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Estimating tree growth from complex forest monitoring data

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Abstract. Understanding tree growth as a function of tree size is important for a multitude of ecological and management applications. Determining what limits growth is of central interest, and forest inventory permanent plots are an abundant source of long-term information but are highly complex. Observation error and multiple sources of shared variation (spatial plot effects, temporal repeated measures, and a mosaic of sampling intervals) make these data challenging to use for growth estimation. We account for these complexities and incorporate potential limiting factors (tree size, competition, and resource supply) into a hierarchical state-space model. We estimate the diameter growth of white fir (*Abies concolor*) in the Sierra Nevada of California from forest inventory data, showing that estimating such a model is feasible in a Bayesian framework using readily available modeling tools. In this forest, white fir growth depends strongly on tree size, total plot basal area, and unexplained variation between individual trees. Plot-level resource supply variables (representing light, water, and nutrient availability) do not have a strong impact on inventory-size trees. This approach can be applied to other networks of permanent forest plots, leading to greater ecological insights on tree growth.

Key words: Abies concolor; *competition intensity; hierarchical model; individual variation; Markov chain Monte Carlo; OpenBUGS; permanent plots; state-space model.*

INTRODUCTION

Understanding the limitations on tree growth is important in many ecological and management applications. Not only is tree growth a basic demographic process that profoundly influences tree population dynamics (Harcombe 1987, Metcalf et al. 2009), but it is also one of the primary means of evaluating forest management goals (Chojnacky 2001). Tree growth rates partly determine tree mortality (Das et al. 2007), and individual-based forest simulators require growth data to parameterize their models (e.g., SORTIE [Pacala et al. 1996]). Cambial growth underlies estimates of carbon sequestration (Mohan et al. 2007, Berner et al. 2011) and tree growth as a function of size is an important element in dendrochronological analysis (Bunn 2008). A tree's growth is metabolically limited by its size (Macfarlane and Kobe 2006, Coomes et al. 2011) and competition is a fundamentally limiting factor in closed-canopy conditions (Lines et al. 2010, Kunstler et al. 2011). In addition, the supply of energy, water, and nutrients (typically measured by proxies such as insolation, water deficit, and soil type) can strongly limit tree growth and can mask density dependence (He and Duncan 2000). Permanent forest plot data are an ideal way to learn about growth limitation. Typically these data include tagged trees whose diameter at breast height (dbh, breast height = 1.37 m) is measured at regular intervals. Changes in dbh are often used to measure tree growth (e.g., U.S. Forest Service Forest Inventory and Analysis network and Smithsonian Center for Tropical Forest Science network).

Unfortunately, long-term monitoring data are typically highly complex, including observation error, missing data and uneven time intervals, spatial nesting and autocorrelation, and repeated measures on the same individuals. Most typical statistical models cannot account for all of these issues. More sophisticated hierarchical models can incorporate these shared sources of variation as well as the error inherent in the observations (e.g., Royle and Dorazio 2008, Cressie et al. 2009, Ponciano et al. 2009, Clark et al. 2010). Hierarchical models can accommodate nested random effects to account for correlations between measurements from the same site, the same plot within site, or the same individual, as well as incorporating crossed random effects for different years. In addition, we can explicitly model measurement error by treating the unmeasured, true sizes as "latent states" that are statistically related to measured sizes. Freely available software (e.g., lme4 in R [Bates and Maechler 2010], OpenBUGS [Lunn et al. 2009]) and multiple textbooks on hierarchical modeling (Clark 2007, Royle and Dorazio 2008, Kery 2010, Kery and Schaub 2012) place this set of tools in the hands of managers and ecologists, allowing them to make better use of complex long-term data sets.

Previous work using hierarchical models with forest inventories has addressed many spatial and temporal

