

Assessing Uncertainty in a Stand Growth Model by Bayesian Synthesis

Edwin J. Green, David W. MacFarlane, Harry T. Valentine, and William E. Strawderman

ABSTRACT. The Bayesian synthesis method (BSYN) was used to bound the uncertainty in projections calculated with PIPESTEM, a mechanistic model of forest growth. The application furnished posterior distributions of (a) the values of the model's parameters, and (b) the values of three of the model's output variables—basal area per unit land area, average tree height, and tree density—at different points in time. Confidence or credible intervals for the output variables were obtained directly from the posterior distributions. The application also provided estimates of correlation among the parameters and output variables. BSYN, which originally was applied to a population dynamics model for bowhead whales (Raftery et al. 1996, JASA 90:402–442), is generally applicable to deterministic models. Extension to two or more linked models is discussed. A simple worked example is included in an appendix. *For. Sci.* 45(4):528–538.

Additional Key Words: Loblolly pine, mechanistic models, confidence intervals, posterior distributions.

AS CONCERNs OVER POTENTIAL GLOBAL CHANGE have intensified, forest growth modelers have become increasingly interested in mechanistic models of forest growth. Such models, which quantify our knowledge and theories of tree physiology and morphology, promise to provide understanding, as well as useful predictions, of the responses of forests to atmospheric and climatic variables. Unfortunately, however, a deterministic, mechanistic model ordinarily doesn't furnish, for its predictions, interval estimates with associated statements of coverage probabilities. Since the point predictions from a model have probability zero of being *exactly* correct, this presents a problem for those who would use a mechanistic model for decision-making purposes. The predictions should be *close* to the true value of the quantity of interest, but close is undefined. Thus an analysis of model uncertainty must be undertaken.

The Bayesian synthesis method, first proposed by Raftery et al. (1995), furnishes interval estimates with associated probability statements for outputs of mechanistic models. In this article we use a variant of Raftery et al.'s original method to obtain interval estimates for predictions from PIPESTEM, a mechanistic model of forest stand growth. A non-Bayesian, Monte Carlo approach for determining interval estimates for PIPEstem predictions was presented by Gertner et al. (1996). With the latter procedure, it is not readily apparent how to incorporate prior distributions and data or likelihoods into the analysis in a formal manner. This occurs naturally with Bayesian synthesis.

The plan of this article is as follows: in the next two sections, we summarize PIPEstem and Bayesian synthesis, respectively. These sections are followed by an application of Bayesian synthesis to PIPEstem. Finally, the last section includes concluding remarks and suggested future directions.

Edwin J. Green is Professor, Department of Ecology, Evolution & Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901-8551—Phone: (732) 932-9152; Fax: (732) 932-8746; E-mail: green@crssa.rutgers.edu. David W. MacFarlane is Graduate Research Assistant, Department of Ecology, Evolution & Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901-8551—E-mail: mcfarln@crssa.rutgers.edu. Harry T. Valentine is Research Forester, Louis C. Wyman Forest Sciences Laboratory, USDA Forest Service, Durham, NH 03824-0640—E-mail: hvalentine/ne_du@fs.fed.us. William E. Strawderman is Professor, Department of Statistics, Rutgers University, 110 Frelinghuysen Road, Piscataway, NJ 08854—E-mail: straw@stat.rutgers.edu.

Acknowledgments: Supported by NSF grant #DEB-9602201; a grant from the USDA Forest Service, Northern Global Change Program; and New Jersey Agricultural Experiment Station funds. The authors thank R.L. Amateis and H.E. Burkhart for contributing data to this study, R.L. Bailey and M.A. Buford for help in assembling growth and yield model information, and A.E. Raftery and G.H. Givens for helpful discussions on Bayesian synthesis. Thanks are also extended to P. Radtke, anonymous reviewers, and the editor for helpful suggestions which greatly improved the manuscript.

PIPESTEM

The mechanistic model PIPESTEM describes the carbon balance and growth of an even-aged monospecific stand on an annual basis (Valentine 1988, 1990, Valentine et al. 1997). The version we used was calibrated for loblolly pine.

The mathematical model consists of 16 differential equations and additional ancillary functions. The differential equations completely describe the dynamic properties of a single model stand. The state variables that characterize the model stand ordinarily are initialized with measurements from a real stand that has aged one or more years since planting. Simultaneous numerical integration of the differential equations provides values of the state variables at any subsequent point in time, and these values serve as predictions for the real stand.

The growth rate of the model stand is defined as the difference between rates of production and loss of dry matter. Dry matter is measured in units of carbon (C) and the rate of growth per unit land area is measured in units of C/ha/yr. The rate of production of dry matter is defined as the difference between the rate of production of C substrate and the consumption of C substrate through maintenance and constructive respiration. These metabolic rates also have dimensions with units of C/ha/yr.

Dry matter is partitioned into foliar, feeder-roots, and woody components. The proportion of C substrate allocated to the production of dry matter of each component is constrained to keep the morphological dimensions of the model stand in accord with pipe model theory (Shinozaki et al. 1964a,b). Losses of dry matter result from the turnover of foliage and feederroots, the death and self-pruning of branches associated with crown rise, and the death of trees associated with self-thinning.

In addition to the information about the carbon balance and production and loss of dry matter, PIPESTEM also furnishes total basal area (m^2/ha), average tree height (m), dominant tree height (m), average height to the base of a live crown (m), and tree density (stems/ha) on an annual timestep. Estimates or measurement of these four variables (ordinarily obtained from a real stand aged 1 yr or more) suffice to initialize the PIPESTEM model.

Valentine et al. (1997) modeled the growth of loblolly pine stands at four sites: Buckingham, Halifax, and Middlesex Counties in Virginia and Northampton County in North Carolina. These areas were chosen because they are the locations of sample plots for the Virginia Tech Loblolly Pine Growth and Yield Research Cooperative, and the data from the sample plots could be used to evaluate the predictions from PIPESTEM. Predictions from the model matched observed data well (Valentine et al. 1997).

In this study, we use a version of PIPESTEM that includes a routine which allows the user to specify the site index. The total number of model parameters in this version of PIPESTEM is 24.¹ Users must specify values

for the 24 parameters, and a solution of the model is available for all feasible combinations.

Bayesian Synthesis

Raftery et al. (1995) developed the Bayesian synthesis (BSYN) method to characterize uncertainty in mechanistic models. The original application was a population dynamics model for bowhead whales, but the methodology is applicable in other situations. The basic approach is to use all available information to generate a *joint premodel distribution* on all model inputs, θ , and model outputs, ϕ . The model is then used to translate the premodel distribution to a *joint postmodel distribution* on θ and ϕ by importance sampling. We can think of the model as a mapping $\{(\theta, \phi) : \phi = \Phi(\theta)\}$, where $\Phi(\cdot)$ is a submanifold in ϕ -space. In other words, the outputs of the model are functions of the inputs. Let $p(\theta, \phi)$ represent the joint premodel distribution of θ and ϕ , and let $\pi(\theta, \phi)$ be the joint postmodel distribution. A key feature of Bayesian synthesis is that

$$\pi(\theta, \phi) \propto p(\theta, \Phi(\theta)) \text{ if } \phi = \Phi(\theta), \quad (1)$$

$$\propto 0 \text{ otherwise.}$$

The joint postmodel distribution can be marginalized to obtain a postmodel distribution of any quantity of interest. Interval estimates with valid posterior probability statements are available from the marginalized posterior distributions. For more details, consult Raftery et al. (1995) (including discussion and rejoinder).

