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Making decisions about the optimal selection environment using Gibbs sampling

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Abstract The use of Gibbs sampling in making decisions about the optimal selection environment was demonstrated. Marginal posterior distributions of the efficiency of selection across sites were obtained using the Gibbs sampler, a Bayesian method, from which the probability that the efficiency of selection lay between specified values and the variance of the distribution were computed, providing a lot of information on which to make decisions regarding the location of genetic tests. The heritability, genetic correlations and efficiencies of selection estimated using REML and Gibbs sampling were similar. However, the latter approach showed that the point estimates of the efficiencies of selection were subject to substantial error. The decision regarding selection at maturity was consistent with that obtained using point estimates from REML, but Gibbs sampling allowed the efficiencies of selection to be interpreted with more confidence. The decision regarding early selection differed from that based on REML point estimates. Generally, the decisions to make early selections at site B for planting at both site B and A, and to make selections at maturity at each individual site, were robust to different priors in the Gibbs sampling.

Keywords Gibbs sampling · REML · Bayesian analysis · Selection efficiency

Introduction

Forest sites are heterogeneous due to variations in soils, weather conditions, or other factors. The manner in which genetic tests are deployed affects genetic gain in production populations in the presence of genotype \times environment (GE) interactions. The question faced by breeders is where one should locate genetic tests so as to ultimately maximise gain in production populations. The conventional method of determining the optimal selection environment is to estimate the efficiency of selecting at one site for planting at another site, using the method of indirect selection described by Falconer (1989). In order to estimate the efficiency of selection, heritabilities and genetic correlations need to be known.

It is usual for these parameters to be known with errors, perhaps after estimation using restricted maximum likelihood (REML, Paterson and Thompson 1971). A major limitation of this process is that whilst an estimate of the efficiency of selection may be calculated its distribution and variance are difficult to obtain, adversely influencing the efficiency of decision-making. This problem is made more error-prone if sample sizes are low, since this increases the chance that the decision may be sensitive to the sampling errors. The large standard errors associated with the genetic correlation estimates, particularly in tree breeding designs with few parents, are an example where this sensitivity may occur. Hence, decisions on whether or not genetic tests should be located at one site may lack conviction through incomplete information.

An alternative approach that might overcome this lack of confidence is to use Monte Carlo Markov Chain methods such as Gibbs sampling. This method can generate random samples from the joint distribution of the parameters, and can assist in decision making because for each sample of parameters the decision can be made as if they are true values. Thus by repeating the process over and over, a number of samples are obtained from the true distribution of the decision-making process. Furthermore, notwithstanding the complexity of decision,

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Gibbs sampling enables one to estimate the probability that certain decisions will provide the desired results, producing considerably more information on which to base decisions compared to the point estimates from REML. Finally, the approach can make use of prior information, and nuisance parameters are integrated out.

The Gibbs sampler has recently been used for estimating variance components in animal-breeding applications (Jensen et al. 1994; Sorensen et al. 1994; Wang et al. 1994; Van Tassell et al. 1998; Yazdi et al. 1999). In addition, Sorensen et al. (1994) used the Gibbs sampler to estimate uncertainty in response to selection. It appears that Gibbs sampling has not been used in tree breeding, but has been used in forest inventories (Green et al. 1992; Green and Strawderman 1996). The present study will investigate use of the Gibbs sampling in decision-making on the choice of site for locating progeny tests. These results will be compared to those obtained by REML. The paper is an extended version of an abstract presented at the 24th Southern Forest Tree Improvement Conference (Gwaze and Woolliams 1997).