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particulars of these data, as well as inevitable observation error. Spatial autocorrelation is a chief issue in permanent plot data, and has been accounted for using correlated spatial random effects in Banerjee and Finley (2007) and Finley (2011). One temporal issue in inventory data is the difficulty of inferring annual growth rates from tree diameter censuses taken at longer and sometimes uneven time intervals. Gregoire et al. (1995) used a continuous-time temporal autocorrelation between measurements to account for these uneven intervals, but comment that their measure of elapsed time as a distance measure may not be meaningful. This temporal mosaic of sampling intervals is common in permanent plot networks as it can be difficult to maintain regular measurement intervals. Even if regular intervals are maintained in any particular network, mismatched time intervals are inevitable when analyses include data from different plot networks. Diameter censuses are easy to execute and typically can include many trees, but are prone to errors due to improper diameter tape placement and bark loss. Therefore, unrealistic negative growth increments are common and many ad hoc methods are used to account for this issue (e.g., by adding an arbitrary amount to all growth increments, which biases estimates toward larger annual growth rates). A way of realistically accounting for observation error is needed (Clark et al. 2007). Previous studies have balanced the strengths and weaknesses of diameter censuses by estimating hierarchical models combining diameter measurements on all trees in some years with tree ring data on some trees in all years in order to infer annual growth (Clark et al. 2007, 2010). Some of these studies include tree size and limiting factors such as canopy cover and climate variables (Clark et al. 2010, 2011, 2012). Other studies have incorporated random effects for spatial nesting with measures of competition and methods of accounting for uneven time intervals (Weiskittel et al. 2007). But none of these existing models have demonstrated how to infer annual growth from a mosaic of sampling intervals by explicitly estimating the unmeasured sizes as well as modeling the repeated measures on individual trees as a random effect.

In this study, we develop a hierarchical model to infer annual growth rates from a mosaic of sampling intervals while incorporating multiple sources of unexplained variation. This state-space model (de Valpine 2003) includes growth as a function of tree size, resource supply, and competition; random effects to account for year-to-year variation, repeated measures on trees, and spatial nesting; and explicit modeling of unmeasured tree sizes and the associated observation error. Our model incorporates the conceptual sophistication of many previous models in such a way that these effects can be estimated simultaneously and compared. While previous studies do include limiting factors, we include interactions between tree size and both fixed and random variables to more completely incorporate size dependence in every aspect of growth, allowing us to explain which of these has the biggest impact. In addition, our model handles time by including random year effects as well as latent states. This approach results in crossed random effects between time and spatial nesting factors, which are technically challenging to estimate. Due to the combination of these crossed and nested random effects, unequal time intervals, and observation error, standard statistical analysis software packages will not suffice and we use Markov chain Monte Carlo (MCMC) to estimate parameters in OpenBUGS. We then compare the relative magnitudes of each estimated source of variation and of the effects of different explanatory variables. This case study illustrates the utility of these tools for forest monitoring data and suggests how these methods can be extended to other such data sets.

METHODS

Study site

Blodgett Forest Research Station (BFRS) is located in the central western slopes of the Sierra Nevada (38°52′ N; 120°40′ W), California, USA. The research station's 1780 ha are divided into compartments (8–80 ha each) containing plots (0.04 ha each) measured periodically to monitor forest composition and structure. (See Appendix A for number of trees, plots, and compartments in this study as well as sampling intervals.) The data we use in this study comes from the reserve compartments, which have seen no management other than fire suppression in the last 100 years. As such, the reserve compartments at Blodgett are representative of much of the western slopes of the Sierra Nevada, which have seen a similar management history and experience similar abiotic conditions.

BFRS currently consists of mature second-growth mixed conifer forest. Trees have not yet reached their maximum size, and diameter growth appears to be an approximately linear function of diameter. Due to fire exclusion in the reserve compartments, later-successional shade-tolerant coniferous species are most common. White fir (*Abies concolor*) is one of these dominant species and is becoming more dominant over time throughout the Sierra Nevada (Ansley and Battles 1998, Collins et al. 2011). Due to the fact that the forest is still recovering from a clearcut in the early 1900s (Battles et al. 2008), tree diameter is a good representation of tree canopy position. The explanatory variables we include in our model are the following: tree size (dbh) in cm, plot basal area in m^2/ha, insolation in $W \cdot h \cdot m^{-2}$, topographic slope in percent, elevation in m, annual water deficit in mm (Table 1), and categorical soil type (as a proxy for soil nutrients). We detail both the measurement methods and the auditing of these data in Appendix B.

Statistical model and estimation

Given the importance of annual growth in assessing tree performance, and that we have a mosaic of

TABLE 1. Explanatory variables.

