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Bayesian parameter estimation and interpretation for an intermediate model of tree-ring width

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Abstract

We present a Bayesian model for estimating the parameters of the VS-Lite forward model of tree-ring width. The scheme also provides information about the uncertainty of the parameter estimates, as well as the uncertainty of VS-Lite itself. By inferring VS-Lite's parameters for synthetically-generated ring-width series at several hundred sites across the United States, we show that the Bayesian algorithm is skillful and robust to climatic nonstationarity over the interval tested. We also infer optimal parameter values for modeling observed ring-width data at the same network of sites. The estimated parameter values cluster in physical space, and their locations in multidimensional parameter space provide insight into the dominant climatic controls on modeled tree-ring growth at each site.

1 Introduction

Forward models of the physical or biological processes by which climate variability is imprinted on natural archives provide important tools for understanding such “proxies” as recorders of climate (Evans et al., 2012). The VS-Lite model (Tolwinski-Ward et al., 2011) provides one such forward model for the climate controls on tree-ring width chronologies. Under this model, just four parameters determine a simulated chronology's response to mean monthly air temperature and monthly model-simulated soil moisture. These parameters connect the local climatology to the modeled controls on growth and the climatic signal contained in the simulated chronology. Thus, in order to use VS-Lite to study the relationship between climate and proxies in the real world, an objective method for choosing the model parameters for any particular site or region is necessary.

Ideally, parameterization should be based on a first-principles understanding of the science represented by the model. The growth response parameters in the VS-Lite model are loosely interpretable as temperature and soil moisture thresholds above

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which growth begins or is no longer sensitive to climatic fluctuations, respectively. This interpretation is consistent with the well-established biological Law of the Minimum (Taylor, 1934), expressed in dendrochronology by the idea that tree growth is determined by the most limiting factor (Fritts, 2001). However, it is debatable whether each of these VS-Lite parameters have directly measurable analogs in the natural world. Recent physiological studies have advanced the scientific community's understanding of climatic thresholds for xylogensis (e.g. Rossi et al., 2007; Deslauriers et al., 2008), but the results are not well-enough developed or catalogued across tree species or climate regimes to be generalizable to all forward model runs. Even if they were, it is not clear how measurable quantities in the real world are related to vastly simplified model quantities. In particular, VS-Lite operates using monthly data, while the cellular-level processes it is intended to mimic vary at daily and shorter timescales. Minimum and optimum parameters therefore represent a simplification that may be inferred from, but not be strictly interpretable as, biophysical limits on cambial activity itself. Given the limited ability of direct observations to constrain the model parameters, it is necessary to estimate VS-Lite's parameters numerically using monthly climate inputs, observed ring-width series, and partial knowledge of the model error structure. At sites where VS-Lite is believed to provide a reasonable intermediate complexity proxy system model for tree-ring width variations, such a parameter estimation procedure can improve upon the characterization of errors arising from the model's incomplete representation of the proxy system.

Two general approaches to numerical parameterization of forward models of tree-ring growth have been explored in the literature. The first is presented by iterative local schemes that optimize the fit of simulated model quantities to their observed counterparts under changing parameter combinations. In the iterative scheme of Fritts et al. (1999), for example, one model parameter is changed at a time in a search over a continuous region of parameter of space for the set of parameters producing optimal model fit. Modern computing power makes such schemes possible to run at many locations, but the approach does not account for potential interactions between parameters. The

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scheme may also locate a local optimum in parameter space but miss information, including other optima, provided by a more global search. A second class of approaches attempts to avoid this last pitfall by running growth models at a preselected, discretized set of parameter combinations believed to cover the entire physically plausible regions of parameter space (e.g. Misson et al., 2004; Misson, 2004; Tolwinski-Ward et al., 2011). The single combination which produces the best match of modeled outputs to its observed counterparts is deemed optimal (e.g. Misson et al., 2004; Misson, 2004; Tolwinski-Ward et al., 2011). This parameterization method is only practical where the number of parameters to be constrained by the available data is relatively small. Both local and global previous parameterization schemes have the shortcoming that they provide only point estimates of optimal parameters, and their results do not include any information about model sensitivity to the parameter choices. In addition, while the ranges of the parameters included in the search space are generally chosen through consideration of physically plausible bounds on their values, the search algorithms lack any more sophisticated use of science-based understanding of where the most likely parameter values lie.

Here we present and test a Bayesian statistical scheme to infer parameter estimates for VS-Lite. The scheme is computationally efficient, combines expert prior information about scientifically reasonable values for the parameters, and automatically provides information pertaining to model sensitivity to parameter choices. The method also automatically safeguards against over-tuning of inferred parameters in cases where the data series are either very short or very noisy. Code for the scheme is freely available with the VS-Lite v2.2 model at the National Oceanic and Atmospheric Administration (NOAA) Paleoclimatology software library (<http://www.ncdc.noaa.gov/paleo/softlib/softlib.html>). We test the skill of the parameterization approach in an idealized experiment using synthetically-generated tree-ring width data. As an application of the method to observed ring-width chronologies, we also present a graphical method for interpreting the fitted model parameters in terms of climatic controls on tree-ring growth at each site.