Materials and methods

Data

Data for the Gibbs sampler were heights assessed at ages 10 years and 23 years in genetic tests located at two sites in Zimbabwe. These two ages were selected because early selection at 10 years was predicted to be effective in *Pinus taeda* (Gwaze et al. 1996) and 23 years was close to the harvest age (since, alternatively, the rotation age of *P. taeda* is 25 years). The tests were located at Tarka (site A) and Martin (site B) in Chimanimani, Zimbabwe, and the sites differed mainly in mean annual rainfall, being 2,156 mm at the former and 1,016 mm at the latter. The two sites were selected because they represented the region where most of the commercial plantations of *P. taeda* are located, and therefore making decisions regarding the location of progeny tests between these two heterogeneous sites are critical. Details of the genetic tests are given by Gwaze et al. (1997). Briefly, the tests were planted in 1972, and the genetic material comprised 140 full-sib families that originated from an incomplete factorial mating design involving 8 male and 15 female parents. Trees were planted at 2.4 × 2.4 m spacing and each plot comprised ten trees. The tests comprised three replicates and ten blocks per replicate, in a triple-lattice design. Systematic thinning was carried out by removing every other tree in each plot at 10 years of age. At that age height was assessed on trees that were felled after thinning.

Overview of the Bayes theorem

The objective of the Bayes methods is to compute the posterior distribution of the parameter of interest. To start with, a prior distribution, which represents the belief about the parameter before any data are observed, is assumed. The posterior distribution then represents the updated belief after viewing the data. The posterior distribution is expressed as proportional to the product of the prior distribution of the parameter and the conditional distribution of the data, given the parameter (likelihood) (Gilks et al. 1996):

$$p(\theta|\mathbf{y}) \propto p(\theta)p(\mathbf{y}|\theta), \quad (1)$$

where \mathbf{y} is the data and θ is the parameter. Therefore, when a uniform prior, a lack of prior-knowledge for the distributions of the parameter, is used, the posterior distribution is simply the likelihood of the parameter given the data (van Tassell and van Vleck 1996).

Gibbs sampling

Gibbs sampling is a method of numerical integration that allows inferences to be made about joint or marginal distributions of the parameters of interest. The Gibbs-sampling algorithm is an updating sampling scheme that requires random independent draws of variables from all of the full conditional distributions. The full conditional distribution is the distribution of a variable given all other parameters in the model. Gibbs sampling integrates out the other parameters leaving the distribution of the parameter in question conditional on the data (i.e. the marginal posterior distribution of the parameter), unlike REML where only joint inferences are possible. After obtaining samples from the marginal distributions, the means and variances of the distribution can be estimated. For derivation of the joint and conditional posterior distributions of parameters see Jensen et al. (1994), Wang et al. (1994), van Tassell and van Vleck (1996).

The following quadrivariate tree model was used to estimate covariance components for height across the two sites and the two ages (hence four traits):

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 \\ 0 & 0 & X_3 & 0 \\ 0 & 0 & 0 & X_4 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 & 0 \\ 0 & Z_2 & 0 & 0 \\ 0 & 0 & Z_3 & 0 \\ 0 & 0 & 0 & Z_4 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix}, \quad (2)$$

where:

y_i = the vector of observations for trait i ,

b_i = the vector of fixed effects for trait i ,

a_i = the vector of random tree (additive genetic) effects for trait i ,

X_i = the incidence matrix for fixed effects for trait i ,

Z_i = the incidence matrix for additive direct effects for trait i ,

e_i = the vector of residual effects for trait i . For $i = 1, 2, 3, 4$.

The conditional distributions of a_i and e_i were each assumed to be quadrivariate normally distributed, and to be independent of each other as follows:

$$\text{var} \begin{bmatrix} y \\ a \\ e \end{bmatrix} = \begin{bmatrix} R + ZGZ' & ZG & R \\ GZ' & G & O \\ R & O & R \end{bmatrix},$$

where $G = A^*G_0$, A is the numerator relationship matrix between the trees and G_0 is the additive genetic variance-covariance matrix of traits, and $R = I^*R_0$, I is the identity matrix and R_0 is the residual variance-covariance matrix of traits. The residual covariances in our study were assumed to be zero because the traits were assessed on separate, but genetically related, trees across sites. Therefore, genetic covariance between any two traits exists, but no environmental covariance. The effect of the replicate was considered fixed. The data was pre-adjusted for the block effects before the analysis. The assessments of height at the two sites and two ages were treated as different traits. At 10 years the trees assessed were those that were removed after thinning. Therefore, trees assessed between the two ages within a site were also different so justifying our assumption of zero residual covariances between ages. The analysis of the four traits simultaneously was done using the Multi Trait Gibbs Sampling for Animal Models program (MTGSAM, Van Tassell and Van Vleck 1995).