Covariate name	Mean	SD	Minimum	Maximum	Units	Level
Insolation	628 688.10	36 106.87	499 531.88	692 878.06	$\mathrm{W{\cdot}h{\cdot}m^{-2}}$	plot
Slope	15.19	10.09	1.00	43.00	%	plot
Elevation	1315.73	35.48	1272.54	1450.85	m	plot
Basal area	62.02	26.17	0.90	135.48	$\mathrm{m^2/ha}$	plot/year
Annual water deficit	−174.87	66.63	−311.93	−66.67	mm	year
Tree size, dbh	30.75	20.56	0.25	131.32	cm	tree/year

Notes: Soil is categorical and is not shown here, but most soil types originate from granites, and Cohasset is more developed than the Holland soil family. See Appendix B for details on soils and other explanatory variables.

sampling intervals for different trees, we choose an annual time step t for our model. Our statistical model for tree growth in each year is hierarchical at several levels. In all the following formulae, subscript i is for compartment, j is for plot, and k is for tree. Superscript m indexes the explanatory variables in Table 1. First, we represent the observation process by modeling observations of tree diameter in cm, $y_{ijk}(t)$, as a function of latent (unknown) tree size $x_{ijk}(t)$ in cm with normally distributed observation error with variance $\sigma^2_{\mathrm{dbh}} : y_{ijk}(t) \sim \mathcal{N}[x_{ijk}(t), \sigma^2_{\mathrm{dbh}}]$. Next, our process model representing annual tree growth is

$$x_{ijk}(t+1) \sim \mathcal{N}\left[\alpha_{ijk}(t) + \beta_{ijk}(t)x_{ijk}(t) + \sum_m \gamma^m z^m_{ij}(t) + \sum_m \kappa^m z^m_{ij}(t)x_{ijk}(t), \sigma^2_\varepsilon\right]. \quad (1)$$

We assume that size in the next year is a linear function of several other explanatory variables, which are denoted $z^m_{ij}(t)$ and have parameters for slope γ^m and interaction with size κ^m. The modeling framework does allow for more complex functional forms (e.g., Weiskittel et al. 2007) as needed, but our data do not warrant this complexity. The z^m are centered and scaled based on these variables as measured in our inventory. The scale of the latent states x is established using the measured inventory sizes y (see Appendix C for details on standardization). The z^m are measured at plot and/or year level: insolation, topographic slope, elevation, and soil category are all measured at plot level, i.e., z^{insol}_{ij}, z^{tslope}_{ij}, z^{elev}_{ij}, and a group of five indicator variables representing a tree's soil type (z^{C}_{ij}, z^{H}_{ij}, z^{HB}_{ij}, z^{HM}_{ij}, and z^{J}_{ij}; see soil types listed in Fig. 1) ; basal area is measured at plot and year level, $z^{\mathrm{ba}}_{ij}(t)$; and annual water deficit is measured at year level, $z^{\mathrm{def}}(t)$ (Table 1). We assume that size in the next year $x_{ijk}(t+1)$ is a linear function of size in the previous year, $x_{ijk}(t)$, with soil-type-dependent slope and intercept (e.g., for Jocal soil type, slope $b_{\mathrm{J}} = \beta_{ijk}(t) + \kappa^{\mathrm{J}}$ and intercept $a_{\mathrm{J}} = \alpha_{ijk}(t) + \gamma^{\mathrm{J}}$). In *Results*, we report the average growth increment $\bar{a}$ and average effect of size on growth increment $\bar{b} - 1$, which are weighted averages over soil types and for average values of explanatory variables. Residual error, with variance σ^2_ε, accounts for additional unexplained variation in growth.

At the next hierarchical level, we model the collective random effects on intercept $\alpha_{ijk}(t)$ and slope $\beta_{ijk}(t)$ with respect to size x as a combination of random effects for tree (q^{α}_{ijk} and q^{β}_{ijk}), plot (p^{α}_{ij} and p^{β}_{ij}), compartment (c^{α}_{i} and c^{β}_{i}), and year ($w^{\alpha}(t)$ and $w^{\beta}(t)$). The intercept effects reflect differences in overall growth increment while the slope effects reflect differences in growth as a function of size. The random effect intercept for a specific tree is determined by the random tree, compartment, plot, and year effects as follows: $\alpha_{ijk}(t) = q^{\alpha}_{ijk} + c^{\alpha}_{i} + p^{\alpha}_{ij} + w^{\alpha}(t)$. The slope is similar: $\beta_{ijk}(t) = q^{\beta}_{ijk} + c^{\beta}_{i} + p^{\beta}_{ij} + w^{\beta}(t)$. The random effects for tree, compartment, plot, and year follow normal distributions and, in *Results*, we display the standard deviations for each of these random effects (e.g., $\sigma_{\alpha,c}$ for the standard deviation of compartment intercept effects). At each level of nesting, random effects are assumed to be independent (see Appendix C for more details on model specification).