Borel's Paradox

Unfortunately, the original BSYN method suffered from Borel's Paradox (Wolpert 1995), which was manifested in a basic incoherence in the procedure. The problem may be stated as follows: the user specifies premodel distributions on the model inputs and outputs. As was noted earlier, however, the model is a transformation from θ to ϕ . Thus the model together with the premodel distribution of the inputs, θ , provides an implied premodel distribution on the outputs. Similarly, the specified prior on the outputs could be used to develop an implied prior on the inputs by running the model backwards. Of course the implied distributions will not be identical to the specified premodel distributions. Hence the incoherence; two different "prior" distributions for both inputs and outputs.

Consider a general situation where information on θ or ϕ or both is represented by a traditional Bayesian prior distribution and/or a likelihood based on whatever data are available, and assume that the premodel information on θ and ϕ is from independent sources, as are the data. Then each premodel distribution may be thought of as composed of two parts: a likelihood and a prior, i.e.,

$$p(\theta, \phi) \propto q_\theta(\theta)L_\theta(\theta)q_\phi(\phi)L_\phi(\phi) \quad (2)$$

where $p(\theta, \phi)$ is the joint premodel distribution; $q_\theta(\theta)$ and $q_\phi(\phi)$ are premodel prior distributions on θ and ϕ , respectively; and $L_\theta(\theta)$ and $L_\phi(\phi)$ are likelihoods for θ and ϕ , respectively. Since likelihoods are known to be invariant

¹ Valentine et al. (1997) report on a version of PIPESTEM with 25 parameters. The number is reduced by one here because we included a routine to derive the parameter s from site index.

to transformation (e.g., see Schweder and Hjort 1996), the difficulty must lie with the premodel prior distributions.

Raftery, Poole, and Givens (1996) (hereafter referred to as RPG) and Givens and Roback (1997, hereafter referred to as GR) suggested a solution to the Borel paradox: pool the implied premodel distribution with the specified premodel distribution. The emphasis in both studies was on pooling the implied and stated prior distributions of the outputs in order to generate samples from the postmodel distribution of the outputs. The methods reported could be used to generate postmodel distributions on the inputs, but only if the model was a 1–1 mapping from θ to ϕ .

Raftery and Poole (1997) and Poole and Raftery (1998), hereafter referred to as RP and PR, respectively, presented the full pooling method for pooling the stated and implied priors on both the inputs and outputs, resulting in samples from the postmodel distributions of θ and ϕ . We used the latter approach, and a brief description of the method follows.

Full Pooling in Bayesian Synthesis

Let $q_\theta^i(\phi)$ represent the prior distribution on the outputs that is implied by the prior on the inputs. Geometric (or logarithmic) pooling of $q_\theta^i(\phi)$ and the specified prior on ϕ , $q_\phi(\phi)$, yields

$$q_\theta^p(\phi) \propto q_\theta^i(\phi)^\alpha q_\phi(\phi)^{1-\alpha} \quad (3)$$

where $q_\theta^p(\phi)$ is the pooled distribution.

RP point out that logarithmic pooling conforms to the Zero Preservation Property (ZPP), while other pooling methods do not. Briefly, the ZPP requires that if one prior-assigns a probability of zero to a particular set of values, then the pooled prior must also assign a probability of zero to that set.

We must have $\alpha = 1/2$ in (3) to ensure that the method is invariant to relabeling of inputs and outputs (i.e., running the model backwards) except in the unusual case of a linear mechanistic model (RP and GR). In addition, setting $\alpha = 1/2$ places equal weight on both the stated and implied priors (RP).

As alluded to earlier, $q_\theta^p(\phi)$ could be used to develop a postmodel distribution for ϕ (RP and GR presented algorithms to do this). Denote the postmodel distribution of ϕ derived in this way by $\pi_\phi(\phi)$. Unless the model is 1–1, the postmodel distribution for θ is not immediately available from $\pi_\phi(\phi)$, because numerous points in θ -space may map onto the same point in ϕ -space. RP and PR solved this problem as follows (see their articles for more details): Let $Z = \{\theta_1, \theta_2, \dots\}$ be the set of θ values that map onto a particular value of ϕ , say ϕ_i , and let θ_z represent any value of θ in the set Z , i.e., $\phi_i = \Phi(\theta_z)$. Then these θ_z 's should be assigned a collective prior probability equal to $q_\theta^p(\phi_i)$; since this is the pooled prior probability of the ϕ value onto which the θ_z 's map. This begs the question: How should this prior probability be allocated to the θ_z 's in Z ? RP and PR distributed the prior probability among the θ_z 's in proportion to the specified prior distribution on θ , $q_\theta(\theta)$. Note that the total specified prior probability over the set Z must equal the implied prior probability of the ϕ value onto which the θ_z 's map, $q_\theta^i(\Phi(\theta_z))$. Then we have

$$q_\theta^p(\theta_z) = q_\phi^p(\Phi(\theta_z)) \frac{q_\theta(\theta_z)}{q_\theta^i(\Phi(\theta_z))} \quad (4)$$

According to (3),

$$q_\phi^p(\phi_i) \propto q_\theta^i(\Phi(\theta_z))^{1/2} q_\phi(\Phi(\theta_z))^{1/2} \quad (5)$$

and hence

$$q_\theta^p(\theta_z) \propto q_\theta(\theta_z) \left(\frac{q_\phi(\Phi(\theta_z))}{q_\phi^i(\Phi(\theta_z))} \right)^{1/2} \quad (5)$$

Once $q_\theta^p(\theta)$ is in hand, Bayes theorem can be readily applied as in (2) to yield the premodel distribution for θ . The invariance problem (and Borel's paradox) vanishes because we no longer have conflicting premodel prior distributions. We invoke (1) to yield the postmodel distribution of θ , i.e.,

$$\pi_\theta(\theta) \propto q_\theta^p(\theta) L_\theta(\theta) L_\phi(\Phi(\theta)) \quad (6)$$

Finally, if we can generate a sample from $\pi_\theta(\theta)$ then we can run the model for each observation in the sample. The resulting outputs would constitute a sample from $\pi_\phi(\phi)$.

Algorithm for Full Pooling and Bayesian Synthesis

RP presented the following importance sampling algorithm to generate samples from $\pi_\theta(\theta)$ and $\pi_\phi(\phi)$. The geometric pooling of the specified and induced priors on both the inputs and the outputs is automatically accomplished by the algorithm.

1. Select a sample of size m of values of θ from the distribution $q_\theta(\theta)$. Denote the sample by $(\theta_1, \theta_2, \dots, \theta_m)$.
2. For each value of θ sampled in step 1, run the model to obtain the corresponding value of ϕ . This will result in the sample $(\phi_1, \phi_2, \dots, \phi_m)$.
3. Use nonparametric density estimation to obtain an estimate of the resulting induced density of ϕ_k , $k = 1, 2, \dots, m$. Denote the estimated density by

$$\hat{q}_\phi^i(\phi_k)$$

4. Form the importance sampling weights

$$w_k = \left(\frac{q_\phi(\Phi(\theta_k))}{\hat{q}_\phi^i(\Phi(\theta_k))} \right)^{1/2} L_\theta(\theta_k) L_\phi(\Phi(\theta_k)), \quad k = 1, 2, \dots, m. \quad (7)$$

5. Sample l values from the discrete distributions (obtained in steps 1 and 2) with values θ and ϕ and probabilities proportional to w_k .