Priors were assigned to unknown parameters (the variance components and fixed effects) in the model. Uniform improper (flat) prior distributions were assumed for fixed effects. Two types of prior distributions were assumed for the additive random genetic covariance matrix: inverted Wishart and uniform distributions. The Wishart (IW) distribution is a matrix generalization of the univariate chi-square distribution (Sorensen 1997). The inverted Wishart distributions are used as prior distributions for covariance because of computational simplicity (van Tassell and Van Vleck 1996). Other prior distributions can be employed but the Gibbs sampling algorithm would be more complex (van Tassell and Van Vleck 1996). Uniform distributions have been used for comparison in order to determine if the assumption of no knowledge of prior distribution would influence the inferences. The mode of the joint posterior should correspond to the REML estimates if a uniform prior is used (Gianola and Fernando 1986).

For a proper prior (IW) distribution, the shape parameter (degrees of freedom) should be 2 more than the order of the matrix (Van Tassell and Van Vleck 1995). Given that the order of the matrix was 4 for the additive covariance matrix (four traits), a shape parameter 6 was the minimum necessary for the prior to be proper, thereby indicating minimum possible belief in the parameters for the prior distributions of the variance components. When the covariance between two traits is zero, as in the case with the residual covariances, then the traits are considered as members of different groups (Van Tassell and Van Vleck 1996) giving an order of the matrix for residual covariances of 1 and a shape parameter of 3.

The additive genetic and residual (co)variance components estimated using REML were used as the starting values. The rationale for this was that it was difficult to find reports of additive and residual covariances from the literature.

Several priors were used in order to conduct a sensitivity analysis on the effect of changing the priors on the expected values of the posterior distributions. The following four sets of parameters for the priors were employed:

- Prior 1. REML variance and covariance estimates used.
- Prior 2. The additive variances at young age = 20, those at older ages = 15, all additive covariances = 10, and the residual variances = 5 (estimates were 5–10 times the REML estimates used as Prior 1).
- Prior 3. REML variance estimates were used but the covariances were zero.
- Prior 4. REML variances and covariance estimates were used as starting values and the shape parameter of 0 (a flat prior) were used for both the additive and residual covariances. A flat prior indicates no prior knowledge for the distributions of the variance components.

The MTGSAM programs were employed to generate the samples and posterior estimates of the variance components. The first 5,000 iterations were not stored, to ensure that the samples saved were from the proper stationary posterior distributions. Thereafter, a total of 100,000 iterations were made, and samples stored at every 100th iteration to reduce autocorrelations, giving a total of 1,000 samples of ten additive genetic and four residual (co)variance estimates stored. From these, heritability, genetic correlations and efficiencies of selection were calculated for each sample (see below for the calculation of efficiency), and inferences about the efficiencies of selection were made by directly computing summary statistics from the resulting distributions derived from the 1,000 samples. Parameters stored from the analysis were the 14 co(variance) components.

In order to check for convergence, the Gibbs sampler was run several times with different lengths of the Gibbs sampling chain and different numbers of iterations between saving samples to make sure that the similar estimates were obtained each time. This was confirmed, hence convergence was assumed.

For each prior, the independence of samples was tested using autocorrelations of the efficiencies of selection. The samples were moderately correlated: for example, the 1st-order lag-correlations ranged between 0.45 and 0.74, when the saved samples were chosen at every 100th iteration. The behaviour of the higher-order lag-correlations suggested a 1st-order auto-regressive model. Therefore, the sequence of 1,000 samples was analysed using an ARIMA(1,0,0) model to provide estimates of both the auto-correlation (ρ) and the sample mean, and an estimate of its standard error (δ). This was done using GENSTAT 5. The ARIMA (1,0,0) is a first-order autoregressive model with no differencing and no moving average (Box and Jenkins 1976). The sampling variance was calculated as $v^2/(1-\rho^2)+\delta^2$, where v^2 was the innovation variance estimated by the ARIMA model. The innovation variance in time-series models is analogous to the residual variance. Although the results presented concerning efficiency arise from these analyses, the estimates differed very little from the simple sample mean and sample variance.

