Theor Appl Genet (2006) 112: 1441–1451
DOI 10.1007/s00122-006-0246-x

ORIGINAL PAPER

Patrik Waldmann · Tore Ericsson

Comparison of REML and Gibbs sampling estimates of multi-trait genetic parameters in Scots pine

Received: 6 February 2006 / Accepted: 20 February 2006 / Published online: 17 March 2006

Abstract Multi-trait (co)variance estimation is an important topic in plant and animal breeding. In this study we compare estimates obtained with restricted maximum likelihood (REML) and Bayesian Gibbs sampling of simulated data and of three traits (diameter, height and branch angle) from a 26-year-old partial diallel progeny test of Scots pine (*Pinus sylvestris* L.). Based on the results from the simulated data we can conclude that the REML estimates are accurate but the mode of posterior distributions from the Gibbs sampling can be overestimated depending on the level of the heritability. The mean and median of the posteriors were considerably higher than the expected values of the heritabilities. The confidence intervals calculated with the delta method were biased downwardly. The highest probability density (HPD) interval provides a better interval estimate, but could be slightly biased at the lower level. Similar differences between REML and Gibbs sampling estimates were found for the Scots pine data. We conclude that further simulation studies are needed in order to evaluate the effect of different priors on (co)variance components in the genetic individual model.

Introduction

In breeding for best benefit, there is generally a primary key trait that receives most attention. Nevertheless there are regularly other traits that deserve consideration since they make a contribution to the final or future results in case the key trait or its qualities are affected. Examples are health traits of domestic animals and trunk quality traits of wood-producing trees, where quantity-production capacity is generally the primary trait that is bred for. A favourable development of all traits that are of some importance calls for methods for simultaneous evaluation, such as multi-trait restricted maximum likelihood (REML) covariance estimation that has been used since long in the breeding industry (e.g. Meyer and Thompson 1986; Meyer 1991). The principal ambition is to reveal whether interrelationships are favourable or unfavourable for future selection (i.e. evaluating if traits are positively or negatively correlated depending on the objectives of the study). The multi-trait 'animal (or tree or individual) model' was introduced in quantitative genetics by Henderson and Quaas (1976). Techniques based on the individual model are well known to perform better than traditional family-based methods in the estimation of variance components and prediction of breeding values because they can use all the information from the pedigree and are less sensitive to bias introduced by selection (Sorensen and Kennedy 1984; Henderson 1986; Borralho 1995).

Historically, most analyses in quantitative genetics have been conducted with classical (also called frequentist) ANOVA methods. Probability is here viewed from the framework of hypothetically repeating an experiment a large number of times under identical conditions. Nowadays ANOVA methods have largely been replaced by REML methods for the estimation of (co)variance components and prediction of breeding values using (approximate) best linear unbiased predictors (BLUPs). The REML method, first described by Patterson and Thompson (1971) for unbalanced mixed models, has been extensively used in, principally, animal breeding. However, the REML approach requires an iterative technique that usually tends to be computationally very demanding, especially for multivariate data sets, and much effort has therefore been devoted to development of more efficient

Communicated by J.-L. Jannink

P. Waldmann (✉)
Department of Forest Genetics and Plant Physiology,
SLU, 901 83, Umeå, Sweden
E-mail: Patrik.Waldmann@genfys.slu.se
Tel.: +46-90-7868599
Fax: +46-90-7865901

T. Ericsson
Forestry Research Institute of Sweden (Skogforsk),
Box 3, 918 21, Sävar, Sweden

algorithms. Various computational procedures have been developed for REML estimation in multi-trait models, e.g. the derivative-free (DF) method (Meyer 1991), the expectation maximization (EM) method (Misztal and Perez-Encisco 1993) and the average information (AI) method (Jensen et al. 1996). In common, these REML methods use iterative algorithms for finding the maximum of the likelihood. Unfortunately, whilst it is easy to obtain estimates of the variance of the resulting estimates of parameters (the variance components), it is much more difficult to calculate reliable confidence intervals around functions of these parameters (Harville and Fenech 1985; Burch and Iyer 1997; Soria et al. 1998).

The current advance in computing power has virtually resulted in a Bayesian revolution in the development of statistical methods in genetics (Shoemaker et al. 1999; Sorensen and Gianola 2002; Xu 2003; Beaumont and Rannala 2004). In the Bayesian paradigm, a probability can be understood as a measure of uncertainty or degree of belief. Bayesian methods are especially useful in complex situations and are often easier to interpret than ordinary frequentist methods. Given the complexity of many genetic problems, it is clear that Bayesian methods could contribute considerably to improve analyses. Bayesian Markov chain Monte Carlo (MCMC) methods were introduced in quantitative genetics in the first half of the 1990s (Wang et al. 1993; Sorensen et al. 1994), facilitated by the development of the Gibbs sampling procedure (Geman and Geman 1984; Gelfand and Smith 1990). The Gibbs sampler successively samples from conditional distributions of all parameters in a model in order to generate a random sample of the marginal posterior distribution, which is the target for Bayesian inference. Gibbs sampling has been extensively practised in animal breeding and different algorithms have been developed for multi-trait evaluation (e.g. Jensen et al. 1994; van Tassel and Van Vleck 1996). However, Gibbs sampling in plant applications are still scarce (e.g. Soria et al. 1998; Gwaze and Woolliams 2001; Zeng et al. 2004; Waldmann et al. 2005).

The primary goal of this study is to compare REML and Gibbs sampling estimates of genetic parameters from multi-trait individual tree models. The methods are applied to simulated data and data from a Scots pine (*Pinus sylvestris* L.) diallel progeny test from northern Sweden, measured for three traits (bole diameter, tree height and branch angle). We restrict the analysis to an additive model because the additive components are most easily applicable in practical breeding based on recurrent selection from sexually propagated populations.

Material and methods

Multi-trait mixed model equations

Following Henderson and Quaas (1976), the multi-trait individual model can be formulated as

$$\mathbf{y}_i = \mathbf{X}_i\beta_i + \mathbf{Z}_i\mathbf{a}_i + \mathbf{e}_i, \quad (1)$$