We estimated the parameters, random effects, and latent states in a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling techniques in OpenBUGS (Lunn et al. 2009). While the MCMC needed some adjustments to produce useful results, ultimately we were able to estimate the full, complex model with all explanatory variables and sources of variation. We used R (R Development Core Team 2009) to format the data and generate initial values for random effects. We could not use completely arbitrary initial values generated by BUGS because we encountered difficulties with slow mixing due to the complexity of the model. Instead we used spline-interpolated sizes (Wood 2006) in a linear mixed-effects model (lmer; Bates and Maechler 2010) to generate plausible starting values for random effects and latent sizes. Initial values for intercept and slope parameters for explanatory variables were set to zero.

We used uninformative priors, with the exception of observation error standard deviation. When we included very small values in our prior distributions for this parameter, MCMC chains mixed poorly. As we expect at least a small amount of observation error, we chose an inverse gamma or a uniform prior with a nonzero minimum, based on the minimum rounding error inherent in the diameter tape. In *Results*, we report estimates from the uniform prior model for all parameters other than observation error (for which we report results for both priors). We assessed convergence both visually and using Gelman-Rubin diagnostics in the coda package (Plummer et al. 2010). See Appendix

D for details on priors, initial values, trace plots, and convergence tests. Finally, while we do not demonstrate a formal model selection procedure here, we do estimate several simpler models to check the robustness of our estimates to removal of other model components and to different choices for observation error priors (Appendix G).

RESULTS

The mean for growth increment $\bar{a}$ was 0.463 (with a 95% credible interval of 0.339, 0.600) cm per year, and for change in growth increment with size $\bar{b} - 1$ was 0.013 (0.006, 0.020) per year. We thus confirm that size has a significant effect on growth and should be included in the model. For all explanatory variable parameters on the same standardized, unitless scale, we list means and 95% credible intervals in Appendix E. The credible intervals of parameters for insolation, elevation, and annual water deficit overlap zero. On the other hand, basal area's effect on growth increment γ^{ba} and its interaction with size κ^{ba} do not significantly overlap zero. The effect of topographic slope on growth increment γ^{tslope} is borderline significant as well, though its interaction with tree size κ^{tslope} is not (Fig. 1). Note that some of the parameters such as the effect of annual water deficit (γ^{def} and κ^{def}) are poorly determined (have a flatter posterior and consequently a broader credible interval). Though several of the soil type effects also overlap each other, some are distinct from each other and from their average, and all of their intercepts are significantly different from zero. Of the soil types, Cohasset has the highest slope κ^{C} and the second highest intercept γ^{C}, consistent with the typically high productivity of these soils (see Appendix E for parameter estimates). The estimates for these significant variables (basal area, topographic slope, and soil effects) are robust to the removal of the others (insolation and elevation), and vice versa (e.g., removal of topographic slope does not render insolation significant). In contrast, when annual deficit is removed, the magnitude of random year effects increases (see Appendix G for comparisons between the full model and several simplified models).

The way these explanatory variables interact with size is more apparent when growth increment as a function of size is shown for low and high values of the explanatory variables (Fig. 2). These results on the original size scale allow biological interpretation (see Appendix C for algebra underlying the rescaling of covariates after estimation). The slope of all lines is significantly greater than zero, indicating that size is significant for all values of the other explanatory variables. Several of the effects of the high and low values of specific covariates make sense: for higher water deficits, growth is lower, and growth is higher overall in Cohasset soils. However, variables other than basal area show high overlap between high and low values and thus do not substantially affect tree growth (soils overlap considerably as well).