Although there was no explicit need for the decision-making process to derive single-point estimates of genetic parameters, these were examined from the means and modes of the posterior

distributions that were computed directly from the Gibbs samples. Since the posterior distributions were asymmetric, small differences between the Gibbs estimates of the posterior mean and REML estimates (the joint mode of the likelihood) would be expected irrespective of the prior assumption. A likelihood-ratio test was performed to examine the differences between the Gibbs posterior means and REML estimates: the difference in the log-likelihoods with and without fixing the (co)variance components of the Gibbs sampling estimates were multiplied by -2 , and compared with a chi-square distribution with the degrees of freedom equal to the number of fixed parameters (i.e., 14).

Efficiency of selection

The efficiency of selecting at site A (trait \mathbf{x}) for planting at site B (trait \mathbf{y}), relative to both selecting and planting at site B, was estimated using the following equation, assuming that selection intensities and generation intervals are equal (Falconer 1989):

$$\mathbf{E} = \mathbf{h}_x \mathbf{r}_A \mathbf{h}_y^{-1}, \quad (3)$$

where \mathbf{r}_A is the genetic correlation between traits \mathbf{x} and \mathbf{y} , \mathbf{h}_x and \mathbf{h}_y are the square root of the heritability of traits \mathbf{x} and \mathbf{y} , respectively. These efficiencies indicate the relative loss in genetic gain from selecting at one site for planting at another. The above equation is normally used when the trees at different sites are assessed at the same ages (e.g., Pswarayi et al. 1997).

Since forest trees have long generation intervals, early selection, which is an indirect selection where performance at a young age is used as an indicator of mature age performance, is preferred. For example, the optimum selection age for height in *P. taeda* in the USA can be as young as 4 years (Newman and Williams 1991). Efficiencies of early selection are mainly determined within a site (King and Burdon 1990; Riemenschneider 1988) or on data pooled across sites (Gwaze et al. 1997; McKeand 1988). The efficiency of early selection across sites has not been given much emphasis in forest trees despite its importance for identifying the best selection site. Given two ages and two sites, our study investigated the efficiency of early selection on the mature performance within and between sites. This gives the reliability of early selection at different sites. Assuming that the selection intensities are equal, the relative efficiency of early selection at site A (trait \mathbf{x}) and B (trait \mathbf{z}) on the mature performance at site B (trait \mathbf{y}) was calculated as:

$$\mathbf{E} = \frac{\mathbf{h}_x \mathbf{r}_{xy} \mathbf{h}_y^{-1} \mathbf{L}_x \mathbf{L}_y^{-1}}{\mathbf{h}_z \mathbf{r}_{zy} \mathbf{h}_y^{-1} \mathbf{L}_z \mathbf{L}_y^{-1}}, \quad (4)$$

where \mathbf{r}_{xy} is the genetic correlation between traits \mathbf{x} and \mathbf{y} ; \mathbf{r}_{zy} is the genetic correlation between traits \mathbf{z} and \mathbf{y} ; \mathbf{h}_x , \mathbf{h}_z and \mathbf{h}_y are the square root of the heritability of traits \mathbf{x} , \mathbf{z} and \mathbf{y} , respectively; \mathbf{L}_x , \mathbf{L}_z and \mathbf{L}_y are the generation intervals of traits \mathbf{x} , \mathbf{z} and \mathbf{y} , respectively. Since $\mathbf{L}_x = \mathbf{L}_z$ in our study, the ratio of the efficiencies of early selection across and within sites reduces to:

$$\mathbf{E} = \mathbf{h}_x \mathbf{r}_{xy} \mathbf{h}_z^{-1} \mathbf{r}_{zy}^{-1}. \quad (5)$$

In this study, calculations of the efficiency of early selection were based on selection at 10 years, because selecting at 10 years was found to be the most efficient (Gwaze et al. 1996).