where in our study the traits are $i = 1, 2, 3$ (see below). Moreover, the design and incidence matrices are the same over traits (i.e. $\mathbf{X}_1 = \mathbf{X}_2 = \mathbf{X}_3 = \mathbf{X}$ and $\mathbf{Z}_1 = \mathbf{Z}_2 = \mathbf{Z}_3 = \mathbf{Z}$) and relate the fixed ($\beta_i$) and additive ($\mathbf{a}_i$) effects to the data ($\mathbf{y}_i$), respectively, and $\mathbf{e}_i$ are vectors with residual effects. The data ($\mathbf{y}_i$) and fixed effects (β_i) can be merged into joint vectors ($\mathbf{y}$) and (β), respectively. To complete the mixed model equations (MME) it is necessary to specify the covariance matrix $\mathbf{R}$ that is associated with the combined residual $\mathbf{e}^{\mathrm{T}} = (\mathbf{e}_1^{\mathrm{T}}, \mathbf{e}_2^{\mathrm{T}}, \mathbf{e}_3^{\mathrm{T}})$ vector and the genetic covariance matrix $\mathbf{G}$ that relates to $\mathbf{a}^{\mathrm{T}} = (\mathbf{a}_1^{\mathrm{T}}, \mathbf{a}_2^{\mathrm{T}}, \mathbf{a}_3^{\mathrm{T}})$. If $\mathbf{R}_0$ is an error covariance matrix with the ijth element being σ_{E} (i, j) the Kronecker product can be used to obtain $\mathbf{R} = \mathbf{R}_0 \otimes \mathbf{I}$, where $\mathbf{I}$ is the identity matrix. Equivalently, let $\mathbf{G}_0$ be a submatrix with additive genetic covariances $c_{ij} = \sigma_A$ (i, j) and using the Kronecker product the following result is obtained: $\mathbf{G} = \mathbf{G}_0 \otimes \mathbf{A}$, where $\mathbf{A}$ is the relationship matrix associated with the studied individuals. Given these definitions, the final multi-trait MME can be expressed as

$$\begin{pmatrix} \mathbf{X}^{\mathrm{T}}\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}^{\mathrm{T}}\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}^{\mathrm{T}}\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}^{\mathrm{T}}\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{pmatrix} \begin{pmatrix} \hat{\beta} \\ \hat{\mathbf{a}} \end{pmatrix} = \begin{pmatrix} \mathbf{X}^{\mathrm{T}}\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}^{\mathrm{T}}\mathbf{R}^{-1}\mathbf{y} \end{pmatrix}. \quad (2)$$

Likelihood and AI REML computation

Defining $\mathrm{Var}(\mathbf{y}) = \mathbf{V} = \mathbf{Z}\mathbf{G}\mathbf{Z}^{\mathrm{T}} + \mathbf{R}, \mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1}\mathbf{X}\left(\mathbf{X}^{\mathrm{T}}\mathbf{V}^{-1}\mathbf{X}\right)^{-1}\mathbf{X}^{\mathrm{T}}\mathbf{V}^{-1}$ and assuming multivariate normality, -2 times the restricted log-likelihood can be written as

$$L(\theta) = -2\ln(l) = c + \ln|\mathbf{V}| + \ln\left|\mathbf{X}^{\mathrm{T}}\mathbf{V}^{-1}\mathbf{X}\right| + \mathbf{y}^{\mathrm{T}}\mathbf{P}\mathbf{y}, \quad (3)$$

where θ is a collection of all parameters in $\mathbf{G}$ and $\mathbf{R}$ and c a constant. For calculation of the REML estimates, it is necessary to compute the first and second order derivatives of the log-likelihood as

$$\frac{\partial L(\theta)}{\partial \theta_j} = \mathbf{tr}\left(\frac{\partial \mathbf{V}}{\partial \theta_j}\mathbf{P}\right) - \mathbf{y}^{\mathrm{T}}\mathbf{P}\left(\frac{\partial \mathbf{V}}{\partial \theta_j}\right)\mathbf{P}\mathbf{y} \quad (4)$$

and

$$\frac{\partial^2 L(\theta)}{\partial \theta_j \partial \theta_{j'}} = -\mathbf{tr}\left(\frac{\partial \mathbf{V}}{\partial \theta_j}\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_{j'}}\mathbf{P}\right) + 2\,\mathbf{y}^{\mathrm{T}}\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_j}\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_{j'}}\mathbf{P}\mathbf{y}. \quad (5)$$

The AI REML algorithm is an efficient, flexible and fast method that was first described by Gilmour et al. (1995) and consequently has been implemented in various computing programs for breeding purposes. How to obtain the solutions for Eqs. 4 and 5 in a multi-trait model is presented in Jensen et al. (1996). Here we just note that the key step in the AI algorithm is the calculation of an average information matrix ($\mathbf{I}_{\mathrm{A}}$) for evaluation of Eq. 5, instead of calculating the observed and expected information matrices:

$$I_{\mathrm{A}} = \frac{1}{2}\left[\frac{\partial^2 L(\theta)}{\partial\theta_j\,\partial\theta_{j'}} + \mathrm{E}\left(\frac{\partial^2 L(\theta)}{\partial\theta_j\,\partial\theta_{j'}}\right)\right] = \mathbf{y}^{\mathrm{T}}\mathbf{P}\frac{\partial\mathbf{V}}{\partial\theta_j}\mathbf{P}\frac{\partial\mathbf{V}}{\partial\theta_{j'}}\mathbf{P}\,\mathbf{y}. \tag{6}$$

Further details and description of the iterative scheme for computation of the parameters is described in Jensen et al. (1996).

Sampling precision of estimated REML parameters and their functions

In addition to the maximum likelihood estimates, with the AI REML algorithm, one can obtain the variance (and thus the standard deviation) estimates of the parameters through the inverse of the negative average information matrix, $\mathrm{Var}\left(\hat{\theta}\right) = (-\mathbf{I}_{\mathrm{A}})^{-1}$. Unfortunately, it is more difficult to obtain exact estimates of the variance of functions of the variance components (for example the heritability) with REML methods (Harville and Fenech 1985; Burch and Iyer 1997). However, the variance of a function of random variables can be computed approximately with the 'delta method' based on Taylor expansion (Kendall and Stuart 1977; Hohls 1996; Lynch and Walsh 1998). If we estimate the heritability as the ratio of the additive genetic variance and the phenotypic variance (i.e. $\hat{h}^2 = \hat{\sigma}^2_{\mathrm{A}}/\hat{\sigma}^2_{\mathrm{P}}$), the standard error of $\hat{h}^2$ is

$$\mathrm{SE}\left(\hat{h}^2\right) \approx \sqrt{\left(\frac{\partial\hat{h}^2}{\partial\theta'}\right)(-\mathbf{I}_{\mathrm{A}})^{-1}\left(\frac{\partial\hat{h}^2}{\partial\theta}\right)}, \tag{7}$$

which for trait i can be rewritten as

$$\mathrm{SE}\left(\hat{h}^2(i)\right) \approx \sqrt{\left(\hat{h}^2(i)\right)^2\left[\frac{\mathrm{Var}\left(\hat{\sigma}^2_{\mathrm{A}}(i)\right)}{\hat{\sigma}^4_{\mathrm{A}}(i)} + \frac{\mathrm{Var}\left(\hat{\sigma}^2_{\mathrm{P}}(i)\right)}{\hat{\sigma}^4_{\mathrm{P}}(i)} - \frac{2\mathrm{Cov}\left(\hat{\sigma}^2_{\mathrm{A}}(i),\hat{\sigma}^2_{\mathrm{P}}(i)\right)}{\hat{\sigma}^2_{\mathrm{A}}(i)\hat{\sigma}^2_{\mathrm{P}}(i)}\right]}, \tag{8}$$

where $\mathrm{Var}\left(\hat{\sigma}^2_{\mathrm{P}}(i)\right) = \mathrm{Var}\left(\hat{\sigma}^2_{\mathrm{A}}(i)\right) + \mathrm{Var}\left(\hat{\sigma}^2_{\mathrm{E}}(i)\right) + 2\mathrm{Cov}\left(\hat{\sigma}^2_{\mathrm{A}}(i),\hat{\sigma}^2_{\mathrm{E}}(i)\right)$ and $\mathrm{Cov}\left(\hat{\sigma}^2_{\mathrm{A}}(i),\hat{\sigma}^2_{\mathrm{P}}(i)\right) = \mathrm{Var}\left(\hat{\sigma}^2_{\mathrm{A}}(i)\right) + \mathrm{Cov}\left(\hat{\sigma}^2_{\mathrm{A}}(i),\hat{\sigma}^2_{\mathrm{E}}(i)\right)$.