2 Model, data, and methods

2.1 Summary of VS-Lite and parameters

A complete description of the VS-Lite model is given by Tolwinski-Ward et al. (2011). However, we briefly summarize the basic structure of the model and its parameterization here. VS-Lite is a substantially simplified, monthly time-step version of the full Vaganov-Shashkin model of tree-ring growth (Vaganov et al., 2006, 2011). At its core, VS-Lite is a parsimonious representation of the Principle of Limiting Factors with respect to monthly temperature and soil moisture, and with growth modulated by insolation. In its current version (version 2.2), insolation is determined from site latitude, and soil moisture is determined from monthly temperature and precipitation via a simple leaky bucket model (Huang et al., 1996). Non-dimensional scaled growth responses $g_T(m, y)$ and $g_M(m, y)$ to monthly time-step temperature and soil moisture content, respectively, are key to determining the extent of simulated growth at each modeled timestep, indexed by the month-year pair (m, y) . These responses have the piecewise linear forms

$$g_T(m, y) = \begin{cases} 0 & T(m, y) \leq T_1; \\ \frac{T(m, y) - T_1}{T_2 - T_1} & T_1 \leq T(m, y) \leq T_2; \\ 1 & T_2 \leq T(m, y) \end{cases} \quad (1)$$

and

$$g_M(m, y) = \begin{cases} 0 & M(m, y) \leq M_1; \\ \frac{M(m, y) - M_1}{M_2 - M_1} & M_1 \leq M(m, y) \leq M_2; \\ 1 & M_2 \leq M(m, y) \end{cases} \quad (2)$$

The parameters T_1 and M_1 thus represent thresholds in temperature and soil moisture content below which growth cannot occur, while T_2 and M_2 are thresholds above which growth is insensitive to climatic variability. The overall monthly growth rate is given

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by $g(m, y) = \min\{g_T(m, y), g_M(m, y)\}$, to mimic the Principle of Limiting Factors (Fritts, 2001) that the more limiting environmental variable controls growth. The simulated annual-resolution ring-width series result from taking an inner product of these overall growth rates with estimates of mean relative monthly insolation derived from trigonometric functions of latitude. Thus, the climatic variable that tends to produce lesser values in its growth response function controls the modeled climate signal contained in the simulated proxy series. The relationship of the parameter values T_1, T_2, M_1, M_2 to the model's climate inputs is therefore critical in determining which variable gets “recorded” by the synthetic trees.

We model the residuals between modeled and observed ring-width chronologies as independent and identically-distributed Gaussian white noise, which fits the model errors at the sites studied in this paper better than noise with AR(1) or AR(2) temporal structure. The error variance σ_W^2 (where the subscript W denotes that this is the variance of error associated with the model estimate of tree-ring width W) may be viewed as a fifth model parameter. Its value provides information about the model uncertainty causing misfit between simulated and observed tree-ring width indices.

2.2 Approach to model parameter estimation

We follow a Bayesian approach to calibrating the model parameters. Let θ denote the vector of model parameters we would like to estimate, $\mathbf{W}(T, P)$ the vector of observed ring-width data, which depends on vectors of monthly temperature and precipitation data covering the same interval in time as the ring width data. The Bayesian paradigm allows inference on the parameters via the posterior distribution $\pi(\theta|\mathbf{W}(T, P))$ of the parameters given the climate and ring width data. The posterior is obtained in terms of the likelihood $f(\mathbf{W}(T, P)|\theta)$ of the ring-width data given the climate and the parameters, as well as a prior distribution $\pi(\theta)$ on the parameters via Bayes' law:

$$\pi(\theta|\mathbf{W}(T, P)) \propto f(\mathbf{W}(T, P)|\theta)\pi(\theta) \quad (3)$$

Given the likelihood and prior parameter models, Markov Chain Monte Carlo techniques produce an ensemble of draws from the posterior distribution (Gilks et al., 1996), from which estimates of the parameters and their associated uncertainties can be made.

The deterministic VS-Lite model plus stochastic error provides the likelihood in Eq. (3). A forward modeling study comparing observed ring-width chronologies to simulations using VS-Lite at 277 sites across the continental United States suggested that independent and identically-distributed Gaussian noise provided a reasonable fit to the model residuals (Tolwinski-Ward et al., 2011). Thus the likelihood model is given by a multivariate normal with mean given by the deterministically-simulated ring-width series, and covariance matrix $\sigma_W^2 I$. For our problem, then, the components of θ are given by VS-Lite's growth response parameters and the variance associated with model uncertainty:

$$\theta = (T_1, T_2, M_1, M_2, \sigma_W^2)' \quad (4)$$

Note that in its current version, VS-Lite also requires several parameters of the Leaky Bucket model of soil moisture. We do not estimate those here, as the soil moisture model may be viewed as an ancillary component of VS-Lite that may be replaced by a more sophisticated hydrological model or direct measurements of soil moisture. In effect, our current approach transfers the uncertainty associated with these parameters to uncertainty in the soil moisture response parameters M_1 and M_2 .

In modeling the prior distribution of the parameters, we first make the assumption that each parameter is independent of the others. This assumption allows us to model their joint prior distribution as the product of individual prior models for each. We put relatively broad but informative priors on the growth response parameters, with shapes and supports consistent with current scientific understanding of tree growth responses to temperature and moisture.

Of the four growth response parameters, the literature provides the most information about T_1 , the threshold temperature for growth to begin. The physiological experiments

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of Körner and Hoch (2007) at a montane site in Switzerland indicate that mean seasonal soil temperatures below 6–7 °C will not permit growth. An assessment of root and air temperatures at a few dozen treeline sites by Körner and Paulsen (2004) give a value of 6.7 °C ± 0.8 °C for this growth threshold, and histological measurements and analyses of Rossi et al. (2007) and Deslauriers et al. (2008) for conifers in the Alps give a range of 5.8–8.5 °C. Hoch and Körner (2009) found that two montane conifer species maintained cambial activity even when grown at 6 °C. Körner (2012) inferred a global mean treeline isotherm near 6 °C and cessation of growth at 5 °C (Körner, 2008). 0 °C is the theoretical limit below which plant tissue formation cannot occur (Körner, 2012). We thus chose to model the temperature threshold for growth by $T_1 \sim \beta(9, 5, 0, 9)$, a four-parameter beta distribution with first and second shape parameters 9 and 5 supported on the interval [0, 9]. This choice puts the mode of the pdf at 6 °C, assigns zero probability below freezing 0 °C or above 9 °C, and places 90 % of the total probability in the interval (3.8 °C, 7.5 °C) (see blue curve in Fig. 1a).