Decision-making

The decision-making process was used to compare the effectiveness of: (1) early selection when tests on different sites are measured at a young age to improve performance at maturity, and (2) mature selection when both tests are measured at a mature age to improve performance at maturity. The probability that the efficiency of selection was greater than 0.7 and 1.0 was estimated. An efficiency of 0.7 was selected because efficiencies lower than 0.7 would justify extra costs of having separate progeny tests (unpublished result). The standard error of the probability was estimated as:

$$SE(p) = \sqrt{\frac{p(1-p)}{n_E}}, \quad (6)$$

where p is the probability and n_E is the effective number of samples. An effective number of samples was calculated for each efficiency with each prior as $n_E = 1,000(1 - \rho)/(1 + \rho)$ (Tierney 1991).

Results

Genetic parameters using prior 1

Using a log-ratio test, covariance estimates from Gibbs sampling and those from REML were not significantly different.

The estimated heritabilities and genetic correlations using Gibbs sampling and REML are shown in Tables 1 and 2, respectively. The heritability estimates from Gibbs sampling (0.58–0.78) were slightly larger compared to those from REML (0.39–0.73), but the genetic correlations were similar. However, the differences were small, and therefore unlikely to be important. In all cases the genetic correlations across sites appear lower at older ages.

Selection efficiencies using prior 1

The estimated selection efficiencies are shown in Table 3. While the estimates of efficiencies of early selection across sites showed variations between sites, those for selection at maturity across sites did not. The distributions of the selection efficiencies were slightly skewed. For mature-age selections, the posterior modes were similar to calculations based on estimates from REML, but those for early selection were not (Table 3).

The probability that the efficiency of early selection at site B for planting at site A was greater than 0.70 was 0.95 (Table 3), indicating that early selection at site B would result in little-loss in gain at site A at harvest age, compared to early selection at site A. In fact, the probability that more gain would be obtained from early selection at site B compared to site A is 0.59. The high efficiency of selection at site B was attributed to a high genetic correlation between heights at 10 years at site A and those at site B at 23 years, which was as high as that between the 10- and 23-year heights at site B (Table 1).

Due to much lower across-site genetic correlations than within-site correlations, the probability that the efficiency of early selection at site A for planting at site B was greater than 0.70 was only 0.35, and the probability that early selections at site A would result in higher gain at site B at harvest age than early selections at site B was 0. The results suggest that site B is a better progeny test site since selections made here will result in little loss in gain at site A, and may even result in higher gain at site A at harvest age than early selection at site A, whereas early selection at site A would severely reduce progress at site B. Therefore, there was little risk of failure when selections were made at site B.

Table 1 Estimated heritabilities (in bold) and genetic correlations for height based on Gibbs sampling using prior 1; standard deviations of the marginal posterior distributions are in parenthesis

Item	HT10 (site A)	HT10 (site B)	HT23 (site A)	HT23 (site B)
HT10 (site A)	0.78 (0.09)			
HT10 (site B)	0.88 (0.07)	0.66 (0.11)		
HT23(site A)	0.71 (0.15)	0.67 (0.17)	0.58 (0.16)	
HT23 (site B)	0.57 (0.17)	0.80 (0.11)	0.49 (0.21)	0.62 (0.17)

Table 2 Estimated heritabilities (in bold) and genetic correlations for height based on REML; their standard errors are in parenthesis

Item	HT10 (site A)	HT10 (site B)	HT23 (site A)	HT23 (site B)
HT10 (site A)	0.73 (0.14)			
HT10 (site B)	0.90 (0.05)	0.59 (0.14)		
HT23(site A)	0.77 (0.08)	0.72 (0.15)	0.40 (0.14)	
HT23 (site B)	0.55 (0.21)	0.82 (0.07)	0.51 (0.25)	0.39 (0.15)

If selection were carried out at 23 years of age (harvest age), the probabilities that the efficiencies of selection at alternative sites are greater than 0.7 were all low: 0.20 for selection at site A for planting at site B, and 0.25 for selection at site B for planting at site A, indicating that these sites were different. Therefore, if selections are to be made at maturity, separate progeny tests should be established for the sites since selections at alternative sites would result in substantial losses in gain at the sites. The low efficiencies of selection are attributed to the low genetic correlation between heights assessed at these two sites at 23 years.

Sensitivity analysis

The heritability estimates obtained from using the different priors were similar, but some genetic correlations showed sensitivity. However, the main interest lay in the sensitivity of the efficiency of selection to the different priors. These results are shown in Tables 4 and 5.