In order to calculate the standard errors for the phenotypic, additive and environmental correlation coefficients ($\hat{r}_{\mathrm{P}}, \hat{r}_A$ and $\hat{r}_{\mathrm{E}}$, respectively), $\hat{h}^2$ in Eq. 7 can be substituted with $\hat{r}_k(i,j) = \hat{\sigma}_k(i,j)/\left(\hat{\sigma}^2_k(i)\,\hat{\sigma}^2_k(j)\right)^{1/2}$ (where k is P, A or E and i, j trait numbers) resulting in

$$\mathrm{SE}(\hat{r}_k(i,j)) \approx \sqrt{\hat{r}^2_k(i,j)\left[\frac{\mathrm{Var}\left(\hat{\sigma}^2_k(i)\right)}{4\hat{\sigma}^4_k(i)} + \frac{\mathrm{Var}\left(\hat{\sigma}^2_k(j)\right)}{4\hat{\sigma}^4_k(j)} - \frac{\mathrm{Var}(\hat{\sigma}_k(i,j))}{\hat{\sigma}^2_k(i,j)} + \frac{2\mathrm{Cov}\left(\hat{\sigma}^2_k(i)\right)\hat{\sigma}^2_k(j)}{4\hat{\sigma}^2_k(i)\hat{\sigma}^2_k(j)} - \frac{2\mathrm{Cov}\left(\hat{\sigma}^2_k(i)\right)\hat{\sigma}_k(i,j)}{2\hat{\sigma}^2_k(i)\hat{\sigma}_k(i,j)} - \frac{2\mathrm{Cov}(\hat{\sigma}_k(i,j))\hat{\sigma}^2_k(j)}{2\hat{\sigma}_k(i,j)\hat{\sigma}^2_k(j)}\right]}. \tag{9}$$

The program Asreml (Gilmour et al. 2002), which is based on the AI REML algorithm and can estimate standard errors for functions of the variance components through the delta method, was used in this study. Based on the standard errors from the delta method, approximate 95% confidence intervals (ΔCI) were computed as $\hat{\theta} \pm 1.96\hat{\sigma}_{\hat{\theta}}$.

Bayesian inference using Gibbs sampling

Bayesian methods are based on formulating a joint probability distribution over the data ($\mathbf{y}$) and the collection of the model parameters and the missing data (θ). The joint distribution consists of two parts: the prior distribution and the likelihood. The posterior distribution is then obtained using Bayes' theorem. Usually, the focus of inference is on θ and Bayes' theorem can therefore be written as the probability $p(\theta|\mathbf{y}) \propto p(\mathbf{y}|\theta)p(\theta)$, which says that the posterior distribution is proportional to the product of the likelihood and the prior. In the Bayesian paradigm, a probability is a direct measure of uncertainty (Gelman et al. 2004).

First, similar to the frequentist model in Eq. 1, assume that the phenotypic data in $\mathbf{y}$ follows a multivariate normal (MVN) distribution:

$$\mathbf{y}\,|\,\beta,\mathbf{a},\mathbf{R}_0 \sim \mathrm{MVN}(\mathbf{X}\beta + \mathbf{Z}\mathbf{a},\mathbf{R}), \tag{10}$$

where parameters are as specified earlier. To perform Bayesian analysis, it is required to assign prior distributions to both the location effects ($\beta, \mathbf{a}$) and all the variance and covariance components ($\mathbf{G}_0, \mathbf{R}_0$). Usually, if no information from earlier studies exists, it is common practice to use non-informative priors. A non-informative flat prior for the fixed effects is

$$p(\beta) \propto \text{constant}, \tag{11}$$

which needs to be given upper and lower bounds ($\beta_{\min}, \beta_{\max}$) in order to become a proper prior. The vector of additive genetic effects is assumed to follow an MVN distribution (which can be thought of as the

vaguely informative prior for these effects):

$$\mathbf{a} \mid \mathbf{G}_0, \mathbf{A} \sim \text{MVN}(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A}). \tag{12}$$

For the covariance matrices $\mathbf{G}_0$ and $\mathbf{R}_0$, the scaled inverted Wishart distributions,

$$p(\mathbf{G}_0 \mid \nu_A, \mathbf{V}_A) \propto |\mathbf{G}_0|^{-(1/2)(\nu_A+k+1)} \exp\left[-\frac{1}{2}\mathbf{tr}\left(\mathbf{G}_0^{-1}\mathbf{V}_A^{-1}\right)\right] \tag{13}$$

and

$$p(\mathbf{R}_0 \mid \nu_E, \mathbf{V}_E) \propto |\mathbf{R}_0|^{-(1/2)(\nu_E+k+1)} \exp\left[-\frac{1}{2}\mathbf{tr}\left(\mathbf{R}_0^{-1}\mathbf{V}_E^{-1}\right)\right], \tag{14}$$

are used as priors, where $k = 3$ for a trivariate model. The hyperparameters ν_τ and $\mathbf{V}_\tau$ (τ = A or E) generate a uniform (non-informative) inverse Wishart (IW) distribution by setting $\nu_\tau = -(k+1)$ and $\mathbf{V}_\tau = \mathbf{0}$ (Sorensen and Gianola 2002).

In the current study we have no missing data and therefore we can write the joint posterior density of all parameters as

$$p(\beta, \mathbf{a}, \mathbf{G}_0, \mathbf{R}_0 \mid \mathbf{y}) \propto p(\mathbf{y} \mid \beta, \mathbf{a}, \mathbf{R}_0) p(\mathbf{a} \mid \mathbf{G}_0) p(\mathbf{G}_0) p(\mathbf{R}_0). \tag{15}$$

Note that the prior of the fixed effects cancels out in Eq. 15 because we have chosen to treat them as constants. For implementation of a Gibbs sampling algorithm it is necessary to derive the fully conditional posterior distributions from Eq. 15 by consecutively fixing the conditioning variables of this joint density. If there had been missing data we should first have generated values for those observations, for example with multivariate data augmentation. However, in our study we first derive the full conditional posterior distribution for the location effects. Therefore, rewrite the MME in Eq. 2 as

$$\mathbf{C}\,\hat{\mathbf{u}} = \mathbf{y}. \tag{16}$$

The full conditional posterior distribution of $\mathbf{u}$ (the location effects) is then

$$\mathbf{u} \mid \mathbf{R}_0, \mathbf{G}_0, \mathbf{y} \sim \text{MVN}\left(\hat{\mathbf{u}}, \mathbf{C}^{-1}\right). \tag{17}$$