The resulting samples of size l are approximate samples from $\pi_\theta(\theta)$ and $\pi_\phi(\phi)$, the geometrically pooled postmodel distributions for θ and ϕ , respectively. The postmodel distributions incorporate everything that is known about θ and ϕ , including data and prior opinion. They can be regarded as posterior distributions, constrained [by (1)] to agree with the

mechanistic model. A simple, worked example application of BSYN and the above algorithm to a two-parameter model is provided in Appendix A.

Application

PIPESTEM is calibrated for loblolly pine. Given initial stand conditions (site quality, average diameter, height, and height to the live crown, and number of stems per hectare, and stand age), the model projects the growth of the stand over time. In the remaining text we will refer to the 24 model parameters as *inputs*. Among the outputs produced by the model are basal area (m^2/ha), average stand height (m), and number of stems per hectare. Denote these variables by B , H , and N , respectively. We used PIPESTEM to simulate the growth of a model loblolly pine stand on the Upper Coastal Plain of North Carolina.

Spacing Trial Data

The Loblolly Pine Growth and Yield Cooperative at Virginia Tech has installed spacing trials at four locations in Virginia and North Carolina. At each location, there are three replications of a number of spacings. The plots have been measured annually. Available data afforded calculation of average stand height, basal area, and number of stems per hectare. We arbitrarily assumed our model stand was planted at location 3 (Roanoke Rapids, North Carolina). Data from plots at this location were used to compute $L_\phi(\theta)$, the likelihood for the outputs. We did not specify a likelihood on the inputs, since we had no data on which to base one. In essence this means we assumed a constant likelihood for θ .

Premodel Distributions

Likelihood for Model Outputs

Four of the spacings in the Spacing Trial data (1.2 m \times 3.6 m, 3.6 m \times 1.2 m, 1.8 m \times 2.4 m, and 2.4 m \times 1.8 m) yielded identical planting densities of 2242 trees/ha. Hence, we chose this as our planting density. At the time of this research, the latest data available were for age 12; hence, we used age 12 data. The likelihood was assumed to be a three-dimensional Gaussian distribution, and the 12 observations (3 replications \times 4 spacings) on basal area per hectare, average stand height, and number of stems per hectare were assumed to be independent realizations from this distribution. The mean basal area, height, and number of stems on these 12 plots were 31.5 m^2/ha , 10.9 m, and 2101.3 stems/ha, respectively.

Prior Distribution on Model Inputs

A key feature of Bayesian Synthesis is that the premodel prior distributions $q_\theta(\theta)$ on the inputs should reflect all that is known regarding their feasible values. Consequently, we researched each of the 24 inputs (i.e., parameters) of PIPESTEM. This was a lengthy and somewhat tedious process, but such endeavors are critical to the valid application of Bayesian procedures. The results of this study are contained in MacFarlane et al. (1999). For brevity, we will summarize the findings here.

We assumed that the inputs were premodel independent. We recognized that this was unlikely to be true, but we were

unable to specify reasonable prior covariances. Hence we decided to allow the model and available data to induce covariances in the postmodel distributions (in fact, one of the virtues of Bayesian synthesis is that such covariances are available at the end of the procedure).

The inputs are defined in Appendix B, while their premodel prior means, standard deviations, and densities are presented in Table 1. With five exceptions, we assumed the premodel prior distributions to be Gaussian. For z_f and z_w we were able to specify upper and lower bounds in addition to means and standard deviations. Hence rather than using unbounded Gaussian densities for these parameters, we chose to use beta densities. The beta density parameters were computed from the bounds, means, and standard deviations using the method described in Johnson and Kotz (1970, p. 44).

Our premodel prior distributions for μ_1 , μ_2 , and ρ were rectangular. We could find no published information on these three parameters. Hence we made liberal guesses regarding the minimum and maximum values, and specified the distributions to be flat in between.

Prior Distribution on Model Outputs

We obtained a site index of 23.4 m (base age 25) for location 3 as follows: for all plots at this location except those planted at 2242 trees/ha, we determined the average height at age 12 of the 7 tallest trees per plot. The mean of these averages was then input into the Amateis et al. (1984) Coastal Plain site index equation to determine a site index value. Using this site index and the planting density, we derived prior distributions on three of the model outputs (basal area per hectare, average stand height and number of stems per hectare) at age 12 with the aid of four common growth and yield models (Bailey et al. 1985, Amateis et al. 1984, Clutter et al. 1984, and Hafley et al. 1982). Unfortunately, it is not common for model developers to provide sufficient information to develop variance estimates. Hence we

Table 1. Mean, standard deviation, and density for premodel prior distributions on model inputs (parameters).

Parameter	Mean	SD	Density
c_f	0.222	0.058	Gaussian
c_r	0.290	0.108	Gaussian
c_w	0.213	0.057	Gaussian
z_f	282.300	14.500	Gaussian
z_r	179.000	76.000	Beta
z_w	235.000	105.000	Beta
m_f	0.730	0.254	Gaussian
m_r	1.060	0.217	Gaussian
m_w	0.057	0.020	Gaussian
α	0.734	0.023	Gaussian
β	1.900	0.440	Gaussian
γ	0.762	0.110	Gaussian
ζ	14.422	4.503	Gaussian
θ_1	1.510	0.220	Gaussian
θ_2	0.535	0.116	Gaussian
λ	0.713	0.014	Gaussian
μ_1	8.500	3.750	Uniform
μ_2	7.000	2.890	Uniform
v_f	1.600	0.040	Gaussian
v_r	0.489	0.282	Gaussian
ρ	50.000	14.430	Uniform
ϕ	0.990	0.040	Gaussian
ψ	0.510	0.230	Gaussian
ω_1	0.273	0.027	Gaussian

assumed a Gaussian prior distribution on the outputs with a mean equal to the average of the predictions from the four models, and a covariance matrix derived from observations on these variables from plots planted at densities of 2242 trees/ha at locations 1, 2, and 4 in the Spacing Trial data. The mean ($\tau = (B, H, N)'$) and covariance matrix Σ were

$$\tau = \begin{bmatrix} 31.6 \\ 12.6 \\ 1,942.4 \end{bmatrix} \quad \Sigma = \begin{bmatrix} 14.77 & -1.02 & 685.08 \\ & 0.69 & -94.42 \\ & & 55,266.42 \end{bmatrix}$$

Model Stand Specification

In all runs of PIPESTEM, we initialized our stand at 2242 trees/ha on an area with a site index of 23.4 m. The initial (age 1) average diameter (d_{av}) and height (h_{av}) were specified to be equal to the averages calculated from the plots planted at 2242 trees/ha at location 3 ($d_{av} = 1.12$ cm, $h_{av} = 0.41$ m). Initial average height to the base of the live crown was arbitrarily specified to be 0.1 m.

Details of Bayesian Synthesis for PIPESTEM

We used the algorithm in section 3. In step 3, we used nonparametric density estimation with a Gaussian kernel and Terrell's constant (e.g., see Scott 1992 or Terrell 1990). The sample sizes were $m = 50000$, and $l = 5000$.