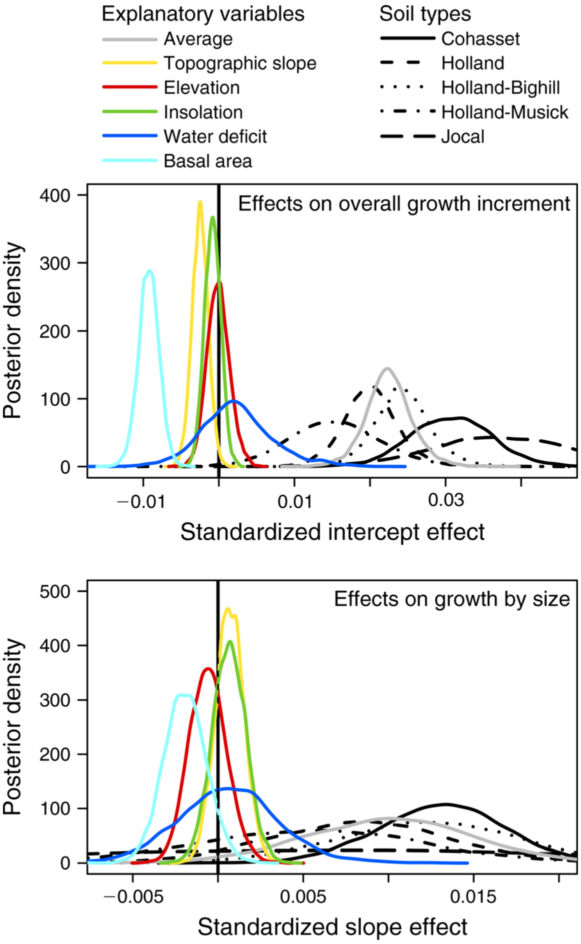

FIG. 1. Parameter posterior densities for main effects of explanatory variables on overall growth increment (γ) and interaction with tree size (κ). In addition to these continuous explanatory variables, the effects due to different categorical soil types are shown in black. The gray line indicates the average growth increment (upper figure, $\bar{a}$) and effect of tree size on growth increment (lower figure, $\bar{b} - 1$). (Top) Effects of continuous explanatory variables and soil types on the overall growth increment ($\bar{a}$ and γ's). (Bottom) Effects of explanatory variables on the slope of future size with respect to current size ($\bar{b} - 1$ and κ's).

Observation error standard deviation σ_{dbh} is estimated at 0.149 (0.082, 0.218) cm with a uniform prior and 0.111 cm (0.073, 0.175) with an inverse gamma prior. Residual standard deviation σ_{ε} is estimated at 0.387 (0.358, 0.414) cm. Because standard deviations can never be less than zero, determination of significance is not simple. However for our results a practical choice was to calculate a ratio of the lower credible bound to the width of the credible interval to represent the posterior's separation from zero. The posteriors that were visually distinct from zero had ratios ranging from 0.22 to 3.76, while those that were not separated from zero had ratios on the order of 10^4 or 10^3. We consider