The mean of the posterior distributions were generally comparable for all the efficiencies considered. However, some differences were evident: means tended to be lower with the flat improper prior (Prior 4), and E_{A1B2} (i.e., the efficiency of selecting at site A at 10 years for planting at site B compared with early selection at site B) was notably higher when using Prior 2 compared to

Table 3 REML and Gibbs sampling estimates of efficiencies of selection for height, standard deviations (SD) of the marginal posterior distributions, and the probabilities that the selection efficiencies (E) are greater than 0.7 and 1.0

Item	REML estimate	Posterior mode	Posterior mean	SD	$P(E > 0.7)^a$	$P(E > 1.0)$
E_{A1B2}^b	0.84	0.68	0.59	0.22	0.35	0.0
E_{B1A2}^c	0.75	1.04	1.11	0.34	0.95	0.59
E_{A2B2}^d	0.53	0.49	0.48	0.27	0.20	0.01
E_{B2A2}^e	0.49	0.53	0.50	0.28	0.25	0.02

^a SE of the probabilities were less than 0.045

^b E_{A1B2} = efficiency of selecting at site A at 10 years for planting at site B compared with early selection at site B at 10 years

^c E_{B1A2} = efficiency of selecting at site B at 10 years for planting at site A compared with early selection at site A at 10 years

^d E_{A2B2} = efficiency of selecting at site A at 23 years for planting at site B compared to direct selection at site B

^e E_{B2A2} = efficiency of selecting at site B at 23 years for planting at site A compared to direct selection at site A

Table 4 Sensitivity of the efficiency of selection to different priors (see Materials and methods for descriptions of priors). Results are the means of marginal posterior distributions and the efficiencies of selection for height. The estimated standard deviations of the posterior distribution are in parentheses

Item	Prior 1	Prior 2	Prior 3	Prior 4
E_{A1B2}	0.59 (0.22)	0.82 (0.79)	0.65 (0.35)	0.52 (0.28)
E_{B1A2}	1.11 (0.34)	1.03 (0.26)	1.07 (0.29)	1.05 (0.78)
E_{A2B2}	0.48 (0.27)	0.41 (0.18)	0.40 (0.24)	0.31 (0.29)
E_{B2A2}	0.50 (0.28)	0.45 (0.20)	0.47 (0.28)	0.32 (0.30)

other priors (Table 4). The standard deviations of the posteriors also showed general agreement, but E_{A1B2} for Prior 2 and E_{B1A2} (i.e., the efficiency of selecting at site B at 10 years for planting at site A compared with early selection at site A) for Prior 4 had larger standard deviations due to a small number of extreme outliers. The autocorrelations for Prior 2 (range 0.09 to 0.41) were notably lower than for other Prior distributions (range 0.41 to 0.83).

Whilst the differences between priors were evident again in the proportions of samples with $E > 0.7$ and $E > 1.0$, the comparisons among the efficiencies were generally robust (Table 5). Thus efficiency of early selection at site B for planting at site A was consistently high using different prior information, and more promising than selection at site A for planting at site B. Selection at maturity across sites was not efficient (Table

5). This indicates that the decision on site preference was robust to the prior information included in the Gibbs sampling.

Discussion

The use of Gibbs sampling in decision-making in progeny test location was demonstrated. Variance components were estimated using MTGSAM, and the estimated components were employed to derive heritability estimates and genetic correlations, which were in turn used to estimate the efficiencies of selection. The study illustrated that the point-estimates of the efficiencies of selection were subject to substantial error, particularly those involving selections at maturity. Gibbs sampling provided a method for constructing the posterior distribution of the efficiencies of selection from which the variations of the estimates were obtained, and the probabilities that the estimates were within a specified range were also estimated. A further advantage of the Gibbs sampling approach was that it allowed a simultaneous estimation of the components of variances and covariances for the four traits. However, heritability and genetic correlation estimates from a series of bivariate REML analyses and those from multivariate Gibbs sampling analyses were not significantly different.