Let $\pi_\theta(\theta)$ and $\pi_\phi(\phi)$ denote the postmodel distributions of θ and ϕ , respectively. The Bayesian Synthesis method yields arbitrarily large samples from $\pi_\theta(\theta)$ and $\pi_\phi(\phi)$. Due to the duality between large samples and their generating distributions, we can base our inferences on the samples. Note that the sample from $\pi_\theta(\theta)$ may be thought of as a sample of model trajectories. Thus, although $\pi_\phi(\phi)$ is a sample from the postmodel distribution of ϕ at age 12, we can easily obtain postmodel distributions for ϕ at any age by running the model to the desired age for each combination of inputs in the sample from $\pi_\theta(\theta)$.

Results

Histograms from the postmodel distributions of B , H , and N at ages 12 and 50 are presented in Figure 1, and the corresponding smoothed densities are shown in Figure 2. With these samples it is possible to construct valid credible intervals. For example, in Table 2 we present the mean, and the 2.5 and 97.5 percentiles for the samples in Figure 1. The percentiles may be regarded as endpoints of approximate 95% credible intervals.

Several of the histograms and/or smoothed densities suggest bimodal distributions. Another noteworthy outcome is that while the specified prior mean for B of 31.6 m²/ha was near the center of the age 12 posterior density, the specified prior values for H (12.6 m) and N (1942.4 stems/ha) do not appear to be plausible values according to the age 12 posterior densities. On the other hand, the observed means from location 3 which entered through the likelihood (31.5 m²/ha, 10.9 m, 2101.3 stems/ha) all appear to be very reasonable values according to Figures 1 and 2. This is usual in Bayesian analysis; given a relatively diffuse prior, the posterior is ordinarily strongly influenced by the data.

The posterior density for number of stems at age 50 is somewhat surprising. Of the 5000 observations in the age 50 sample, 8% had fewer than 100 stems/ha. This indicates that about one-tenth of the time we can expect very poor survival. Commonly used yield tables predict somewhat greater survival. For instance, the survival model of Bailey et al. (1985) predicts survival of 335 stems/ha at age 50. However, growth and yield models usually are based on data from much younger stands (loblolly pine stands tend to be harvested well before age 50), and published studies show remarkable variation in predicted numbers of surviving stems per unit area (Burkhart et al. 1981). Long-term studies with many replications would be required to determine whether our results are reasonable.

It is possible to gauge the influence of the 12 plots from location 3 on the marginal posterior distributions by eliminating the likelihood on the outputs from the procedure, and proceeding as if we had no data. In this case the marginal posteriors depend only on the prior distributions for the inputs and outputs, and the model. We did this and the results are presented for age 12 in Figure 3. A comparison of Figure 3 with Figures 1 and 2 indicates that the data exerted considerable influence, as would be expected. In particular, the posterior distributions have a much wider spread than their counterparts in Figures 1 and 2. The means from the samples in Figure 3 are 31.5 m²/ha for basal area, 12.2 m for height, and 1951.6 stems/ha for tree density. Hence when the likelihood is included, the posterior means for height and density are closer to the observed means at location 3 than when the likelihood is removed. For basal area, the prior mean and the mean of the location 3 data are very close (31.6 m²/ha and 31.5 m²/ha, respectively) and the posterior mean obtained without incorporating the data from location 3 (31.5 m²/ha) is marginally closer to both than is the posterior mean obtained using the location 3 data (33.7 m²/ha). However, the differences among the marginal posterior means shown in Figures 1–3 are minor compared with the changes in scale. As mentioned above, it is usual in a Bayesian analysis for the data to exert more influence on the posterior distributions than the prior distributions (e.g., see Green et al. 1994). The obvious impact of the data in the present study was such that we did not feel that additional explorations with alternative prior distributions were warranted, especially since the priors employed represented our best understanding of the potential values of the model parameters.

In addition to posterior distributions on the outputs, Bayesian synthesis also yields posterior distributions on the inputs. These may be useful for future development of the mechanistic model, or as prior distributions for the next application of the model. In this case, we were interested in assessing posterior correlations among the inputs. With 24 inputs, we were able to compute 276 pairwise posterior correlation coefficients. The average posterior pairwise correlation was 0.005, while the average of the absolute values was 0.14. Of the 276, 36 were greater than 0.25 in absolute value, and 2 were greater than 0.5 in absolute value. Using a standard normal significance test (see, e.g., Sokal and Rohlf 1995, p. 574), 47% of the correlations were significantly

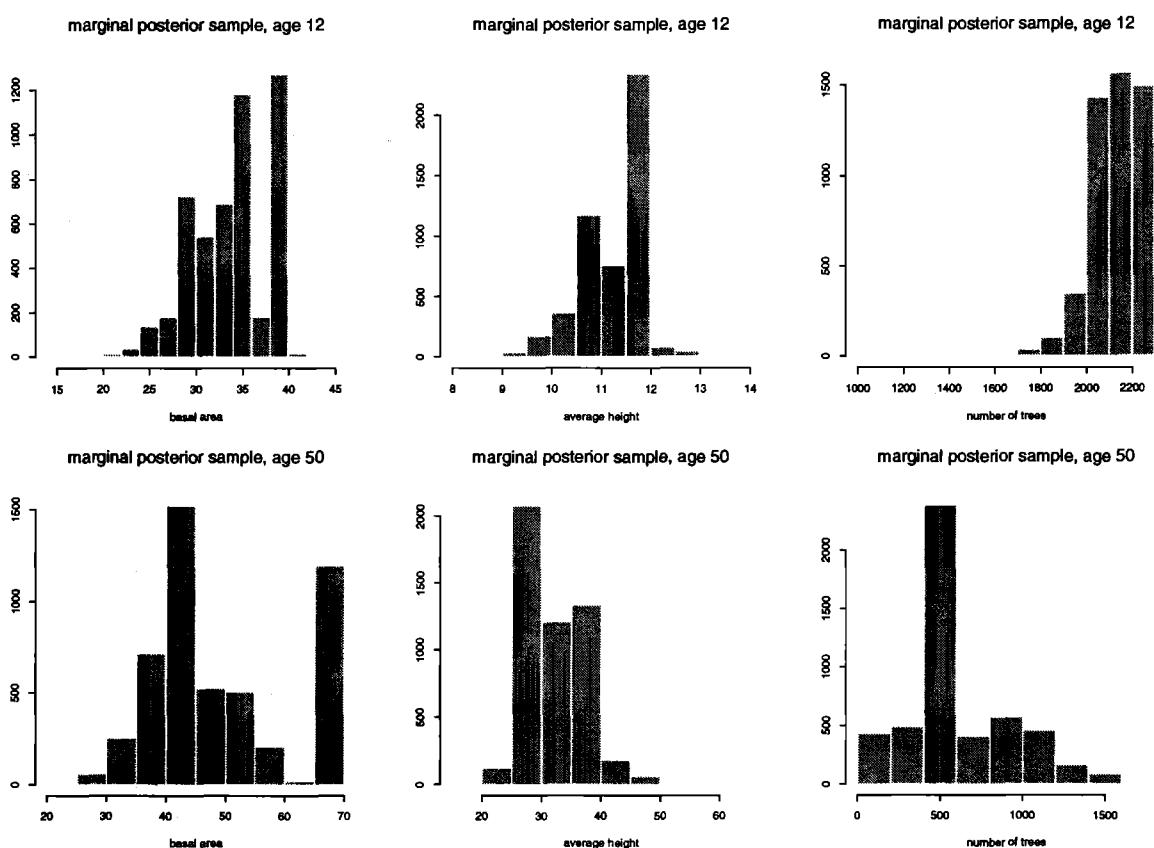


Figure 1. Histograms from marginal posteriors at ages 12 and 50.