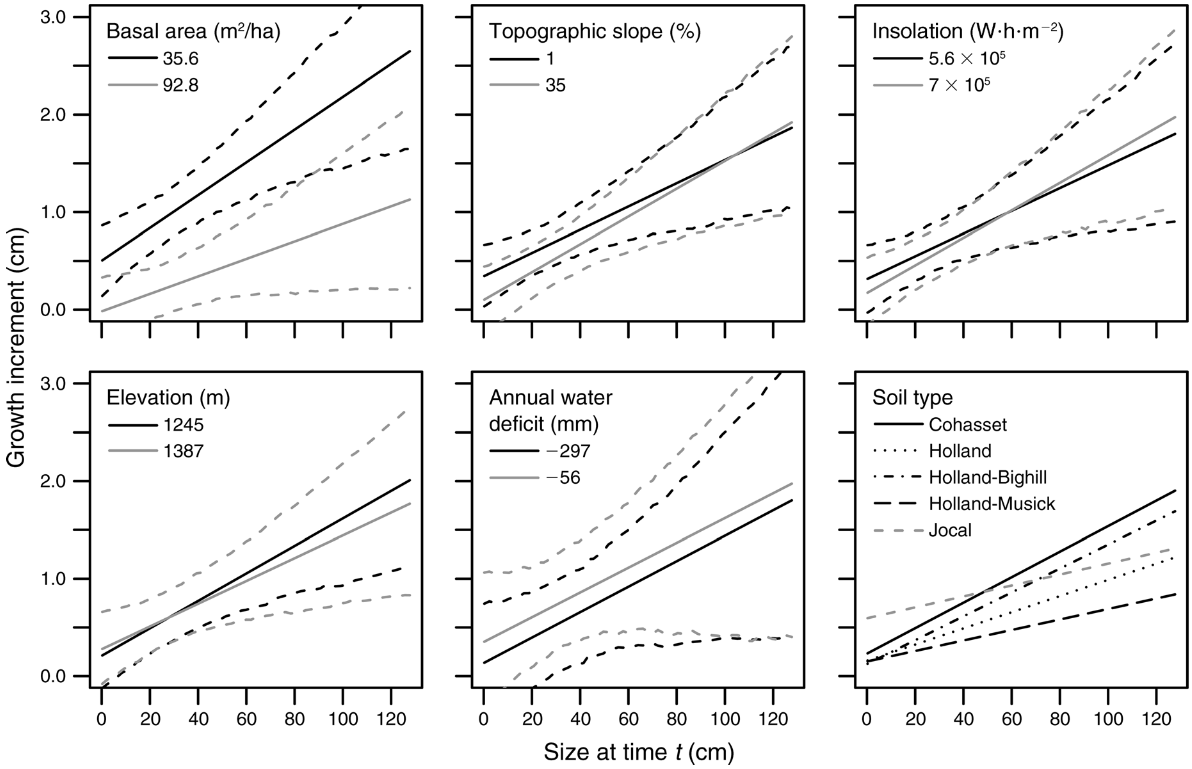

FIG. 2. Explanatory variable effects on growth increment (measured as change in dbh) as a function of size (dbh), rescaled to centimeters. All plots show that growth increases with tree size in the previous year. Solid lines are the means from posteriors of parameter estimates; dashed lines are 95% credible intervals. For all explanatory variables other than soil type, black shows growth increment for a low value of the explanatory variable (−2 SD) and dark gray for a high value (+2 SD). Credible intervals for soil type overlap a great deal and are not shown for clarity.

those in the first group to be significant and those in the second group not to be significant (see Table E2 in Appendix E for these ratios). Based on this reasoning, among the intercept random effect standard deviations, the year, tree and plot effects are significant ($\sigma_{\alpha,w}$, $\sigma_{\alpha,q}$, and $\sigma_{\alpha,p}$; Fig. 3). Of the slope random effect standard deviations, only plot ($\sigma_{\beta,p}$) is significant (see Appendix E and Fig. 3). Though several of the sources of unexplained variation have a significant effect on the overall growth increment, the variation they introduce is substantially less than the variation introduced by overall residual variation. Several of the random effect standard deviations are not well determined: year and compartment intercept effects have particularly broad, flat posteriors. Finally, we also examined explicitly estimated latent tree sizes $x_{ijk}(t)$ for nine trees in the inventory. Some trees' unmeasured sizes are better constrained by the data than others (small trees in particular are poorly estimated, with wide credible bands); but for several larger trees the annual growth between censuses has narrow credible bands and reasonable values (Appendix F: Fig. F1).

DISCUSSION

Our study demonstrates the feasibility of estimating a hierarchical model from forest inventory data with the full richness of both categorical and continuous explanatory variables, many sources of variation, and observation error. We have successfully estimated annual growth from a mosaic of sampling intervals. Backward model selection strategies require one to start with the most complex model available, and we have shown that this most complex model can be estimated. Forest inventory data sets with this kind of sampling structure and with individually marked trees are becoming more common, so this modeling approach could be applied to many other forest dynamics problems.

Tree size, basal area, and resource supply

Our estimations confirm that dependency of tree growth on size and competition intensity cannot be ignored when modeling growth, e.g., in other applications such as population dynamics or dendrochronology. Our annual average growth increment of 0.463 cm per year at average conditions on these plots is high but reasonable, as BFRS is a productive site and its second-growth forests are still increasing in biomass. We chose a linear model for diameter growth for this study, but the modeling framework easily accommodates other functional forms for dependency on size and competition (see Cao [2000], Nord-Larsen [2006], Weiskittel et al.

[2007], and Cao and Strub [2008], who have incorporated complex functional forms with uneven inventory time intervals). In particular, we could explore nonlinear functions that allow tree growth to slow as trees reach very large sizes (as in Clark et al. 2007, 2010, 2011, 2012), although forests at BFRS are young enough not to show this behavior.

Basal area's dominance among the remaining explanatory variables has two possible explanations. First, competition is a likely limiting factor in forests like BFRS. As in many Sierra Nevada forests, fire suppression has allowed shade-tolerant species to dominate younger cohorts and regeneration. Tree density is high and recruitment to the canopy is only possible in distinct canopy gaps. Second, though we conclude that elevation and insolation are not important at plot level, these variables occur in a narrow range at BFRS relative to the species' fundamental niche (Lutz et al. 2010). Variation in these variables at BFRS is small relative to the U.S. Forest Service's permanent plot data in a similar latitude range (see Appendix H for details of comparison to Forest Inventory and Analysis data), and other studies show larger responses when larger ranges of covariates are available (Clark et al. 2012). The fact that annual water deficit did not have a strong effect on growth is surprising given the documented relationship between growth and climate for white fir trees in northern California (Yeh and Wensel 2000). One explanation for this result is that water deficits at BFRS tend to be lower than comparable forests in the region (see Appendix H). Also recall that when water deficit is removed from the model, the intercept year standard deviation increases (see Appendix G). So although the effect of annual water deficit cannot be precisely estimated, its magnitude may be biologically important. Finally, this data set does not include many trees smaller than 11.4 cm dbh, and these smallest individuals may be more strongly influenced by resource supply than larger, more established individuals, and also at a spatial scale below plot level.