Using this approach, site B emerged as a better site to locate progeny tests than site A if early selection is

Table 5 Sensitivity of the efficiency of selection to different priors (see Materials and methods for descriptions of priors). Results on probabilities that the selection efficiencies (E) are greater than 0.7 and 1.0, with standard errors in parentheses

Item	Probability ($E > 0.7$)				Probability ($E > 1.0$)			
	Prior 1	Prior 2	Prior 3	Prior 4	Prior 1	Prior 2	Prior 3	Prior 4
E_{A1B2}	0.35 (0.037)	0.62 (0.016)	0.50 (0.029)	0.27 (0.036)	0.0 (-)	0.22 (0.014)	0.07 (0.015)	0.03 (0.014)
E_{B1A2}	0.95 (0.015)	0.82 (0.016)	0.95 (0.015)	0.82 (0.019)	0.59 (0.035)	0.49 (0.021)	0.64 (0.033)	0.53 (0.024)
E_{A2B2}	0.20 (0.041)	0.03 (0.008)	0.08 (0.027)	0.08 (0.027)	0.01 (0.010)	0.0 (-)	0.01 (0.01)	0.0 (-)
E_{B2A2}	0.25 (0.043)	0.11 (0.015)	0.19 (0.036)	0.08 (0.028)	0.02 (0.014)	0.0 (-)	0.02 (0.013)	0.0 (-)

practised. This decision arose from the data despite the relatively few parents in the dataset. However, if selections are made at maturity, which is highly unlikely, separate progeny tests should be established for the two sites. The decision regarding selection at maturity is consistent with that obtained using point estimates from REML, but Gibbs sampling allowed the efficiencies of selection to be interpreted with more confidence. However, the decision regarding early selection with Gibbs sampling differed from that based on REML point estimates. Using REML, the efficiencies of early selection at both site A and site B were greater than 0.7 indicating that either of the two sites could be a suitable location for progeny tests; in contrast, with Gibbs sampling, it was clear that site B was a better site to locate progeny tests. Furthermore, if a choice had to be made between the two sites, site A would be selected using point estimates from REML, resulting in different decisions arising from the two approaches. The difference between the results from Gibbs sampling and REML is attributable to the greater information derived using the former method, and an improved risk analysis. The study demonstrates the advantage of having some measure of variability associated with the estimates of the efficiency of selection.

A sensitivity analysis was conducted to study the influence of priors. Changing the shape of the priors and the magnitude of their parameters made no serious impact on the posterior distributions of the efficiencies of selection, nor upon the outcome of the selection decision. Assuming that the prior distributions were flat and improper gave a higher variance of the marginal posterior distribution of early selection at site B than assuming that the priors were inverted Wishart distributions. Sorensen et al. (1994) also found that variances were higher when flat priors were used. The lack of agreement might be due to improper distributions when flat distributions are assumed as the priors were combined with a weak likelihood due to poor information in the data. The use of uniform priors for variance components was discouraged because the chance of obtaining an improper posterior distribution was high (Van Tassel and Van Vleck 1995). However, the decision to establish progeny tests at site B was insensitive to prior information despite the limited data.

The present study indicate that, even in this simple decision problem, Gibbs sampling can be an attractive approach to decision-making in progeny test location, as more information to make inferences about the parameter of interest can be derived from the analyses than is possible from REML. In this example we have used a relatively simple decision rule based on the estimated parameters. A fuller analysis of the problem may develop a more-complex decision process than considered here and these benefits would be expected to be sustained, or even possibly be greater. The major advantage of Gibbs sampling is that it gives a full marginal posterior distribution of a parameter of interest, and any feature of this distribution can be computed including the proba-

bility statements, giving a richer analysis than is possible with REML. Therefore, Gibbs sampling offers tree breeders the possibility of making better-informed decisions and, over time, its use will become less limited by high computational demands.