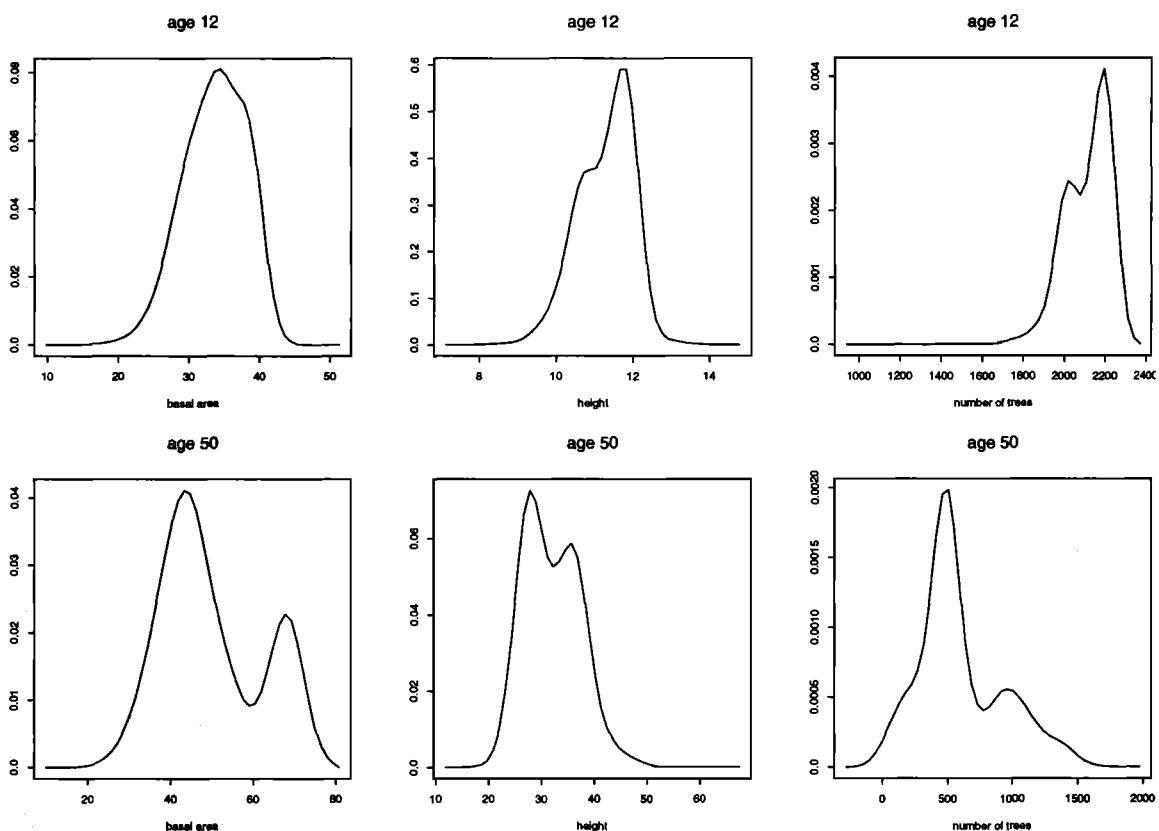


Figure 2. Smoothed marginal posterior densities at ages 12 and 50.

Table 2. Means and approximate 95% credible intervals for posterior distributions in Figure 1.

Attribute	Mean	Lower limit (2.5 percentile)	Upper limit (97.5 percentile)
B, age 12	33.7	24.9	38.6
B, age 50	49.7	32.1	68.0
H, age 12	11.3	9.8	12.0
H, age 50	32.0	25.0	41.6
N, age 12	2,110.8	1,869.5	2,212.1
N, age 50	596.5	74.9	1,377.0

different from zero at the 0.05 level, and 44% were significant at the 0.01 level.

The maximum observed posterior correlation was 0.61, between ρ and γ . As an example of the type of information available from an application of BSYN, we present the

marginal posterior distributions for these two parameters and a scatterplot of their 5000 values from the joint posterior distribution in Figure 4.

There was no particular pattern with regard to the parameters represented in the 20 highest absolute posterior correlations. Of the 24 parameters, only ϕ and ω_1 were not represented among the 20 highest absolute posterior correlations, while ζ , c_w , λ , and μ_1 were each represented three times. At present, the patterns and implications of these correlations are not clear.

Conclusion

Bayesian synthesis is a useful means of generating posterior distributions and/or interval estimates for the

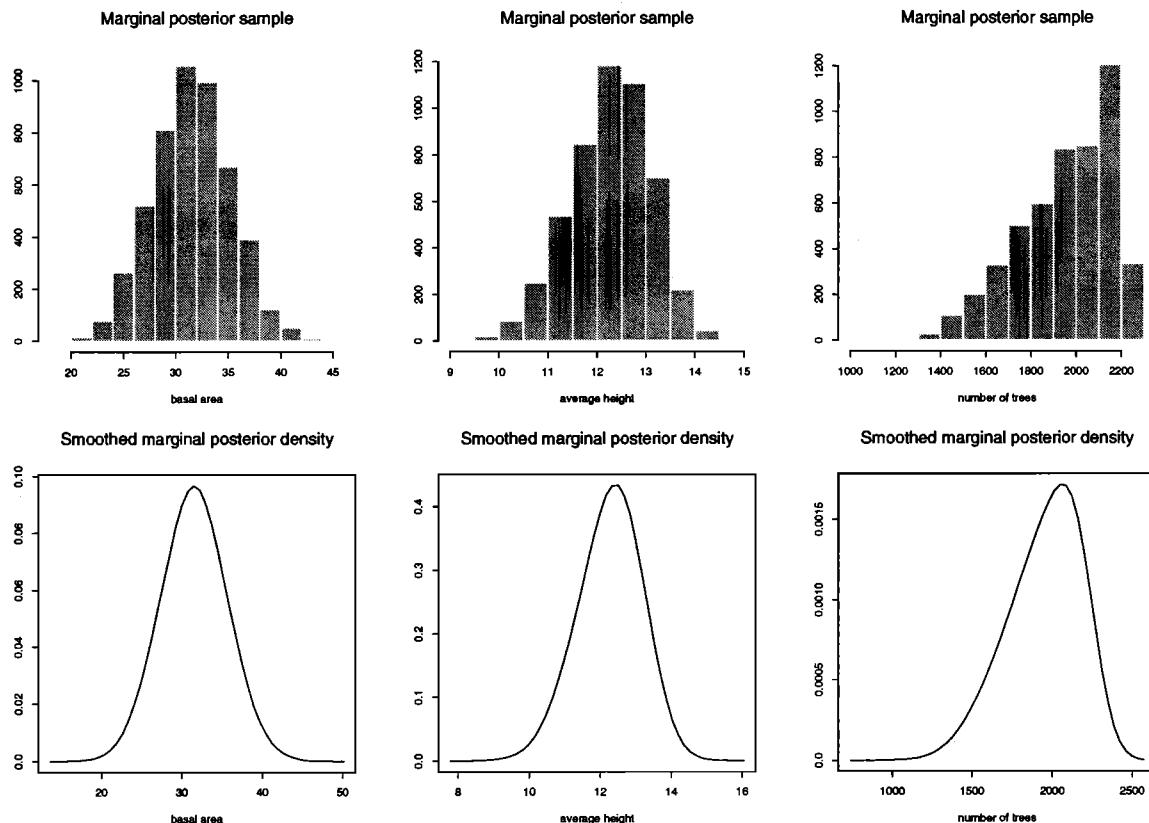


Figure 3. Marginal posterior densities at age 12 without likelihood for outputs.