The biologically-based information available about T_2 , the threshold above which growth is no longer sensitive to temperature variations, is more uncertain. Vaganov et al. (2006) give a default value of 18 °C for the full Vaganov-Shashkin model based on a few intensive case studies at a limited number of Russian tree-ring sites, but use a value of 15 °C in an example model run, demonstrating the range of uncertainty associated with this parameter. The analogous parameter in the TreeRing2000 model has a default value of 23 °C (Fritts et al., 1999). Data shown by Williams et al. (2011) suggests a broad plateau where ring width in Alaskan *Picea glauca* ceased increasing with June and July means temperature between approximately 10 °C and 13 °C, depending on site hydrology. On the other hand, Garfinkel and Brubaker (1980) showed no change in the regression of ring width on temperature in the same species even at temperatures approaching 15 °C. Carrer et al. (1998) inferred a lower optimal summer temperature threshold of 13 °C for *Picea abies* and 16 °C for *Larix decidua*. Although this information sheds some light on the threshold for sensitivity to temperature, the majority of these studies are based on empirical data at monthly to seasonal time scales,

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as opposed to direct studies of cambial activity in response to temperature. To reflect the uncertainty inherent in the wide range of these estimates, as well as uncertainty in their direct applicability as parameter estimates in VS-Lite, we model the prior by $T_2 \sim \beta(3.5, 3.5, 10, 14)$. This choice limits probability mass to the interval ($10^\circ\text{C}, 24^\circ\text{C}$), and distributes probability symmetrically about a mean of 17°C with a standard deviation of 2.5°C (blue curve, Fig. 1b).

Very little biologically-based information is available to constrain either moisture parameter. We use the default parameters developed by Vaganov et al. (2006) to define broad priors on M_1 and M_2 . Default values for M_1 , interpretable as soil wilting point, are 0.02 v/v (Vaganov et al., 2006) and 0.01 v/v (Fritts et al., 1999). The latter source also sets a moisture optimum at 0.109 v/v, so the value of M_1 should certainly fall well below this value. We set the prior mean at 0.035 with standard deviation of 0.02 v/v, with no probability mass outside of (0 v/v, 0.1 v/v), by letting $M_1 \sim \beta(1.5, 2.8, 0, 0.1)$ (blue curve, Fig. 1c). The default for M_2 is 0.8 of typical soil saturation levels, and the Leaky Bucket model of soil moisture employed by VS-Lite never allows soil to be saturated to a value more than 0.75 v/v. We set $M_2 \sim \beta(1.5, 2.5, 0.1, 0.4)$. This gives the prior a mean of 0.25 v/v, standard deviation of 0.1 v/v, and nonzero probability on (0.1 v/v, 0.5 v/v) (blue curve, Fig. 1d).

The prior for the model noise σ_w^2 is inverse gamma with shape and scale parameters 5 and 10, respectively. The inverse gamma distribution is a common choice for the prior of the variance of a Gaussian process, since it is a conjugate prior; that is, the posterior distribution also has an inverse gamma distribution. The conjugacy feature simplifies the sampling. The shape and scale parameters are chosen to make the prior both broad and vague, with a mean of 2.5 and a variance around 2.1, to limit the influence of our prior choice on the inferred value of σ_w^2 .

The posterior distribution (Eq. 3) is sampled using a Metropolis-Hastings algorithm embedded within a Gibbs sampler, which is a standard Markov Chain Monte Carlo approach (Chib and Greenberg, 1996). To check for convergence, we run three chains with 4000 iterations each after a burn-in period of 1000 iterations. In the rare case that

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the R-hat statistic (Gelman and Rubin, 1992) indicates the MCMC has not converged, we re-run the sampler with a greater number of iterations until the sampler has converged. The autocorrelation functions of the MCMC chains indicate that at most sites, autocorrelation in the parameter sampling chains is no longer significant past a lag of twenty. We conservatively subsample every fiftieth value of each of the three chains to ensure independence of samples, resulting in a collection of 240 samples for each parameter value at each site.

The ensemble output may be used in several different ways. First, point estimates from the posterior ensemble, such as the posterior median, may be used as calibrated parameter values that optimize the fit between model simulated ring width data and a target ring width series, given fixed input climate data. However, the posteriors contain additional information beyond point estimates. Their spread indicates the uncertainty in the parameter estimates, as well as the degree to which the climate and target ring-width data inform the parameter values. Hence a measure of the model sensitivity to each parameter may also be gleaned from the posterior spread. The Monte Carlo ensemble of parameter values may also be used to run modeling studies where accounting for the effect of parameter uncertainty is important for interpretation of the results.

2.3 Experimental design

We perform our study using estimates of monthly temperature and precipitation from the 4 km × 4 km-resolved gridded Parameter-Elevation Regressions on Independent Slopes Model (PRISM) data product (Daly et al., 2008). We use the mean of the monthly maximum and minimum temperature fields as well as the accumulated precipitation field, and neglect the inherent PRISM measurement and model error. The climate product is used at the grid cells co-located with 277 sites associated with observed tree-ring width chronologies across the continental United States. These sites form the subset of chronologies used in a multi-proxy hemispheric temperature reconstruction by Mann et al. (2008) that also overlap with the PRISM data from 1895–1984.

The choice of this 90-yr interval represents a balance between the availability of proxy observations and climate data. All the associated chronologies are freely available online on the NOAA Paleoclimate Reconstructions Network/Proxy Data webpage (<http://www.ncdc.noaa.gov/paleo/pubs/pcn/pcn-proxy.html>).