For the covariance matrices, first define

$$\mathbf{S}_A = \begin{bmatrix} \mathbf{a}_1^T\mathbf{A}^{-1}\mathbf{a}_1 & \mathbf{a}_1^T\mathbf{A}^{-1}\mathbf{a}_2 & \mathbf{a}_1^T\mathbf{A}^{-1}\mathbf{a}_3 \\ \mathbf{a}_2^T\mathbf{A}^{-1}\mathbf{a}_1 & \mathbf{a}_2^T\mathbf{A}^{-1}\mathbf{a}_2 & \mathbf{a}_2^T\mathbf{A}^{-1}\mathbf{a}_3 \\ \mathbf{a}_3^T\mathbf{A}^{-1}\mathbf{a}_1 & \mathbf{a}_3^T\mathbf{A}^{-1}\mathbf{a}_2 & \mathbf{a}_3^T\mathbf{A}^{-1}\mathbf{a}_3 \end{bmatrix} \tag{18}$$

and

$$\mathbf{S}_E = \begin{bmatrix} \mathbf{e}_1^T\mathbf{e}_1 & \mathbf{e}_1^T\mathbf{e}_2 & \mathbf{e}_1^T\mathbf{e}_3 \\ \mathbf{e}_2^T\mathbf{e}_1 & \mathbf{e}_2^T\mathbf{e}_2 & \mathbf{e}_2^T\mathbf{e}_3 \\ \mathbf{e}_3^T\mathbf{e}_1 & \mathbf{e}_3^T\mathbf{e}_2 & \mathbf{e}_3^T\mathbf{e}_3 \end{bmatrix}. \tag{19}$$

The full conditional distribution for the genetic covariance matrix is obtained by combining the prior 13 with the density $p(\mathbf{a} \mid \mathbf{G}_0)$ as

$$p(\mathbf{G}_0 \mid \beta, \mathbf{a}, \mathbf{R}_0, \mathbf{y}) \propto |\mathbf{G}_0|^{-(1/2)(\nu_A+n+k+1)} \times \exp\left\{-1/2\mathbf{tr}\left[\mathbf{G}_0^{-1}\left(\mathbf{V}_A^{-1} + \mathbf{S}_A\right)\right]\right\}, \tag{20}$$

which is the kernel of the scaled inverse Wishart distribution

$$\mathbf{G}_0 \mid \beta, \mathbf{a}, \mathbf{R}_0, \mathbf{y} \sim \text{IW}_3\left(\left(\mathbf{V}_A^{-1} + \mathbf{S}_A\right)^{-1}, \nu_A + n\right), \tag{21}$$

where n is the number of individuals. Finally, the posterior density of the residual covariance matrix is defined as

$$p(\mathbf{R}_0 \mid \beta, \mathbf{a}, \mathbf{G}_0, \mathbf{y}) \propto |\mathbf{R}_0|^{-(1/2)(\nu_E+n+k+1)} \times \exp\left\{-1/2\mathbf{tr}\left[\mathbf{R}_0^{-1}\left(\mathbf{V}_E^{-1} + \mathbf{S}_E\right)\right]\right\} \tag{22}$$

and the Gibbs sampler simulates updates from the following inverse Wishart distribution

$$\mathbf{R}_0 \mid \beta, \mathbf{a}, \mathbf{G}_0, \mathbf{y} \sim \text{IW}_3\left(\left(\mathbf{V}_E^{-1} + \mathbf{S}_E\right)^{-1}, \nu_E + n\right). \tag{23}$$

There are several ways to implement an algorithm that samples from Eqs. 17, 21 and 23. We have used the program gibbs1f90 (Misztal et al. 2002) which uses block updating by traits.

Point, interval and kernel estimation of posterior densities

After the parameters of the MCMC chains have been checked graphically and for convergence (for example by using the *R* statistic suggested by Brooks and Gelman 1998), it is necessary to summarize the posterior distributions by some suitable point and interval statistics. Commonly used measures of location of the posterior densities comprise the mean, median and mode. For a posterior distribution that is symmetric, the mean, median and mode should all be the same. The mean and median can easily be estimated using standard methods. However, the mode is more difficult to obtain. Here, we will use an approach that is based on finding the maximum of a kernel density. There are many different methods available for estimation of kernel densities, from simple histograms to advanced non-parametric smoothing techniques. However, the kernel density estimator at point u is often calculated as

$$\hat{p}_h(u) = (nh)^{-1}\sum_{i=1}^{n} K[(\theta - u)/h], \tag{24}$$

where n is the number of iterations after burn-in and thinning of the parameter (θ), K (the kernel) a normal

probability density and h the bandwidth. It is important to choose an appropriate bandwidth because this parameter determines the amount of smoothing being applied to the curve. We use the direct plug-in approach for automatic selection of optimal bandwidth as implemented in the KernSmooth package in the R software (Wand and Jones 1995). The mode of the posterior density is

$$\tilde{\theta}_{\mathrm{MODE}} = \max\left[p(\theta|\mathbf{y})\right], \tag{25}$$

which can be obtained by finding the u value at $\max\left[\hat{p}_h(u)\right]$.

In Bayesian statistics, intervals are often termed credible (or posterior) intervals in order to distinguish from frequentist confidence intervals. For symmetric posterior distributions, a two-sided $100(1-\alpha)\%$ credible interval (BCI) can be obtained from the MCMC samples $\theta_{(i)}$ as

$$\left(\theta_{n\alpha/2}, \theta_{n(1-\alpha)/2}\right). \tag{26}$$

However, when the posterior distribution is not symmetric (i.e. skewed), a highest probability density (HPD) interval is more desirable because a standard credible interval will generally contain some parameter values that have lower posterior probability than values outside the interval. An HPD interval is adjusted so that the probability ordinates at each tail are identical. Moreover, HPD intervals are also of the shortest length (Chen and Shao 1999). Unfortunately, HPD intervals are more difficult to compute than credible intervals, but Chen and Shao (1999) described a method where the MCMC sample can be used. This method is based on evaluating all the j $100(1-\alpha)\%$ credible intervals in the sample and then selecting the one (at j^*) with smallest interval width according to

$$\theta_{j^*+n(1-\alpha)} - \theta_{j^*} = \min_j\left(\theta_{j+n(1-\alpha)} - \theta_j\right). \tag{27}$$

The 'boa' package in R was used for calculation of HPD intervals based on the algorithm of Chen and Shao (1999).

Scots pine material

The methods are applied to data from a Scots pine (*P. sylvestris* L.) progeny test site at 64°18'N in north Sweden, where full-sib progenies of 52 assumed unrelated parent trees were planted out in 1971 (identification at Skogforsk: S23F7110264 Vindeln). The parent trees were crossed according to a partial diallel (approximate 'circulant') plan (Table 1; Kempthorne and Curnow 1961). In total about 8,000 seedlings were used, where about 200 full-sib families were represented by 40 one-year-old seedlings per family. The labelled seedlings were planted out unrestricted randomly using 2.2 m^2 spacing, thus taking up roughly 4 ha of normal forest land. The plantation was thoroughly mapped and subdivided into 70 nearly square blocks to be used in subsequent evaluations.