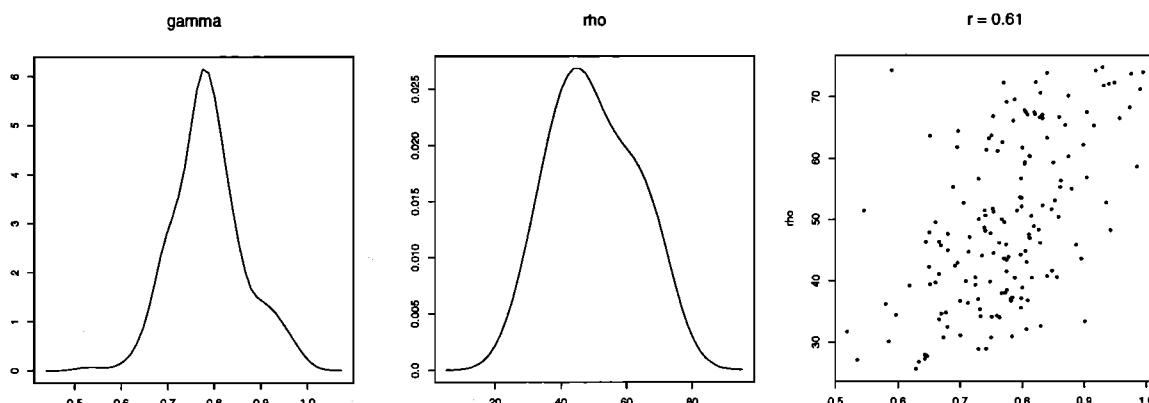


Figure 4. Marginal posterior densities for rho and gamma, and scatterplot of posterior sample for rho and gamma.

outputs from mechanistic models. The method incorporates all the information available to the user regarding the inputs and outputs of the model, in addition to the model itself. It may also prove useful when two or more models are used together. For example, as Valentine et al. (1997) have shown, carbon flux models may be used to develop estimates for one or more parameters used in PIPESTEM. If the carbon flux model is altered to accommodate specified changes in atmospheric carbon concentration, then the two models may be used together to produce an estimate of forest growth under the postulated scenario. However, using current methods, this estimate would simply be a point estimate. We are currently engaged in an effort to perform Bayesian synthesis on a carbon flux model. The posterior distribution from the carbon flux model of PIPESTEM parameters will be used as the premodel (prior) distribution of those parameters for PIPESTEM. In this way we will be able to produce posterior distributions for stand attributes under the various scenarios.

Literature Cited

- AMATEIS, R.L., H.H. BURKHART, B.R. KNOEBEL, AND P.T. SPRINZ. 1984. Yields and size class distributions for unthinned loblolly pine plantations on cutover site-prepared lands. Va. Polytech. Inst. and State Univ. Publ. FWS-2-84. 69 p.
- BAILEY, R.L., G.E. GRIDER, J.W. RHENY, AND L.V. PIENAAR. 1985. Stand structure and yields for site-prepared loblolly pine plantations in the Piedmont and Upper Coastal Plain of Alabama, Georgia, and South Carolina. Univ. Ga. Coll. Agric. Exp. Sta. Res. Bull. 328. 118 p.
- BURKHART, H.E., Q.V. CAO, AND K.D. WARE. 1981. A comparison of growth and yield prediction models for loblolly pine. Va. Polytech. Inst. and State Univ., School of For. and Wildl. Resour. Publ. No. FWS-2-81. 18 p.
- CLUTTER, J.L., W.L. BRISTER, AND J.H. RHENY. 1984. Stand structure and yields of site-prepared loblolly pine plantations in the lower Coastal Plain of the Carolinas, Georgia, and North Florida. USDA For. Serv. Gen. Tech. Rep. SE-27. 173 p.
- GERTNER, G., P. PARYSOW, AND B. GUAN. 1996. Projection variance partitioning of a conceptual forest growth model with orthogonal polynomials. For. Sci. 42:474–486.
- GIVENS, G.H., AND P.J. ROBACK. 1997. Logarithmic pooling of priors linked by a deterministic simulation model. Colorado State University, Dep. of Statist., Tech. Rep. 97-21.
- GREEN, E.J., F.A. ROESCH, A.F.M. SMITH, AND W.E. STRAWDERMAN. 1994. Bayesian estimation for the three-parameter Weibull distribution with tree diameter data. Biometrics 50:254–269.
- HAFLEY, W.L., W.D. SMITH, AND M.A. BUFORD. 1982. A new yield prediction model for unthinned loblolly pine in plantations. N.C. State Univ. Sch. For. Res. Bioecon. Model. Proj. Tech. Rep. 1, 65 p.
- JOHNSON, N.L., AND S. KOTZ. 1970. Continuous Univariate Distributions—2. Wiley, New York. 306 p.
- MACFARLANE, D.W., E.J. GREEN, AND H.T. VALENTINE. 1999. Parameter distribution estimation for a stand-level carbon balance model for loblolly pine. Manuscript in preparation.
- POOLE, D., AND A.E. RAFTERY. 1998. Assessment of the Bering-Chukchi-Beaufort Seas stock of Bowhead whales using Bayesian and full pooling Bayesian synthesis methods. Pap. SC/50/AS5 presented to the IWC Scientific Committee.
- RAFTERY, A.E., G.H. GIVENS, AND J.E. ZEH. 1995. Inference from a deterministic population dynamics model for Bowhead whales. JASA 90:402–442 (with discussion and rejoinder).
- RAFTERY, A.E., D. POOLE, AND G.H. GIVENS. 1996. The Bayesian synthesis assessment method: Resolving the Borel paradox and comparing the backwards and forwards variants. Pap. SC/48/AS16 presented to the IWC Scientific Committee.
- RAFTERY, A.E., AND D. POOLE. 1997. Bayesian synthesis assessment methodology for Bowhead whales. Pap. SC/49/AS5 presented to the IWC Scientific Committee.
- SCHWEDER, T., AND N.L. HJORT. 1996. Bayesian synthesis or likelihood synthesis? What does the Borel paradox say? Rep. Int. Whal. Comm. 46:475–480.
- SCOTT, D.W. 1992. Multivariate density estimation. Wiley, New York. 317 p.
- SHINOZAKI, K., K. YODA, K. HOZUMI, AND T. KIRA. 1964a. A quantitative analysis of plant form: The pipe model theory. I. Basic analyses. Jpn. J. Ecol. 14:97–105.
- SHINOZAKI, K., K. YODA, K. HOZUMI, AND T. KIRA. 1964b. A quantitative analysis of plant form: the pipe model theory. II. Further evidence of the theory and its application in forest ecology. Jpn. J. Ecol. 14:133–139.
- SOKAL, R.R., AND F.J. ROHLF. 1995. Biometry. Ed. 3. W.H. Freeman and Co., San Francisco, CA. 859 p.
- TERRELL, G. 1990. The maximal smoothing principle in density estimation. JASA 85:470–477.
- THORNLEY, J.H.M. 1970. Respiration, growth and maintenance in plants. Nature 227:304–305.
- THORNLEY, J.H.M. 1971. Energy, respiration and growth in plants. Ann. Bot. 25:721–728.
- THORNLEY, J.H.M. 1976. Mathematical models in plant physiology. Academic Press, London.
- VALENTINE, H.T. 1988. A carbon-balance model of stand growth: a derivation employing pipe-model theory and the self-thinning rule. Ann. Bot. 62:389–396.
- VALENTINE, H.T. 1990. A carbon-balance model of tree growth with a pipe-model framework. P. 33–40 in process modeling of forest growth responses to environmental stress, Dixon, R.K. et al. (eds.). Timber Press, Portland, OR. 441 p.
- VALENTINE, H.T., T.G. GREGOIRE, H.E. BURKHART, AND D.Y. HOLLINGER. 1997. Pipestem: A stand-level model of carbon allocation and growth, calibrated for loblolly pine. Can. J. For. Res. 27:817–830.
- WOLPERT, R.L. 1995. Comment on “Inference from a deterministic population dynamics model for Bowhead whales,” by Raftery, A.E., G.H. Givens, and J.E. Zeh, JASA 90:426–427.