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References

- Box GEP, Jenkins GM (1976) Time series analysis, forecasting and control. Holden-Day, Oakland, California
- Falconer DS (1989) Introduction to quantitative genetics, 3rd edition. Longman, London
- Gilks WR, Richards S, Spiegelhalter DJ (1996) Markov chain monte carlo in practice. Chapman and Hall, London, pp 1–19
- Gianola D, Fernando RL (1986) Bayesian methods in animal breeding theory. *J Anim Sci* 63:217–244
- Green EJ, Strawderman WE (1996) Predictive posterior distributions from a Bayesian version of a splash pine yield model. *For Sci* 42:456–464
- Green EJ, Strawderman WE, Thomas CE (1992) Empirical Bayes development of Honduran pine yield models. *For Sci* 38:21–33
- Gwaze DP, Woolliams JA (1997) Decision-making in progeny test location using Gibbs sampling. In: Proc 24th Southern Forest Tree Improvement Conf, 9–12 June, 1997, Florida, USA, pp 366–368
- Gwaze DP, Woolliams JA, Kanowski PJ (1996) Predicted genetic gain in height in 23 year-old progeny tests of *Pinus taeda* L. in Zimbabwe, and inferences for the optimum age of selection. In: Dieters MJ, Matheson AC, Nikles DG, Harwood CE, Walker SM (eds). Tree improvement for sustainable tropical forestry. Proc QFRI-IUFRO Conf, Caloundra, Queensland, Australia, 27 October–1 November, 1996. (Queensland Forestry Research Institute, Gympie), pp 133–137
- Gwaze DP, Woolliams JA, Kanowski PJ (1997) Optimum selection age for height in *Pinus taeda* L. in Zimbabwe. *Silvae Genet* 46:358–365
- Jensen J, Wang CS, Sorensen DA, Gianola D (1994) Bayesian inference on variance and covariance components for traits influenced by maternal and direct genetic effects, using the Gibbs sampler. *Acta Agric Scand Sect A, Anim Sci* 44:193–201
- King JN, Burdon RD (1991) Time trends in inheritance and projected efficiencies of early selection in a large 17 year-old progeny test of *Pinus radiata*. *Can J For Res* 21:1200–1207
- McKeand SE (1988) Optimum age for family selection for growth in genetic tests of loblolly pine. *For Sci* 34:400–411
- Newman DH, Williams CG (1991) The incorporation of risk in optimum selection age determination. *For Sci* 37:1350–1364
- Patterson HD, Thompson R (1971) Recovery of interblock information when block sizes are unequal. *Biometrika* 58:545–554
- Pswarayi IZ, Barnes RD, Birks JS, Kanowski PJ (1997) Genotype-environment interactions in a population of *Pinus elliottii* Engelm. var. *elliottii*. *Silvae Genet* 46:35–40
- Riemenschneider DE (1988) Heritability, age-age correlations, and inferences regarding juvenile selection in jack pine. *For Sci* 34:1076–1082
- Sorensen DA (1997) Gibbs sampling in quantitative genetics. Unpublished internal report no. 82.1996. Danish Institute of Animal Science, Denmark, pp 20–21
- Sorensen DA, Wang CS, Jensen J, Gianola D (1994) Bayesian analysis of genetic change due to selection using Gibbs sampling. *Genet Selec Evol* 26:333–360

- Tierney L (1991) Markov chains for exploring posterior distributions. Technical report no. 560. School of Statistics, University of Minnesota, USA
- Van Tassell CP, Van Vleck LD (1995) A manual for use of MTG-SAM. A set of Fortran programs to apply Gibbs sampling to animal models for variance component estimation. US Department of Agriculture, Agricultural Research Service
- Van Tassell CP, Van Vleck LD (1996) Multiple-trait Gibbs sampler for animal models: flexible programs for Bayesian and likelihood-based (co)variance component inference. *J Anim Sci* 76:2586–2597
- Van Tassell CP, Van Vleck LD, Gregory KE (1998) Bayesian analysis of twinning and ovulation rates using a multiple-trait threshold model and Gibbs sampling. *J Anim Sci* 76:2048–2061
- Wang CS, Rutledge JJ, Gianola D (1994) Bayesian analysis of mixed linear models via Gibbs sampling with application to litter size in Iberian pigs. *Genet Sel Evol* 26:91–115
- Yazdi MH, Johanson K, Näsholm A, Jorjani H, Liljedahal, L-E (1999) Bayesian analysis of birth weight and litter size in Baluchi sheep using Gibbs sampling. *J Anim Sci* 77:533–540