From the measurements in 1997, with about 65% of the trees remaining after the initial mortality period, we used the records of diameter at 130 cm above ground (D), total tree height (H) and branch angle (B). The branch angle was scored such that an average tree was given score 5, and the range 1–9 was used to include all trees including much better to much worse branch angle appearance (that is, horizontal branches were given low scores and upwards vertical branches high scores). It is expected that the two size traits, D and H, are genetically strongly positively correlated. The mortality of 35% implies some patchiness in the originally even-spaced plantation. However, only living trees with complete records were considered (totally 4,970 individuals) in order to avoid a selection effect in the measured sample. D, H and B had mean values of 114 mm and 705 cm and a mean score of 4.86, respectively. In order to facilitate the computational procedures, for each trait, the records were transformed to zero mean and unit variance before analysis.

Simulated data

In order to evaluate the statistical properties of the ΔCI, BCI and HPD intervals, we simulated data for two traits corresponding to a one-way half-sib design with 50 maternal families (each with 25 offspring). The between- and within-family variance were set to 2.5 and 97.5 for trait one (corresponding to a heritability of 0.1). For trait two, the variances were 10 and 70, respectively (resulting in a heritability of 0.5). The exact 95% confidence intervals of the heritabilities were calculated using the mean squares from ANOVA and the quantiles of the F distribution (for details see Lynch and Walsh 1998). We generated 50 replicates and analysed each with AI REML and Gibbs sampling. The root mean squared errors (RMSE) were obtained as a measure of bias for the lower and upper limits of ΔCI, BCI and HPD when evaluated against the exact confidence intervals. We did not test the statistical properties of the variance components because this has recently been thoroughly evaluated elsewhere (Browne and Draper 2006). Moreover, we did not simulate any genetic correlations because of the lack of exact CI for this parameter.

Results

REML analysis of Scots pine data

In multi-trait REML analysis, no iteration algorithm guarantees success unless the iterations are started with parameter values that are sufficiently close to the final estimates. Satisfactory starting values for variances were obtained by univariate pre-runs. Approximate covariances are less readily calculated. Bivariate pre-runs

Table 1 The crossing plan with the number of trees per full-sib family that were used in the study (4,970 trees in total)

	24	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**
1	22	–	–	–	–	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	24	18	30	25	21	25	22	28	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	–	28	26	20	19	26	29	26	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	–	–	29	22	19	19	11	24	28	21	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	–	–	–	21	13	16	22	28	13	24	24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6	–	–	–	–	30	23	14	29	33	25	30	29	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7	–	–	–	–	–	26	22	30	25	20	–	18	24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	–	–	–	–	–	–	25	34	27	16	27	28	24	30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
9	–	–	–	–	–	–	–	35	32	27	33	23	31	16	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	23	29	23	25	24	26	27	23	–	–	–	–	–	–	–	–	–	–	–	–	–
11	–	–	–	–	–	–	–	–	–	34	31	23	20	19	24	23	18	–	–	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–	23	29	18	26	28	30	24	17	–	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–	–	23	27	29	26	28	28	28	–	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	–	–	–	–	22	27	23	27	19	21	–	31	–	–	–	–	–	–	–	–	–
15	–	–	–	–	–	–	–	–	–	–	–	–	–	28	26	26	29	24	15	20	23	–	–	–	–	–	–	–	–
16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	22	26	26	12	26	29	30	–	–	–	–	–	–	–
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25	25	27	29	33	30	29	28	–	–	–	–	–	–
18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	22	–	26	30	26	23	22	–	–	–	–	–
19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	23	15	24	30	28	19	16	28	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	19	27	26	29	12	17	25	–	–	–
21	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	25	23	18	22	24	22	26	–	–
22	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	35	30	26	21	33	25	27	25	–
23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	33	31	20	29	20	22	28	27
24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	26	27	25	29	13	30
25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	32	26	25	19	10
26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	27	27	27	23	25
27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	34	29	27
28	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	22	18
29	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	24
30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	31

The parent trees are numbered in boldface (mothers vertically)

supported by qualified guesses will generally suffice, particularly if correlations are estimated instead of covariances, which belong to a theoretically unlimited parameter space. There is an implemented option in Asreml where to reformulate the multi-trait MME using correlations. Thus, facilitated by the rescaled data representing only three traits, it was quite straightforward to obtain good REML estimates.

The resulting parameter estimates with standard errors and approximate 95% ΔCI are presented in Tables 2 and 3 (the REML columns). A notable result is that the genetic correlation between diameter and tree height, $r_A(D,H) = 0.64$, appears weaker than the corresponding environmental correlation, $r_E(D,H) = 0.83$, though the contrary might equally well be expected under fairly similar test conditions. But, the heritability span is similar to what can be supposed ($h^2 = 0.08$ and 0.21 for D and H, respectively) in an environment that is modifying diameter development much more than height growth due to varying competition between trees caused by patchiness.

Gibbs sampling analysis of Scots pine data

We ran two MCMC chains each of 1,300,000 iterations. Graphical inspection of the trace and autocorrelation plots suggested a burn-in of 50,000 iterations and thinning of every 25th iteration for each chain, yielding a total sample of 100,000 iterations. The Brooks and Gelman (1998) R statistic was close to 1 for all parameters and one could therefore conclude that the MCMC chains had converged.

The relative differences between the mean, median and mode of the posterior densities were larger for the additive variance and covariance components than for the error components. Two additive covariances had negative mean, median and modes (diameter–branch angle and height–branch angle) whereas only the phenotypic covariance between height and branch angle was negative (Table 2). As expected (Chen and Shao 1999), the HPD intervals were narrower than the BCI intervals for all (co)variance components (Table 2).

Differences between the mean, median and mode of the posterior densities were largest for the heritability that was closest to zero (diameter; Table 3). Furthermore, the relative differences between both the lower and upper levels of the BCI and HPD intervals were larger for the diameter heritability. Statistical theory predicts that distributions of a variance ratio like the heritability should follow F-distributions and therefore be more skewed at the margins (i.e. close to zero and one). It can be seen that the posterior density of height is more skewed than the other heritability densities (Figs. 1, 2, 3). The two posterior densities of the additive genetic correlations that are closer to the margins (-1 and 1) are also more skewed (Figs. 4, 5, 6).

