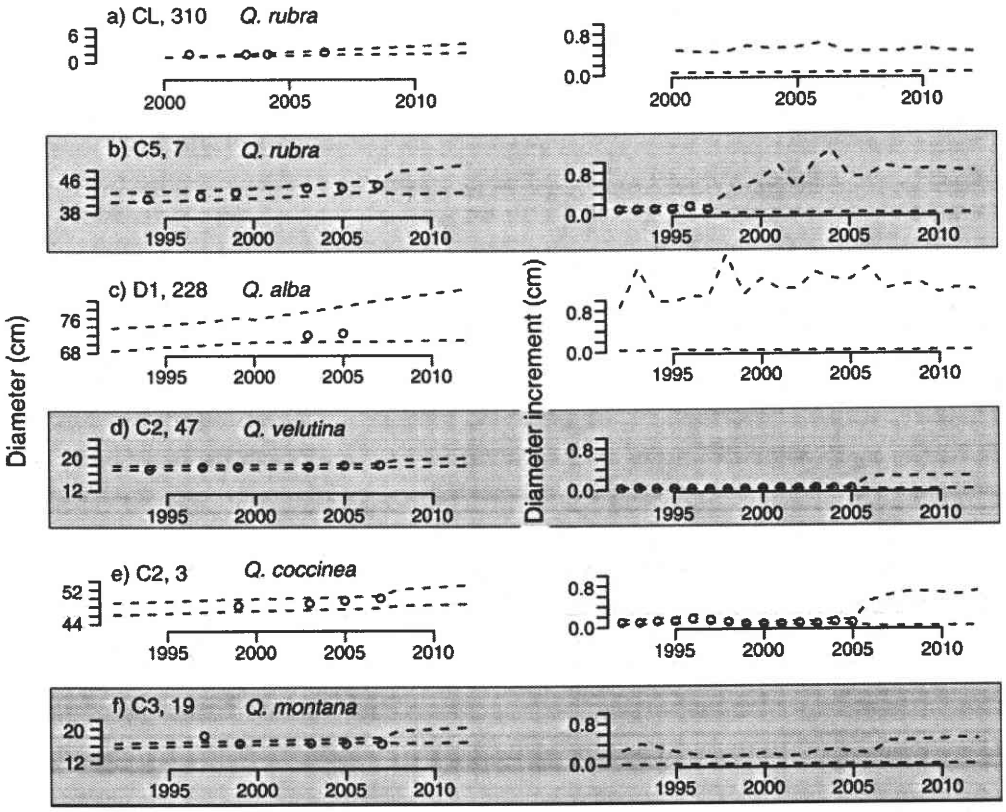

FIG. 5. Predictive intervals for example trees in Fig. 4, showing 10 years ahead. Unlike Fig. 4, diameter increments in this figure are shown on a linear (not log) scale. The label for each panel consists of the stand designation from Table 1 followed by the nominal tree number.

The capacity to identify where the uncertainty lies can guide research. For the example included here, parameter error is not an important source of uncertainty, so collecting more data will not narrow the predictive interval for many trees, only those for which few data are already available, i.e., by filling in data gaps. The widths of credible intervals are largely controlled by errors in data and the process, not in the estimates of parameters themselves.

Although not taken up here, our approach allows for a wide range of options. It readily admits covariates, including crown class observations, such as those used by Clark and Clark (1999), Baker (2003), and Wyckoff and Clark (2005). We could just as easily have modeled stands and species independently, or we could have included terms for one or both in Eqs. 1 and 2. For example, random stand effects could be included in the same fashion as random individual effects. The latter approach is used by Clark et al. (J. S. Clark, I. Ibáñez, S. LaDeau, and M. Wolosin, *unpublished manuscript*) in an extension for tree allocation.

Relationship to traditional methods for tree growth time series

Although our approach appears to overlap with tradition methods applied to tree ring time series, they are more complementary than overlapping. The practice of cross-dating increment cores from different or the same trees can be especially important and productive in environments where interannual variability is large and caused by climate (there is synchronicity across the population at some spatial scale). In our analysis, this source of variation would be taken up by year effects, β_t. A difference here is that we estimate the year effects along with all other parameters of the model, so we have an explicit credible interval for each year. Our approach can be applied just as readily to cross-dated series as it is to non-crossdated series.