2.3.1 Pseudoproxy experiment (PPE)

To evaluate the skill of the Bayesian parameter estimates, we perform a variation on so-called “pseudoproxy experiments” (PPE) (Smerdon, 2012) using synthetically generated tree-ring width data. At each site, we first do a preliminary run of the Bayesian scheme described above using the observed chronologies and estimates of observed climate data for the entire interval 1895–1984. The posterior medians from this step parameterize regionally-realistic tree growth responses to climate, and we use them as our PPE parameter targets. We next run the VS-Lite model over the same interval using the target parameter set and PRISM climate estimates to produce 277 synthetic ring-width series. Finally, we estimate the known target parameters using the Bayesian scheme. We condition on the known climate data and pseudoproxy ring-width data, use the interval 1955–1984 to estimate the growth response parameters, and the interval 1925–1954 to estimate the model noise σ_W^2 . The data from 1895–1924 are withheld to compute estimates of the model noise in an interval independent from the one used to tune the growth response parameters. This PPE is designed as a test of our parameter calibration scheme over a realistic range of tree responses to climate, but in an idealized model world where the VS-Lite model perfectly describes the process by which climate is transformed into noise-free tree-ring width chronologies. The skill of the algorithm measured in such a PPE thus provides an upper bound on its skill in real-world scenarios.

Comparing the growth parameter posterior distributions to the known targets allows us to quantify the skill of the estimation scheme. The numerics return $N = 240$ draws from the posterior distribution, so we compute Monte Carlo estimates of the root-mean-square error and bias in the pseudoproxy context using the “true” target value of each

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(scalar) parameter θ :

$$\text{RMSE} \approx \sqrt{\frac{1}{N} \sum_{n=1}^N (\hat{\theta}_n - \theta)^2} \quad (5)$$

$$\text{Bias} \approx \frac{1}{N} \sum_{n=1}^N (\hat{\theta}_n - \theta) \quad (6)$$

5 The extent to which the prior and posterior distributions differ indicates the degree to which the climate, ring-width data, and the VS-Lite model structure constrain the value of each parameter. To quantify this “Bayesian learning” at each site, we examine the ratio of posterior to prior variance. Parameters whose posteriors are well-constrained by the data will have much smaller posterior variance than prior variance, while parameters that are not well-constrained will have posteriors that resemble their priors, and hence variance ratios close to one. Finally, the parameter σ_w^2 characterizes the model skill in simulating the data, and so must be checked for artificial skill. We compare the posterior median of this parameter to the median of the prior updated by the variance of the residuals obtained by running VS-Lite in the independent validation interval with
10 the estimated growth response parameters.

15 To evaluate the sensitivity of the parameter estimation scheme to the choice of prior distributions, the pseudoproxy experiment described above is also performed with uniform prior distributions. The supports of these uniform priors are chosen to be the same as that for the literature-informed four-parameter beta priors described in Sect. 2.2 for T_1 , T_2 , and M_1 . For M_2 , a uniform distribution with the same lower bound on its support as the four-parameter beta prior is used, but the upper bound is extended slightly out to 0.6 v/v. The uniform prior is a standard noninformative choice against which to check the sensitivity of posterior results to more complicated priors (see Gelman et al., 2003, Sect. 6.8). The posteriors derived under the four-parameter beta priors informed by the
20 literature are compared with those derived using the uniform priors.

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2.3.2 Observed proxy experiment (OPE)

We also calibrate the VS-Lite model parameters using the PRISM data and the observed tree-ring width chronologies at each of the 277 network sites to perform an observed proxy experiment (referred to hereafter by the acronym OPE). We condition the growth response parameter estimates on the data for the interval 1955–1984 and the model noise σ_W^2 on the data from 1925–1954. We withhold the 1895–1924 data to independently validate the estimate of model noise.

We take the posterior medians as point estimates of each parameter, and look at their spatial distribution across the experimental domain. As in the PPE case, we also look at the ratio of posterior to prior variance to assess Bayesian learning, and compare the OPE estimates of the model uncertainty σ_W^2 in calibration and validation intervals to check for robustness in the estimate of model skill. In the case of parameter calibration using real data, the parameters are unknown, and so we cannot compute RMSE or bias. Instead, we seek to interpret the fitted parameters in terms of the climate controls on growth at each site. We first classify each site as having growth which is either temperature-limited, moisture-limited, or as having mixed climatic controls. To do so, we run the VS-Lite model at each site with the parameters' posterior medians and examine the growth response functions during June, July, and August, when insolation is at its peak and allows the bulk of modeled growing to occur. We compute the proportion of summer months over the entire simulation in which the growth response to soil moisture (temperature) is strictly less than the growth response to temperature (soil moisture). If the modeled proportion is significantly more than the null hypothesis of half, than the site is classified as M-limited (T-limited). Sites for which the proportion cannot be statistically distinguished from 0.5 are classified as mixed-control sites. We then examine the structure of the parameter point estimates in multi-dimensional parameter space for each class of sites.

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3 Results

3.1 Pseudoproxy experiment (PPE) results

A plot of prior and posterior distributions of the four growth response parameters and the model uncertainty parameter for one representative site in the network is shown in Fig. 1. A set of such posterior distributions exists for every site in the experimental network. We compute statistics of these distributions to assess the skill of the parameter calibration method as described in Sects. 2.3.1 and 2.3.2.

Both posterior bias and root-mean-squared error tend to be on the order of 20% or less of the length of the prior interval for estimates of the parameters T_1 , T_2 , and M_2 (Fig. 2a, b, d). Only posteriors of the parameter M_1 tend to be systematically biased, with probability mass generally lower than the targets (Fig. 2c) due to prior probability mass generally favoring the lower half of the the prior support and targets that tend toward the upper end. Root-mean-squared error and bias for this parameter ranges up to 40% of the length of the prior intervals. While the posterior distributions of M_1 tend to exhibit greater RMSE and bias than those of the other parameters, these posteriors also have greater variance, and hence greater uncertainty. This result is shown by the comparatively large value of RMSE at values of bias close to zero. The large posterior variance of the M_1 posteriors is also evident in a plot of the ratio of posterior to prior variance, which is close to one at all sites for this parameter (Fig. 3, bottom-left panel). This ratio varies by location for both temperature threshold parameters T_1 and T_2 , and tends to be close to zero at most sites for the parameter M_2 (Fig. 3 remaining panels).