Table 2 Point and interval estimate summary for variance and covariance parameters

Parameter (trait)	REML				Gibbs sampling						
	Estimate	SE[a]	ΔCI2.5[b]	ΔCI97.5[b]	Mean	Median	Mode	BCI2.5[c]	BCI97.5[c]	HPD2.5[d]	HPD97.5[d]
Additive (co)variances											
$\sigma^2_A(D)$	0.06734	0.01746	0.0331	0.1016	0.08120	0.07781	0.06827	0.04563	0.1352	0.04143	0.1278
$\sigma_A(D,H)$	0.07073	0.02222	0.0272	0.1143	0.08702	0.08321	0.07679	0.03938	0.1558	0.03370	0.1467
$\sigma_A(D,B)$	−0.02728	0.02230	−0.0710	0.0164	−0.03228	−0.0313	−0.03001	−0.09479	0.02503	−0.09484	0.02494
$\sigma^2_A(H)$	0.1805	0.03974	0.1026	0.2584	0.2224	0.2143	0.1991	0.1388	0.3532	0.1294	0.3347
$\sigma_A(H,B)$	−0.1213	0.03727	−0.1943	−0.0483	−0.1493	−0.1436	−0.1385	−0.2656	−0.06594	−0.2562	−0.06029
$\sigma^2_A(B)$	0.2524	0.05515	0.1443	0.3605	0.3169	0.3073	0.2912	0.1984	0.4908	0.1857	0.4666
Error (environmental) (co)variances											
$\sigma^2_E(D)$	0.8134	0.01947	0.7752	0.8516	0.8079	0.8083	0.8117	0.7658	0.8484	0.7668	0.8492
$\sigma_E(D,H)$	0.6108	0.01861	0.5743	0.6473	0.6037	0.6047	0.6065	0.5596	0.6431	0.5620	0.6449
$\sigma_E(D,B)$	0.2331	0.01714	0.1995	0.2667	0.2361	0.2358	0.2361	0.1979	0.2763	0.1973	0.2757
$\sigma^2_E(H)$	0.6654	0.02521	0.6160	0.7148	0.6457	0.6487	0.6535	0.5744	0.6990	0.5805	0.7030
$\sigma_E(H,B)$	0.07274	0.02211	0.0294	0.1161	0.08679	0.08442	0.07970	0.03755	0.1493	0.03218	0.1421
$\sigma^2_E(B)$	0.7613	0.03309	0.6964	0.8262	0.7310	0.7348	0.7435	0.6377	0.8019	0.6483	0.8089
Phenotypic (co)variances											
$\sigma^2_P(D)$	0.8807	0.01911	0.8432	0.9182	0.8891	0.8884	0.8878	0.85035	0.9318	0.8489	0.9300
$\sigma_P(D,H)$	0.6815	0.01834	0.6456	0.7174	0.6908	0.6898	0.6898	0.6527	0.735	0.6508	0.7327
$\sigma_P(D,B)$	0.2058	0.01688	0.1727	0.2389	0.2038	0.2039	0.2028	0.1645	0.2415	0.1650	0.2419
$\sigma^2_P(H)$	0.8459	0.02500	0.7969	0.8949	0.8680	0.8650	0.8576	0.8153	0.9383	0.8103	0.9307
$\sigma_P(H,B)$	−0.04859	0.02195	−0.0916	−0.0056	−0.06248	−0.06012	−0.05636	−0.1241	−0.01412	−0.1196	−0.01084
$\sigma^2_P(B)$	1.0140	0.03279	0.9497	1.0783	1.0478	1.0437	1.0393	0.9781	1.1410	0.9716	1.1307

REML: from the restricted maximum likelihood analysis; Gibbs sampling: from posterior distributions of the Gibbs sampling analysis
Traits *D* density, *H* height, *B* branch angle
[a]Standard error
[b]95% confidence interval
[c]95% Bayesian credible interval
[d]95% highest probability density interval

Table 3 Point and interval estimate summary for heritabilities and correlation parameters

Parameter (trait)	REML				Gibbs sampling						
	Estimate	SE[a]	ΔCI2.5[b]	ΔCI97.5[b]	Mean	Median	Mode	BCI2.5[c]	BCI97.5[c]	HPD2.5[d]	HPD97.5[d]
Heritabilities											
$h^2(D)$	0.07650	0.01920	0.0389	0.1141	0.09105	0.08771	0.07863	0.05224	0.1478	0.04863	0.1413
$h^2(H)$	0.2134	0.04220	0.1307	0.2961	0.2546	0.2482	0.2341	0.1676	0.3796	0.1578	0.3638
$h^2(B)$	0.2490	0.04790	0.1551	0.3429	0.3004	0.2946	0.2833	0.2002	0.4329	0.1909	0.4186
Additive genetic correlations											
$r_A(D,H)$	0.6414	0.09890	0.4476	0.8352	0.6418	0.6554	0.6728	0.3970	0.8127	0.4230	0.8261
$r_A(D,B)$	−0.2092	0.1652	−0.5330	0.1146	−0.2033	−0.2096	−0.2144	−0.5238	0.1526	−0.5342	0.1389
$r_A(H,B)$	−0.5684	0.1107	−0.7854	−0.3514	−0.5602	−0.5717	−0.5967	−0.7615	−0.2939	−0.7760	−0.3175
Error (environmental) correlations											
$r_E(D,H)$	0.8302	0.0091	0.8124	0.8480	0.8362	0.8350	0.8325	0.8156	0.8637	0.8135	0.8606
$r_E(D,B)$	0.2962	0.0221	0.2529	0.3395	0.3077	0.3058	0.3038	0.2586	0.3680	0.2560	0.3642
$r_E(H,B)$	0.1022	0.0330	0.0375	0.1669	0.1278	0.1221	0.1104	0.05304	0.2345	0.04325	0.2187
Phenotypic correlations											
$r_P(D,H)$	0.7896	0.0077	0.7745	0.8047	0.7864	0.7870	0.7876	0.7662	0.8026	0.7680	0.8038
$r_P(D,B)$	0.2178	0.0179	0.1827	0.2529	0.2113	0.2121	0.2131	0.1683	0.2493	0.1708	0.2512
$r_P(H,B)$	−0.0525	0.0230	−0.0976	−0.0074	−0.06504	−.06344	−0.06049	−0.1241	−0.01516	−0.1223	−0.01409

REML: from the restricted maximum likelihood analysis; Gibbs sampling: from posterior distributions of the Gibbs sampling analysis
Traits *D* density, *H* height, *B* branch angle
[a]Standard error
[b]95% confidence interval
[c]95% Bayesian credible interval
[d]95% highest probability density interval