Appendix A

Example Application of Bayesian Synthesis

In this section, we provide an example application of Bayesian Synthesis with geometric pooling to a two-parameter model. The model is not mechanistic, but it does serve to illustrate the procedure.

Suppose that our interest is in the distribution of height at age 50 for some species of tree. Suppose, further, that cumulative height can be represented by the following model:

$$H = A (1 - e^{-k(age)}) \quad (\text{A.1})$$

where H = cumulative height (m), A = asymptotic height (m), k = growth rate parameter (year^{-1}), and e is the base of the natural logarithms. Hence, for a given age (years), the two model parameters (or model inputs) are A and k , and the model output is height at that age. Here we let age = 50. In the notation presented in the paper, $\theta = (A, k)$ and $\phi = H$. Let A and k be premodel independent, and let our

prior distributions for these two parameters be $A \sim \text{Gaussian}(60, 5^2)$ and $k \sim \text{Uniform}(0.001, 0.03)$. Furthermore, suppose that our prior expectation for tree height at age 50 is adequately reflected by $H \sim \text{Gaussian}(30, 2^2)$. Finally, suppose that we observe the heights of ten 50-year-old trees and these turn out to be: $\underline{h} = (30, 27, 28, 26, 30, 27, 29, 26, 29, 29)'$, and consistent with our prior belief regarding H , we model these data as realizations from a normal distribution. We apply the BSYN with geometric pooling algorithm as follows:

1. Draw a sample of size m from our premodel (or prior) distribution on A and k . Since we are assuming A and k are independent this just entails drawing m values for A from a Gaussian(60, 5²) distribution, and m values for k from a Uniform(0.001, 0.03) distribution. For this example, let $m = 2000$. This results in the following sample.

A	k
51.09	0.0055
52.86	0.0081
50.39	0.0059
:	:
57.97	0.0214
56.48	0.0145
50.55	0.0188

2. Insert each (A, k) pair into Equation (A.1) and solve for the associated value of H . This results in the following induced sample of size 2000: $\underline{h}^i = (12.28, 17.51, 12.78, \dots, 38.05, 29.66, 30.76)'$.
3. Estimate the density of the induced sample obtained in step 2. In real applications, this should be done using a robust method such as nonparametric density estimation, but for this example we will assume that the sample from step 2 follows a Gaussian distribution. The estimated mean and standard deviation of the sample are 29.71 and 12.55, respectively. We then compute estimated density of each observation in the step 2 sample using this mean and standard deviation, i.e.,

$$\hat{q}_{A,k}^i(\underline{h}^i) = \frac{1}{\sqrt{2\pi}(12.55)} e^{-\frac{1}{2}\left(\frac{(h_j^i - 29.71)^2}{12.55^2}\right)}, j = 1, 2, \dots, 2000$$

The induced densities turn out to be [ignoring the constant $(2\pi)^{-1/2}$]:

$$\hat{q}_{A,k}^i(\underline{h}^i) = (0.012, 0.020, 0.013, \dots, 0.026, 0.032, 0.032)'$$

4. Now we need to find the importance sampling weights using Equation (7). First, we must compute the density, under the specified prior on H , of all the values in the sample obtained in step 2, i.e.,

$$\hat{q}_H^i(h_j^i) = \frac{1}{\sqrt{2\pi}(2)} e^{-\frac{1}{2}\left(\frac{(h_j^i - 30)^2}{2^2}\right)}, j = 1, 2, \dots, 2000$$

The densities turn out to be:

$$q_H(\underline{h}^i) = (1.8 \times 10^{-18}, 6.8 \times 10^{-10}, \\ 1.6 \times 10^{-17}, \dots, 6.0 \times 10^{-5}, 2.0 \times 10^{-1}, 1.8 \times 10^{-1})'$$

Since we have no data on A and k , we do not need to compute the first likelihood on the RHS of Equation (7). We do have height data though, so we need to compute the likelihood of each value in the step 2 sample given the 10 observed heights. For the likelihood computations, we assume the standard deviation is equal to 1.52, the sample standard deviation of the 10 observed heights. Hence, for the first observation in the step 2 sample (12.28), the likelihood given the observed data is

$$L(12.28 | \underline{h}) = \left(\frac{1}{\sqrt{2\pi}(1.52)} \right)^{10} e^{-\frac{1}{2} \sum_{j=1}^{10} \frac{(h_j - 12.28)^2}{1.52^2}} \\ = 1.0 \times 10^{-243}.$$

The likelihoods for the 2,000 values in the step 2 sample are then proportional to:

$$L_H(\underline{h}^i) \propto (9.2 \times 10^{-237}, 1.4 \times 10^{-101}, \\ 3.3 \times 10^{-223}, \dots, 2.1 \times 10^{-89}, 3.9 \times 10^{-1}, 1.7 \times 10^{-3})'$$

As we can see, parameter pairs not supported by the data result in very small likelihoods. Now, we compute the importance sampling weights:

$$w_k = \left(\frac{q_H(h_k^i)}{\hat{q}_{A,K}^i(h_k^i)} \right)^{1/2} L_H(h_k^i), k = 1, 2, \dots, 2000,$$

which results in:

$$w \propto (1.1 \times 10^{-106}, 9.6 \times 10^{-43}, \\ 3.8 \times 10^{-100}, \dots, 2.0 \times 10^{-42}, 1.8 \times 10^{-2}, 2.3 \times 10^{-4})'$$

5. Next, we resample the samples drawn in steps 1 and 2 with the importance weights obtained in step 4. We do this as follows:
 - a. Find the sum of the w_k values, $\Sigma_k w_k$.
 - b. Form a vector of length 2000 containing the cumulative sums of w .
 - c. Divide each of the cumulative sums in the vector computed in (b) by the overall total from (a). Call the resulting vector p . Augment the vector p with a 0 in the first position, i.e., p is of length 2,001.
 - d. Draw a random number u from a Unif(0,1) distribution
 - e. Find the interval (p_a, p_b) such that $p_a \leq u \leq p_b$, where p_a and p_b are adjacent values in p .