Comparisons of parameter estimates using the literature-based priors to those based on uniform priors show that the sensitivity of the parameter estimates to the prior distribution depends on both the site and the specific parameter in question (results not shown). At sites where the model is highly sensitive to any of VS-Lite's growth response parameters, the choice of prior model has little influence on the posterior mean and variance. Meanwhile, the prior model influences parameter estimates heavily at sites where the parameter in question has little effect on modeled growth.

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3.2 Observed proxy experiment (OPE) results

The point estimates of the VS-Lite parameters in the observed proxy experiment, given by the posterior medians, tend to cluster in space (Fig. 4). In particular, the estimated values of T_2 tend to occupy the lower end of the prior support in the West. The spatial structure of M_1 is also notable, with values tending to fall near the upper end of the prior for arid and semi-arid sites in the West. Point estimates of M_2 are close to the upper end of the prior range nearly uniformly across space.

The spatial distribution of Bayesian learning, parameterized by the ratio of posterior to prior variance, does not exhibit any notable spatial structure for T_1 and T_2 . Rather, the sites where the estimates of these parameters are influenced most heavily by the data are scattered throughout the experimental domain (Fig. 5). Estimates of M_1 are influenced very little by the data constraints almost uniformly across the experimental domain, while estimates of M_2 are influenced heavily by the data everywhere, indicating high model sensitivity to this parameter.

The size of the estimated model uncertainty parameter σ_W^2 is comparable across the calibration and validation interval in both the synthetic and observed data experiments (Fig. 6). Although the sites with the greatest values of σ_W^2 in the OPE show greater differences between calibration and validation interval estimates, note that these estimates are also more uncertain, since higher medians for inverse-gamma posteriors also implies higher variance. Finally, the model uncertainty is generally much greater in the OPE than in the PPE, with the median value of validation-interval σ_W^2 point estimates at 1.43 in the former case, and only 0.56 in the latter.

The point estimates of the parameters cluster in anomaly-parameter space according to the sites' classifications as temperature-limited, moisture-limited, or mixed-control sites (Fig. 7). The estimated values of T_1 fall below the mean local JJA temperature (not shown); in other words, the mean summer temperatures all fall above the threshold for nonzero growth at every site. Data at sites classified as temperature-sensitive constrain all estimates of T_2 to values above the mean local summer temperature. Summer

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temperature variations therefore influence modeled growth at these sites. Sites classified as moisture-limited or as having mixed controls tend to have values of T_2 that fall below local summer mean temperatures; thus temperature variability will have less of an effect on modeled growth. The results for the moisture parameters are similar.

All sites have calibrated values of M_1 falling below the climatological mean soil moisture content, so that there is enough moisture for modeled growth to occur across the experimental domain in summer. Calibrated values of M_2 are greater than local climatological mean soil moisture for all sites classified as moisture-limited, but mixed-control and temperature-limited sites tend to have values of M_2 that fall below the climatological summer mean.

Given that the parameter estimates of the lower thresholds T_1 and M_1 fall below mean summer climatological values at all sites, the distribution of the anomaly point estimates in $T_2 \times M_2$ space contains the most information about the modeled climate controls on growth (Fig. 7). In the second quadrant of such a plot (defined by anomaly- $T_2 = T_2' < 0$ and anomaly- $M_2 = M_2' > 0$) one would expect sites where moisture generally limits summer growth, since climatological temperatures tend to fall above the optimal temperature growth limit, but soil moisture tends to fall below its optimal growth limit. Most of the sites whose parameterizations end up in this quadrant are in fact classified as moisture-limited by our classification scheme. The fourth quadrant ($T_2' > 0$, $M_2' < 0$) would seem to define a region of parameter space describing temperature-limited growth, and indeed the sites whose estimated parameters are in this quadrant are nearly all classified this way. The sites that fall within quadrant III are exclusively mixed-control sites, as one would expect for locations where trees are sensitive to both variations in summer moisture and temperature variability.

The modeled climate controls on growth break the continental United States into roughly three regions. In both the pseudoproxy and observed proxy experiments, the Northwest contains mainly temperature-controlled sites (red markers in quadrant IV of Fig. 7), moisture-controlled sites fill the West and Midwest (blue markers in quadrant II of Fig. 7), and mixed-control sites are most common in the Southeast and along the

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eastern seaboard (green markers in quadrant III Fig. 7). This pattern is generally consistent with our knowledge of the climate sensitivity of the North American tree-ring network (e.g. Meko et al., 1993).

4 Discussion

The Bayesian inference scheme is skillful in recovering the known parameters used to create pseudoproxy ring-width series. Although real-world analogs to the pseudoproxy target model parameters may not be known, the skill in the pseudoproxy context supports the notion that the approach will estimate parameters that optimize VS-Lite's fit to observed tree-ring width chronologies. The results of the PPE and OPE are highly similar in terms of their spatial distributions of the modeled controls on growth, as well as the model sensitivities to the growth response parameters. These correspondences support the applicability of pseudoproxy experiment results to studies using observed proxy data.

In addition to point estimates of the parameters, the spread of the posterior distributions also provide measures of the estimation uncertainty and the model sensitivity to the parameters. This is a novel feature among parameter estimation schemes for forward models of tree-ring width. Previous studies either performed simple sensitivity analysis by varying one parameter at a time over a limited region of the parameter space (Evans et al., 2006; Anchukaitis et al., 2006), or else not at all (Fritts et al., 1999; Misson, 2004; Misson et al., 2004). We find that the VS-Lite model is generally least (most) sensitive to the value of M_1 (M_2), as the ratio of posterior to prior variance is very close to one (zero) at all sites in both pseudoproxy and observed proxy experiments (Figs. 3 and 5). The model sensitivity to the temperature thresholds T_1 and T_2 depends on the particular site.