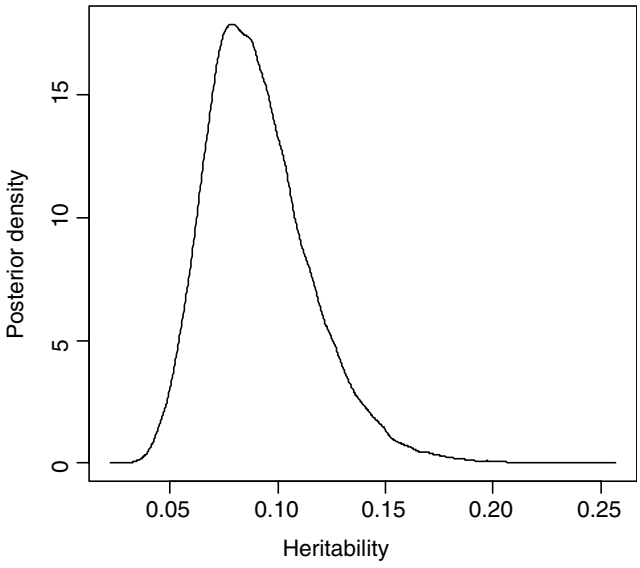

Fig. 1 Posterior density of the heritability of diameter

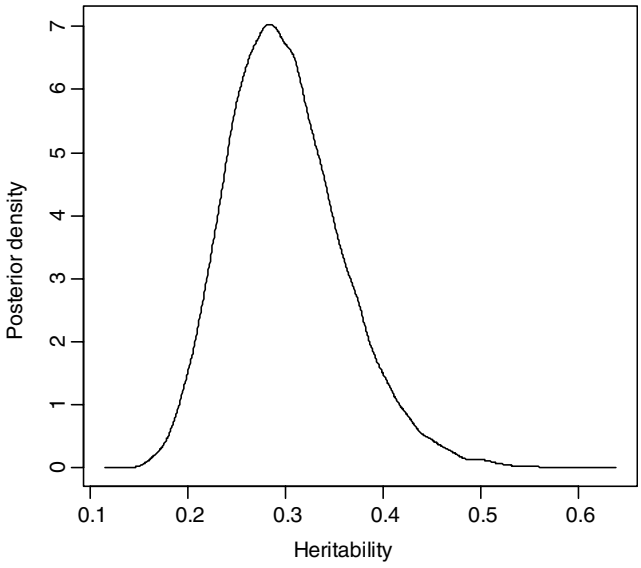

Fig. 3 Posterior density of the heritability of branch angle

REML and Gibbs sampling analysis of simulated data

The Gibbs sampling analysis of each simulated replicate was based on an MCMC chain of 110,000 iterations that were thinned at each 10th iteration and with a burn-in of 10,000. Results from the simulation study are presented in Table 4. The mean of the 50 REML estimates corresponded very well with the exact values for both heritabilities, whereas the 95% confidence intervals were considerably biased downwardly. The mode of the trait with the lower heritability was close to the actual value of 0.1, but the mode of the higher heritability was overestimated. The mean and median of the posteriors were considerably higher than the exact values for both traits. Both BCI2.5 and HPD2.5 were upwardly biased, whereas the HPD97.5 provided accurate estimates. Some explanations of those biases are given in next section.

Discussion

The long-lasting and sometimes infected controversy between practicians of standard frequentist and Bayesian statistics is likely to continue for some time, but methodologically both paradigms seem to be converging (Blasco 2001; Bayarri and Berger 2004). For example, MCMC methods like the Gibbs sampler can be used for both frequentist and Bayesian inference (e.g. Xu 2003), and much of the post-analysis of Bayesian MCMC chains is based on frequentist methods (Bayarri and

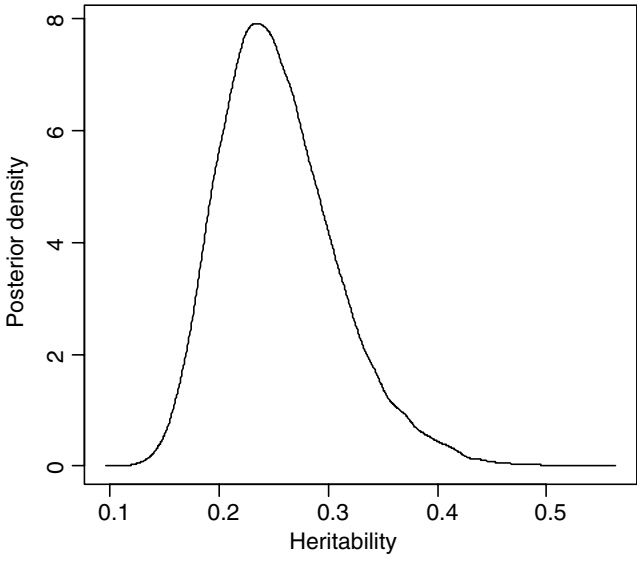

Fig. 2 Posterior density of the heritability of height

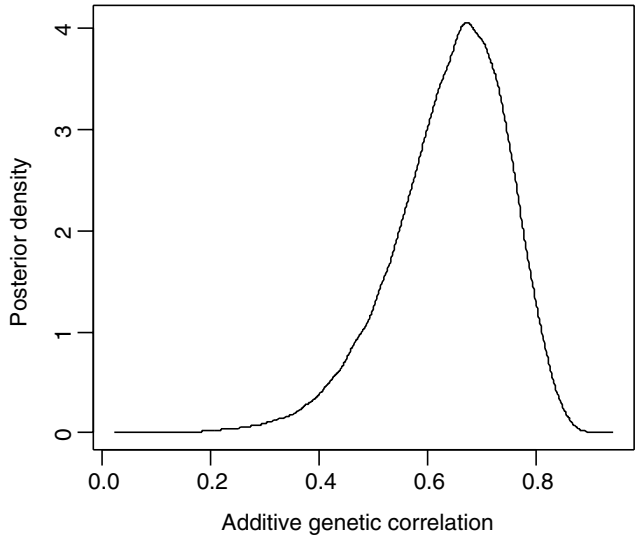

Fig. 4 Posterior density of the additive genetic correlation between diameter and height

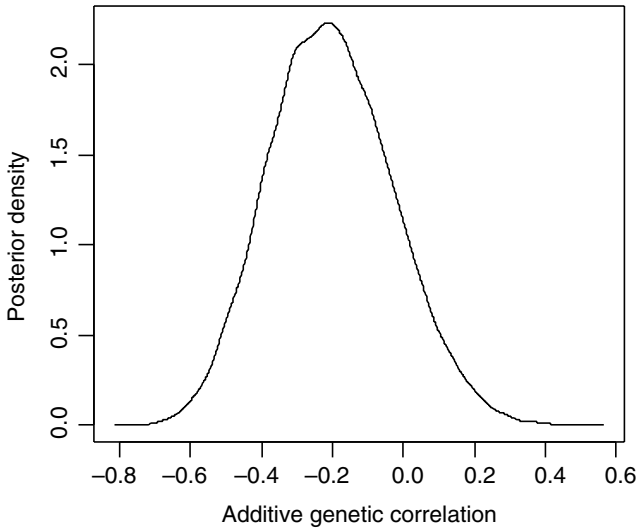

Fig. 5 Posterior density of the additive genetic correlation between diameter and branch angle

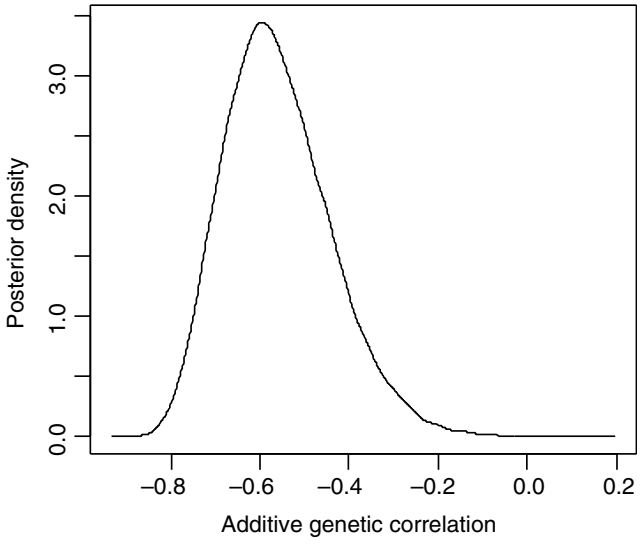

Fig. 6 Posterior density of the additive genetic correlation between height and branch angle

Berger 2004). Moreover, when the parameters of the mixed linear model are assigned non-informative uniform distributions, the maximum likelihood estimates of the variance components from a REML analysis should be identical to the mode of the Bayesian posterior distribution (Sorensen and Gianola 2002).