Sources of variation

The behavior of our model implies that observation error standard deviation may not be independently estimable in this kind of model. Priors allowing the standard deviation to approach zero, including uniform and half-*t*-distribution priors (Gelman 2006, Knape et al. 2008), result in bad mixing as the system struggles to move away from a scenario in which observations perfectly match latent states. This behavior could be due to the MCMC samplers in OpenBUGS; different software may not have this problem. Some observation error in this system is expected, however, and including it should improve other estimates. We chose a minimal lower bound on the observation error standard deviation, based on the rounding error in the measurement tape (0.073 cm; see Appendix D for details of this calculation). Our estimates are larger than this minimum, but still much smaller than the 1 cm (0.8%) reported by Clark et al. in a study combining tree cores with dbh measurements (Clark et al. 2007) and the 2.7% reported by Gonzalez et al. (2010) for repeated dbh measurements made in similar forests (though this latter study included outliers and obvious errors, which we have removed from our inventory; see Appendix B). Models like ours for similar data sets should check to confirm that observation error can be estimated and may likewise consider an informative prior to ensure a minimum amount of observation error. Analysts may also try different MCMC samplers, which may be less sensitive to this behavior.

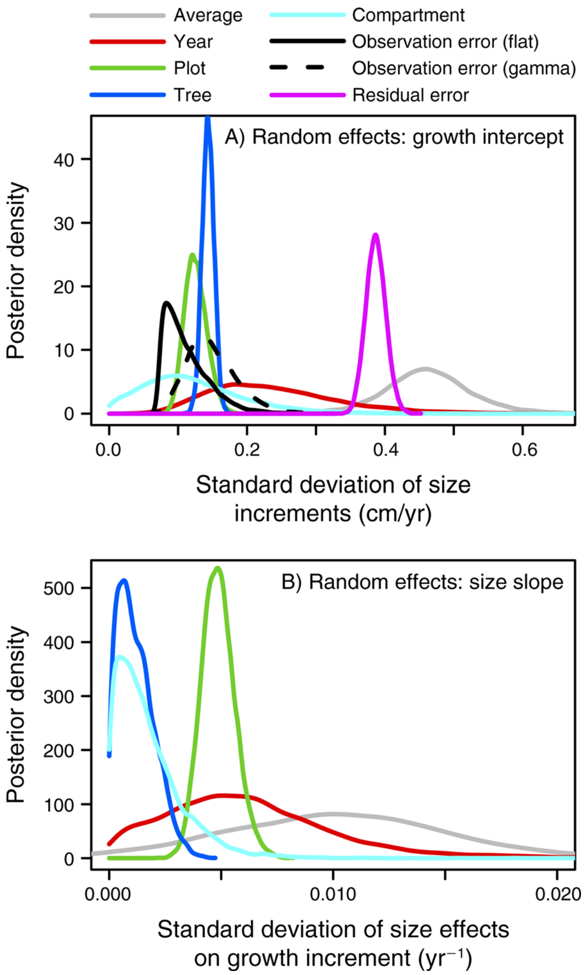

FIG. 3. Random-effect standard-deviation posteriors. (A) The intercept, α, standard deviations (compartment α_c, year α_w, tree α_q, and plot α_p), with the average growth increment $\bar{a}$ from Fig. 1 shown for scale in gray. Observation error standard deviation σ_{dbh} and residual error standard deviation σ_ε are shown on the same plot for comparison. Only for observation error, we show posteriors for both the inverse gamma (dashed) and uniform (solid) prior models. (B) The slope, β, standard deviations ($\sigma_{\beta,c}$, $\sigma_{\beta,w}$, $\sigma_{\beta,q}$, and $\sigma_{\beta,p}$); again, the growth increment slope $\bar{b} - 1$ from Fig. 1 is shown for scale in gray.