Our sensitivity analysis indicates that the shape of prior distributions are of little consequence for parameter-site combinations where a high degree of learning occurs, indicating high model sensitivity to the parameter in question. At such locations, the

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resulting parameter estimates could be viewed as hypotheses for field studies aiming to provide observed physiological evidence either supporting or refuting the inferred values. By contrast, at sites at which the model is insensitive to a given parameter, the posterior inference is determined almost entirely by the prior model. Defaulting to the prior when the data contain little information is a standard feature of Bayesian analysis and underscores the importance of careful prior elicitation based on all available scientific evidence. This situation may occur when the data are very noisy, when the model is insensitive to the parameter in question, or when the length of the data series is limited. In the particular case that the data series is too short to inform the parameter value, the Bayesian approach can be viewed as automatically safeguarding against over-tuning the estimated parameters. This feature is ideal for parameter estimation to the degree that one has faith in the representation of the underlying science and its inherent uncertainty reflected in the prior distributions. Note that our publicly-available code includes flexible options for users to define their own priors, should new information from future field studies of tree growth render the default set of priors described here obsolete.

The choice of finite support or range is another component of prior specification that may heavily influence the posterior inference, as in the case of the parameter M_2 at most sites in this study. The posterior distributions of this parameter at most sites show high probability mass toward the upper bound of the compact prior support (see Fig. 1 and bottom right panel of Fig. 4), indicating that the data alone imply values of this parameter above the region allowed by the prior. However, the upper limit of the prior represents a physical constraint on biological thresholds for optimal moisture conditions for plant growth, as excessive soil moisture values may become detrimental to plant growth (Kozlowski, 1984). Given that the modeling of soil moisture within VS-Lite is known to be simplistic (Tolwinski-Ward et al., 2011), we believe the posteriors here represent an objective compromise between the data and prior knowledge of the parameter, given the uncertainty of VS-Lite.

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Posterior estimates of σ_W^2 computed during the parameter calibration are of similar size to those measured in an independent validation interval (Fig. 6), indicating that the algorithm provides a reasonable estimate of VS-Lite's uncertainty. The skill of the tuned model fit to data might be expected to degrade for periods with mean climatic conditions that differ greatly from those of the parameter calibration interval. However, the PRISM data do display some temperature trends and induce low-frequency modeled soil moisture variability over the period used in this study. The result that the calibration and validation interval model uncertainties are comparable shows that the parameter optimization is robust to at least the type of nonstationarity present in the PRISM data set (Fig. 6). A comparison of the typical size of σ_W^2 in the pseudoproxy experiment to that in the observed proxy experiment provides a sense of the size of model error that can be attributed to parameter uncertainty as opposed to other sources. The differences between the model output and target synthetic ring-width in the pseudoproxy experiments is completely accounted for by the variability of VS-Lite associated with parameter uncertainty. Symbolically, we can write this as $\sigma_{W_{PPE}}^2 = \sigma_{W_{PARAM}}^2$. The model residuals in the OPE can be attributed to both parameter uncertainty and other sources, such as processes unresolved by VS-Lite and non-climatic signal in the observed proxy data. Then we can write $\sigma_{W_{OPE}}^2 = \sigma_{W_{PARAM}}^2 + \sigma_{W_{OTHER}}^2$, assuming the parametric and other sources of noise are independent. Thus, for any given site, contributions to the model noise from sources independent of the parameter uncertainty can be easily estimated by running a PPE and taking the difference between the total variance minus the component $\sigma_{W_{PARAM}}^2 = \sigma_{W_{PPE}}^2$.

The location of parameter point estimates relative to local climatological means in multidimensional anomaly parameter space presents a graphical tool for understanding the climate controls on the modeled ring width signal (Fig. 7). At sites where VS-Lite reasonably represents growth, this type of plot could help identify and predict changes in the climate-proxy relationship that result from climatic nonstationarities driving mean environmental conditions across biological thresholds. In such cases of “divergence” (D’Arrigo et al., 2004; Carrer and Urbinati, 2006), one would expect the

point representing the optimal set of parameter choices to cross from one quadrant into another after the climatic shift.

In future studies, uncertainty in the parameter posteriors can likely be reduced by modeling the fields of parameters spatially, as sites close in space tend to take on similar optimal parameter values (Fig. 4). Since the parameter values are interpretable in terms of the climate controls on growth, any modeled spatial structure of the parameter fields likely holds information about the spatial distribution of climate controls that can be linked to mechanistic causes, such as orography, regional drought patterns, the timing of snowmelt, regional climatological means and variances, or teleconnections to larger global patterns of climatic variability.

5 Conclusions

The Bayesian calibration scheme presented here skillfully recovers parameter estimates near the values used to create synthetic tree-ring width data. The spread of the posterior distributions show that the model fit to data is generally sensitive (insensitive) to the value of the moisture threshold M_2 (M_1), and may or may not be sensitive to the temperature threshold parameters depending on location. Estimates of the VS-Lite model's uncertainty provided by the scheme appear to be robust outside of the interval used for calibration. The location of estimated parameters relative to local climatology in multidimensional parameter space provides insight into the climate controls on modeled tree-ring growth, and may be useful for some studies of the “divergence” phenomenon.

Supplementary material related to this article is available online at:
<http://www.clim-past-discuss.net/9/615/2013/cpd-9-615-2013-supplement.zip>.