Several types of modeling are often applied to tree ring data for purposes of highlighting (or removing) specific scales of variation. Autoregressive (AR) models are a common example (Cook 1987). There are several points to make here. First, our model is effectively an AR(1) model (an AR model of lag 1) due to the fact that we are modeling increments. Second, fixed year effects are used here in preference to autoregression. We adopt this approach, because we wanted year effects to take up interannual forcing, whether or not it is correlated from year to year. For example, climate variation might be sometimes autocorrelated (e.g., multiyear droughts, decadal trends in temperature) and sometimes not. The fixed effects included in our model accommodate both.

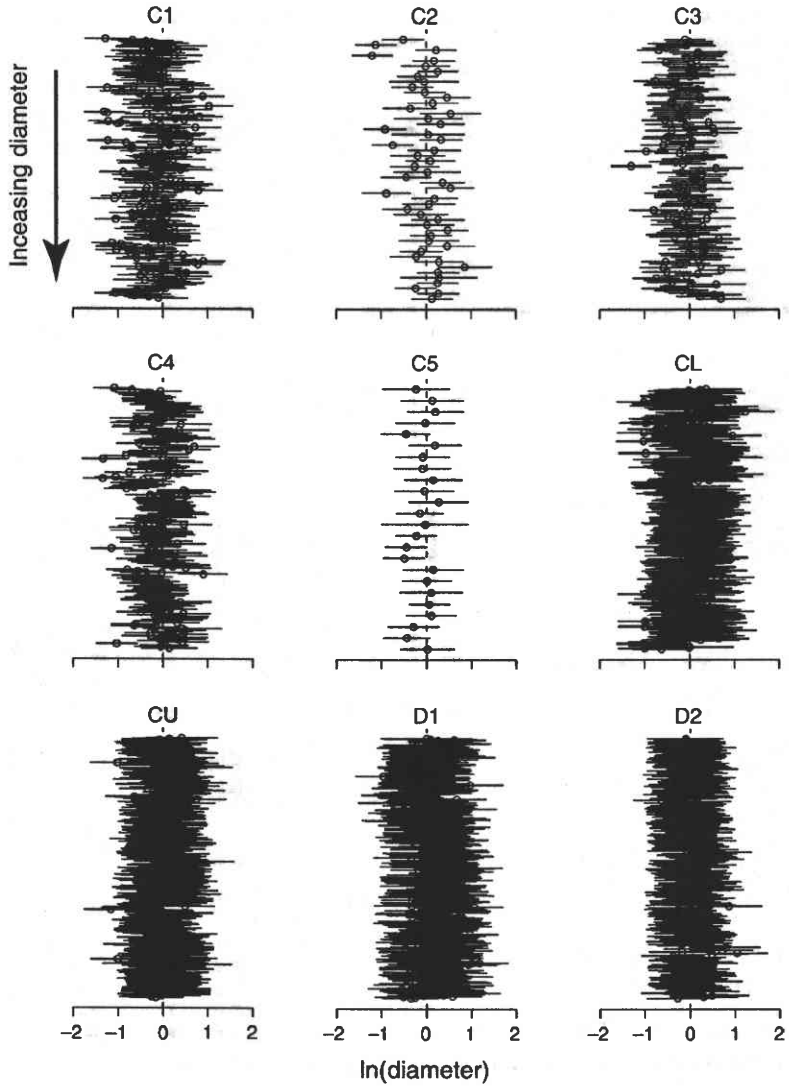

FIG. 6. Uncertainty in estimates of individual effects. Although the point estimates span a broad range above and below zero (open circles are posterior means), the 95% credible intervals for each individual are also large (horizontal lines). The estimates are ordered according to increasing diameter; there is no trend in the individual effect with diameter.

Indeed, we can inspect the posterior estimates of year effects to determine if autocorrelation exists (they do in the example provided here). Likewise, interannual climate variation can itself be included in the model (M. Wolosin, J. S. Clark, and M. Dietze, *unpublished manuscript*). Finally, because our emphasis is on short-term effects, as opposed to decade- to century-scale climate variation, we have not analyzed particular scales of variation in the data. Nonetheless, the simple regression at the core of our model is flexible to a wide range of assumptions. These could include diameter and/or age covariates, if we wished to model reductions in ring width that can occur with size or age (e.g., Swetnam and Lynch 1993). The common practice in dendrochronology of removing long-term trends, due to tree size or age, can be readily incorporated into Eq. 2.

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APPENDIX

Tree growth inference and prediction (*Ecological Archives* A017-077-A1).