Even after accounting for basal area, the significant plot random effect standard deviations essentially give each plot its own size relationship with growth. Plots at BFRS are approximately two to three neighborhoods in size (Canham et al. 2006, Das et al. 2011), so neighborhood effects could be acting below the plot level. Density dependence in closed canopy forests can be complex, so an effect due to plot in addition to an overall basal area measurement at the plot level is reasonable. The importance of slope random effects in addition to intercept random effects implies that models may need to include variation in more than just the overall growth intercept. The broad, flat posteriors of some random effect standard deviations may be the result of a small sample size to estimate them; in particular, the broad posterior for the year effect variance is not surprising as some years do not have data and the annual increment cannot always be precisely estimated.

The nontrivial tree intercept standard deviation, even when size is included in the model, implies that some trees have a growth advantage over their entire lifetime in the inventory. This slightly different average growth of different trees is ecologically important: for example, in population models, individual quality (Ellner and Rees 2006) can have important impacts on population growth. Unfortunately it is impossible with our data to determine whether this individual quality reflects genetic superiority, a favorable microsite when the tree first established, or some other neighborhood factor. The significance of this individual variation highlights the importance of studying forests at the individual tree level (Clark et al. 2012).

Future work and implications for practice

We have demonstrated the use of a complex hierarchical model including explanatory variables and multiple random effects on long-term forest inventory data. Though our model accounts for uneven time intervals effectively, it does not include the sophistication of explicitly including underlying spatial autocorrelation (Banerjee and Finley 2007, Finley 2011). In addition, though we have included a variety of explanatory variables, there is a constellation of possible variables we could have included. Ultimately, one would want to use both knowledge of the system and a model selection procedure to determine what functional form to use and which explanatory variables and random effects to keep in the model, which we do not demonstrate here.

The results of these models can be directly used to parameterize population models (e.g., integral projection population models [Metcalf et al. 2009, Ghosh et al. 2012]) or forest simulators (e.g., SORTIE). Comparative studies using rich long-term data sets can illuminate patterns in ecological processes over large geographical areas. These studies may test basic ecological theories such as resource limitation and niche theory, or applied questions about management practices (e.g., how the effectiveness of fuel hazard reduction treatments could be affected by climate change). Data on individually tagged trees, rather than plot-level data, are becoming the norm, and long-term monitoring data are maturing. Forest permanent plots are common in Long-Term Ecological Research sites (over one-third of the International Long-Term Ecological Research sites are listed as "forest"). Since 1999 when the U.S. Forest Service Forest Inventory and Analysis program moved to annualized inventory, their program includes remeasurement of tagged trees, and numerous other long-term data sets are available from a variety of sources (e.g., the Smithsonian Center for Tropical Forest Studies).

As policymakers, managers, and ecologists alike call for adaptive management strategies (Federal Register 2012), including long-term monitoring as a key component in assessing ecosystem interventions, sophisticated modeling is needed to appropriately analyze these data so that inference can feed back into management planning and therefore complete the adaptive management cycle. Monitoring data are often rich in covariates and highly complex in sources of variation, and uneven time intervals are a common problem. Our study, including the appendices, which detail the modeling process, and the supplements, which include the code and data to run the model, should help more ecologists and managers to try these types of sophisticated models and open up new ways of using inventory data from across the world.

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SUPPLEMENTAL MATERIAL

Appendix A

Number of trees and plots in each compartment, and number and length of time intervals (*Ecological Archives* A023-067-A1).

Appendix B

Measurement methods and auditing of explanatory variables (tree size, basal area, insolation, elevation, slope, annual water deficit, and soil type (*Ecological Archives* A023-067-A2).

Appendix C

Additional details on statistical model and algebra regarding standardization of explanatory variables (*Ecological Archives* A023-067-A3).

Appendix D

Details on model estimation and the evaluation of model results (*Ecological Archives* A023-067-A4).

Appendix E

Table of parameter estimates (*Ecological Archives* A023-067-A5).

Appendix F

Latent unmeasured sizes for nine trees (*Ecological Archives* A023-067-A6).

Appendix G

Examples of simpler models (*Ecological Archives* A023-067-A7).

Appendix H

Comparison of conditions at BFRS with FHA data from a similar latitude (*Ecological Archives* A023-067-A8).

Supplement 1

BUGS model code for full model (*Ecological Archives* A023-067-S1).

Supplement 2

BUGS-formatted *Abies concolor* data suitable for running full model (*Ecological Archives* A023-067-S2).

Supplement 3

Initial values for full model (*Ecological Archives* A023-067-S3).