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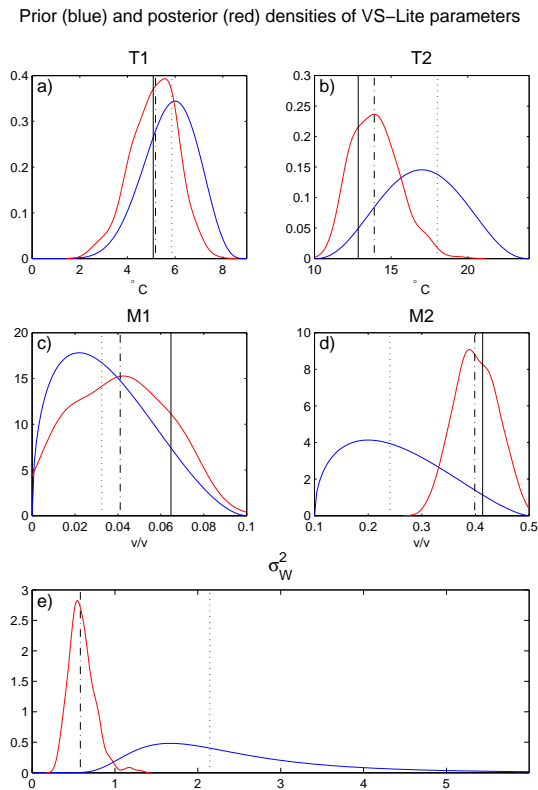


Fig. 1. Prior (blue) and estimated posterior (red) densities for the parameters of VS-Lite, conditioned on pseudoproxy and PRISM climate data at the Sipsey Wilderness site in Alabama. (Plot of posterior density given by a smooth approximation to a frequency plot of ensemble members.) Solid black vertical lines give the target values of the growth response parameters, dotted black lines give prior medians, and dash-dot black lines give the posterior medians.

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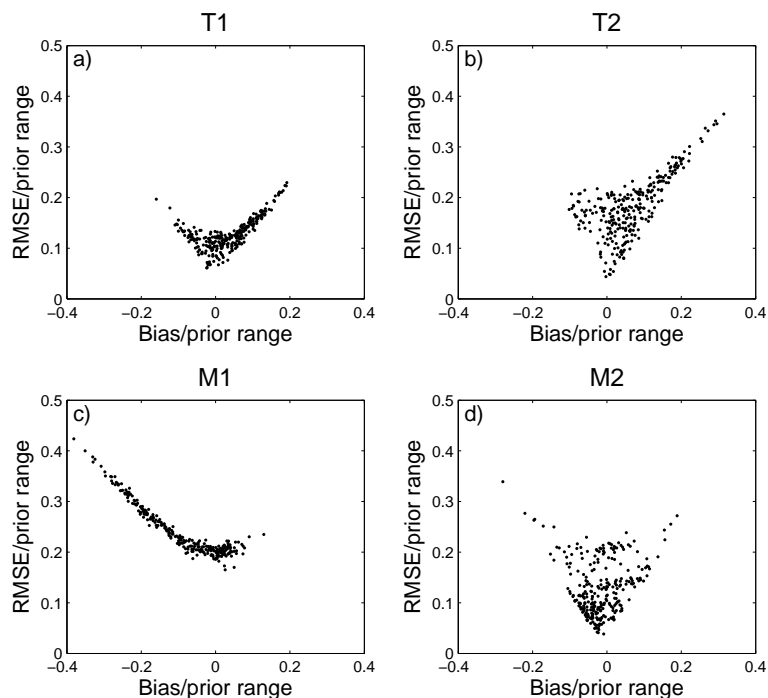


Fig. 2. Root-mean-squared error versus bias of parameter estimates in the pseudoproxy experiment, with both statistics shown relative to the length of each prior's support. Note that the structure in the scatter plots is a result of the fact that by definition $\text{RMSE}(X) = \sqrt{\text{Var}(X) + \text{Bias}^2(X)}$.

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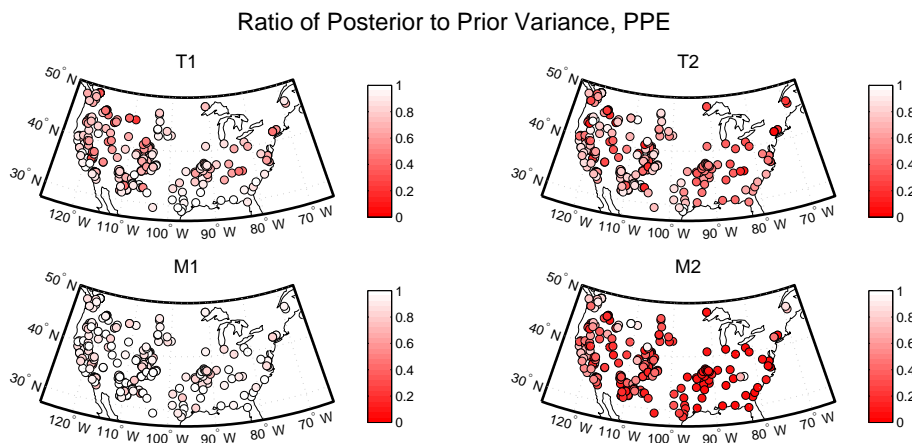
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Fig. 3. Ratio of posterior to prior variance for the four growth response parameters as a measure of Bayesian learning in the pseudoproxy experiment. Color scale calibrated so that sites with smaller (larger) values of the ratio, indicating greater (lesser) Bayesian learning, have darker (lighter) coloration.