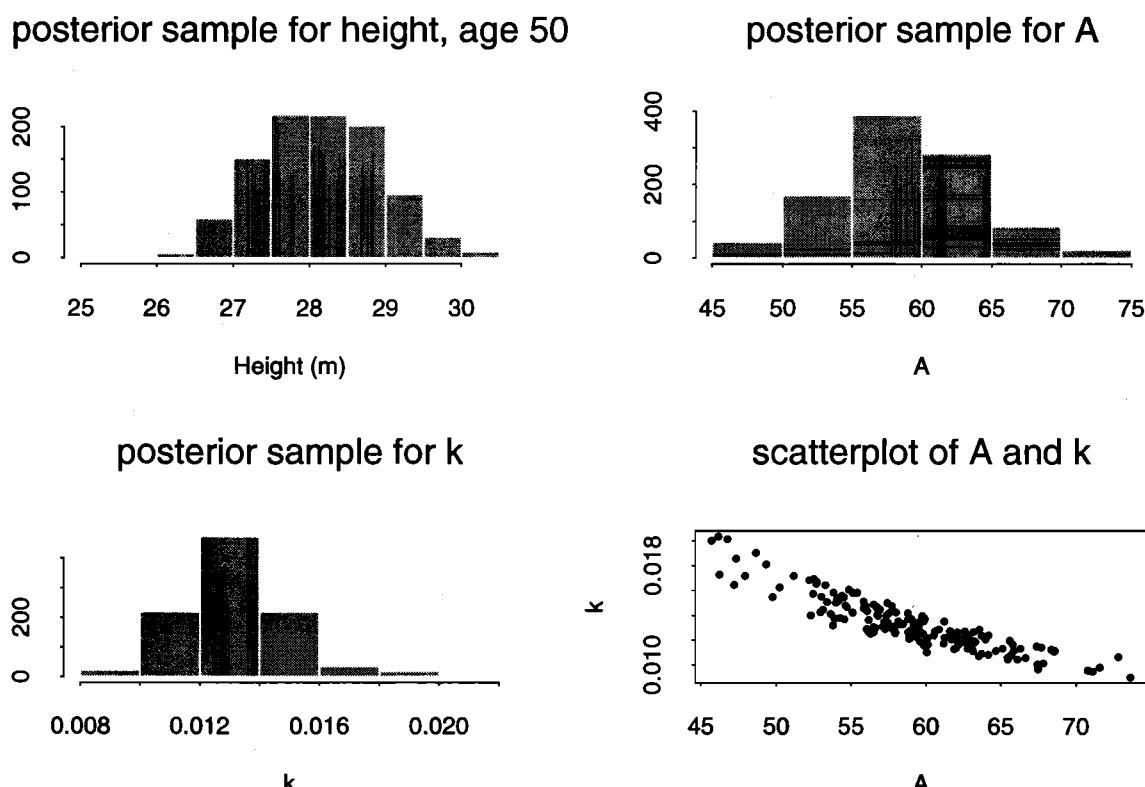


Figure A.1. Marginal posterior samples and scatterplot of model parameters from posterior sample for example application.

f. Suppose that p_a is the j th value in p . Then admit the j th value from the samples drawn in steps 1 and 2 into the joint posterior distribution.

g. Repeat steps (d) through (f) until the desired posterior sample size is achieved.

The result is an approximate sample from the posterior (or postmodel) distribution of (H, A, k) . Samples from the marginal distribution of any of the inputs (A, k) or outputs (H) are available by just selecting the appropriate column from the joint posterior sample of (H, A, k) . For this example, we generated posterior samples of size 1,000.

In Figure A.1, we display histograms of the three marginal posterior distributions. We also present a bivariate scatterplot of the values of A and k in the posterior sample. It is evident that these two parameters are highly correlated. The estimated correlation coefficient of A and k in the posterior sample is -0.94 .

Appendix B

Definitions of Model Inputs (i.e., PIPESTEM Parameters)

c_f units of carbon substrate consumed in constructive respiration for the production of a unit of foliar dry matter ($\text{kg C} \cdot \text{kg C}^{-1}$)

c_r units of carbon substrate consumed in constructive respiration for the production of a unit of feeder-root dry matter ($\text{kg C} \cdot \text{kg C}^{-1}$)

c_w units of carbon substrate consumed in constructive respiration for the production of a unit of woody dry matter ($\text{kg C} \cdot \text{kg C}^{-1}$)

m_f units of carbon substrate consumed in maintenance respiration per unit of foliar dry matter per unit time ($\text{kg C} \cdot \text{kg C}^{-1} \cdot \text{year}^{-1}$)

m_r units of carbon substrate consumed in maintenance respiration per unit of feeder-root dry matter per unit time ($\text{kg C} \cdot \text{kg C}^{-1} \cdot \text{year}^{-1}$)

m_w units of carbon substrate consumed in maintenance respiration per unit of live woody dry matter per unit time ($\text{kg C} \cdot \text{kg C}^{-1} \cdot \text{year}^{-1}$)

z_f units of foliar dry matter per unit cross-sectional area of active pipes ($\text{kg C} \cdot \text{m}^{-2}$)

z_r units of feeder-root dry matter per unit cross-sectional area of active pipes ($\text{kg C} \cdot \text{m}^{-2}$)

z_w units of dry matter per unit wet volume of woody tissue ($\text{kg C} \cdot \text{m}^{-3}$)

α ratio of the average length of the portion of an active pipe within a live crown to the average length of a crown ($\text{m} \cdot \text{m}^{-1}$)

- β ratio, in a closed stand, of the average length of a live crown to the average distance among adjacent trees ($m \cdot m^{-1}$)
 γ proportion, aboveground, of an active pipe
 ζ upper bound of active-pipe area ($m^2 \cdot ha^{-1}$)
 θ_1 ratio of the average length of a disused pipe in a dying tree to the average height to the base of a crown ($m \cdot m^{-1}$)
 θ_2 ratio of the average length of a shed branch to the average distance among adjacent trees ($m \cdot m^{-1}$)
 λ proportion of available substrate allocated to the production and constructive respiration of new active pipes, and foliar and feeder-root dry matter
 μ_1 crown-increment parameter (m)
 μ_2 exponent (dimensionless)
 ρ scaling parameter of C substrate production rate ($m^2 \cdot ha^{-1}$)
 v_f longevity of foliage (yr)
 v_r longevity of feeder roots (yr)
 ϕ ratio of the rate of loss of old basal area to the rate of production of new basal area
 $((m^2 \cdot year^{-1}) \cdot (m^2 \cdot year^{-1})^{-1})$
 ψ ratio of the average basal area of a dying tree to that of a surviving tree ($m^2 \cdot m^{-2}$)
 ω pipe-length parameter (m)