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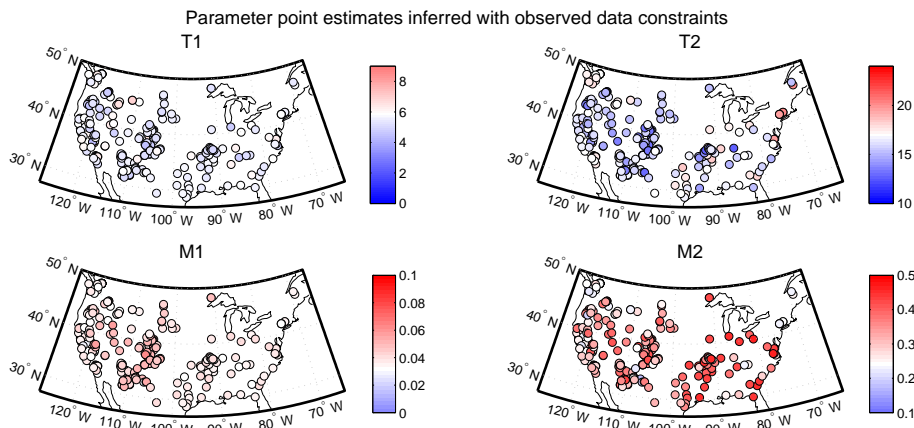


Fig. 4. Posterior medians of VS-Lite growth parameters. Note that the color scale for each parameter ranges over the interval on which the prior is supported, and is calibrated so that white indicates the prior median.

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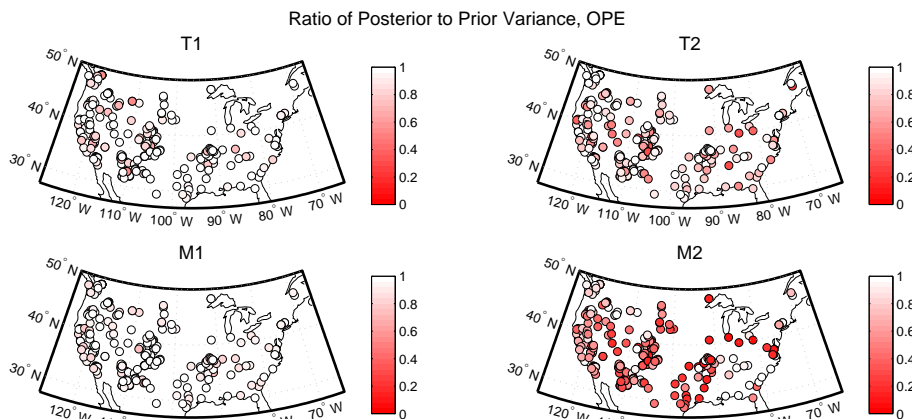


Fig. 5. Ratio of posterior to prior variance for the four growth response parameters as a measure of Bayesian learning in the observed proxy experiment. Color scale calibrated so that sites with smaller (larger) values of the ratio, indicating greater (lesser) Bayesian learning, have darker (lighter) coloration.

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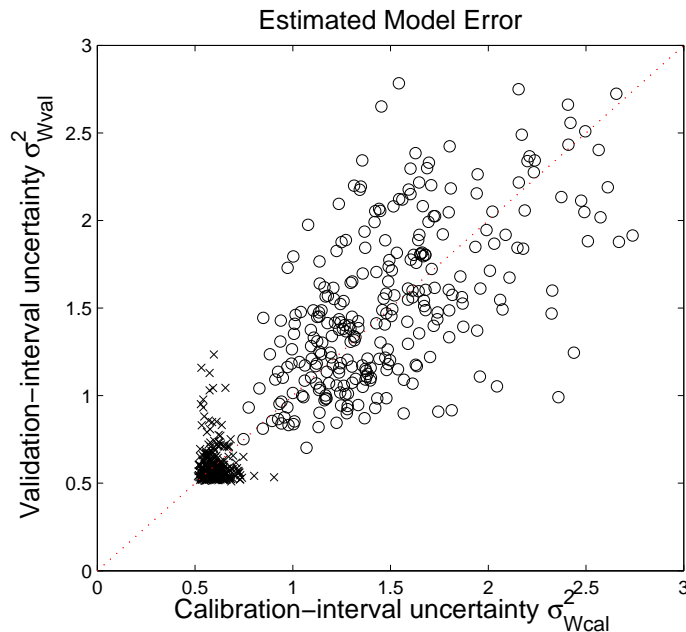


Fig. 6. Validation-interval model uncertainty, versus calibration-interval model uncertainty for pseudoproxy experiment (x-markers) and observed proxy experiment (o-markers). Dotted red line is $y = x$.

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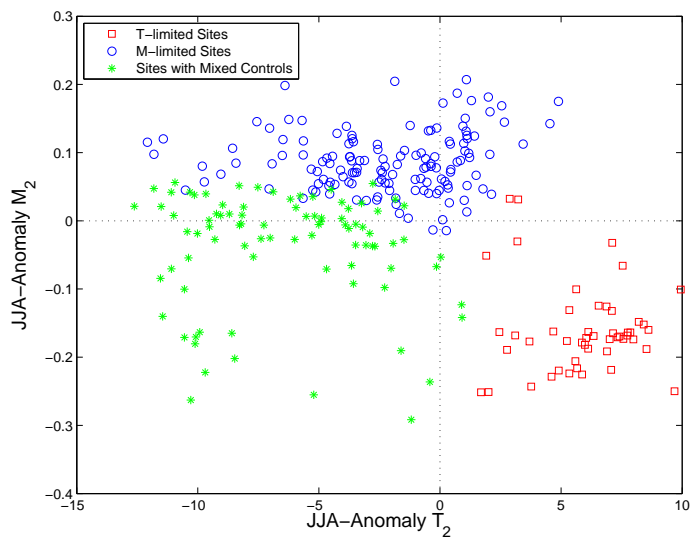


Fig. 7. Plot of estimated M_2 versus estimated T_2 at each site, with both parameters measured as anomalies relative to the local climatological mean summer temperature. Color of points denote the classification of the controls on modeled growth at each site. $x = 0$, $y = 0$ define the mean local summer temperature and soil moisture content, respectively.

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