Based on the results from the simulated data we can conclude that the AI REML estimates are accurate but the mode of posterior distributions from the Gibbs sampling can be overestimated depending on the level of heritability. Moreover, the delta method produced confidence intervals that were biased downwardly. The highest probability density (HPD) interval represents a better interval estimate, but was slightly biased at the lower level. For the point estimates, the RMSE were

Table 4 Point and interval estimate summary from simulations of two traits: heritability parameters from restricted maximum likelihood (REML) analyses and posterior distributions of Gibbs sampling analyses

Parameter (simulated trait)	$h^2(1)$		$h^2(2)$	
	Value	RMSE[a]	Value	RMSE[a]
Expected estimate	0.1000		0.5000	
Expected CI2.5[b]	0.0213		0.3180	
Expected CI97.5[b]	0.2356		0.7891	
Mean values, REML estimation				
ML estimate	0.1100	0.0549	0.5023	0.1166
SE[c]	0.0531		0.1151	
ΔCI2.5[d]	0.0059	0.0385	0.2767	0.0089
ΔCI97.5[d]	0.2141	0.0759	0.7278	0.0258
Mean values, Gibbs sampling				
Posterior mean	0.1263	0.0645	0.5550	0.1207
Posterior median	0.1191	0.0614	0.5484	0.1218
Posterior mode	0.1071	0.0585	0.5330	0.1274
BCI2.5[e]	0.0360	0.0815	0.3509	0.0961
BCI97.5[e]	0.2585	0.0978	0.7906	0.1026
HPD2.5[f]	0.0366	0.0330	0.3472	0.1031
HPD97.5[f]	0.2321	0.0858	0.7824	0.1108

[a]Root mean square error
[b]Exact 95% confidence interval calculated based on quantiles from the *F*-distribution
[c]Standard error
[d]95% confidence intervals based on the delta method
[e]95% Bayesian credible interval
[f]95% highest probability density interval

smaller for REML than for the Gibbs sampler. That both point and interval summaries of the posterior distributions of the heritabilities are overestimated suggests that the lower part of the posterior is truncated. Choice of priors can sometimes have a considerable influence on the result (e.g. Lin and Berger 2001), whereas the opposite can also be the case (Blasco et al. 1998). Unfortunately, we lacked the possibility to change the priors in the program gibbs1f90 (Misztal et al. 2002). Some preliminary simulations with another univariate Gibbs sampler under development suggest that the common procedure to set the parameter ν_i to -2 results in a posterior distribution of the heritability that actually is truncated in the lower part. Better performance was obtained by setting ν_i to 0, but further evaluation of this prior is needed. Moreover, it has recently been argued that the inverse gamma family (which includes the inverse chi-square and inverse Wishart distributions) can be problematic as prior for variances and result in biased estimates (Gelman 2006). Consequently, additional simulation studies of the effect of different priors on the individual model are certainly warranted.

In an earlier simulation study, van Tassel et al. (1995) compared the effect of selection on estimates of variance components using Gibbs sampling (posterior mean and mode) and REML based on populations of 400 individuals. The most important result was that the Gibbs sampling (posterior mean) and REML estimates were quite similar, especially for traits with high heritability.

However, the variance components estimated with the Gibbs sampler had consistently smaller mean squared error (i.e. less bias) than those obtained with REML. A similar result was found in another simulation study where breeding value estimates were compared between REML and Gibbs sampling procedures (Schenkel et al. 2002). For traits with small variance components, van Tassel et al. (1995) found that the posterior mode estimates from the Gibbs sampler tended to be biased and the distributions skewed.

We are aware of only two studies in the tree breeding literature that have compared REML and Gibbs sampling estimates based on the individual model. Soria et al. (1998) compared the mean, median and mode of the posterior distributions of the heritability and additive genetic correlation with its corresponding REML estimate of height and diameter in *Eucalyptus globulus*. They found differences between the mean, median and mode of both the heritabilities and the additive genetic correlation that were similar to the levels in our study. Worth noting in their study is that the REML estimates of the two heritabilities (approximately 0.13 and 0.20 for diameter and height, respectively) were considerably higher than the Gibbs sampling estimates (the REML estimates were higher than the HPD97.5 estimates). However, the Bayesian and frequentist estimates of the additive genetic correlation were more consistent. The other study is a comparison between REML and Gibbs sampling estimates of height at two different ages and two different sites in *P. taeda* (Gwaze and Woolliams 2001). In their study, the heritability estimates (posterior mean) from the Gibbs sampling analyses were larger for all traits than those from REML, whereas the genetic correlations were more similar. Gwaze and Woolliams (2001) concluded that the differences were small and therefore unlikely to be important. However, the Gibbs sampler produced a heritability estimate at age 23 at site B that was 1.6 times larger than that from REML (0.62 compared to 0.39), a difference that can hardly be neglected.

Finally, from a breeding point of view, it is encouraging that the genetic correlations between branch angle and growth traits are low or negative. Both the delta and Bayesian intervals of the additive genetic correlation for D versus B span zero, and the strongly negative value for $r_A(H,B)$ means that faster growing trees develop better branching (lower B scores denote more favourable branch angles; cf. Haapanen et al. 1997, observe their reversed scaling). It is to be noted that the negative phenotypic correlation $r_E(H,B)$ is well in accordance with the other parameter values, including the fact that the highest heritability refers to branch angle, which is expected according to experience (e.g. Haapanen et al. 1997).

Acknowledgements We would like to thank the two reviewers for useful comments. Financial support was provided by the Research School in Forest Genetics and Breeding at the Swedish University of Agricultural Sciences (SLU).

References

Bayarri MJ, Berger JO (2004) The interplay of Bayesian and frequentist analysis. Stat Sci 19:58–80

Beaumont MA, Rannala B (2004) The Bayesian revolution in genetics. Nat Rev Genet 5:251–261

Blasco A (2001) The Bayesian controversy in animal breeding. J Anim Sci 79:2023–2046

Blasco A, Sorensen D, Bidanel JP (1998) Bayesian inference of genetic parameters and selection response for litter size components in pigs. Genetics 149:301–306

Borralho NMG (1995) The impact of individual tree mixed models (BLUP) in tree breeding strategies. In: Potts BM, Borralho NMG, Reid J, Cromer R, Tibbits W, Raymond C (eds) Proceedings of the CRC–IUFRO conference on eucalypt plantations: improving fibre yield and quality, Hobart, Australia, 19–24 February 1995. CRC Temperate Hardwood Forestry, Hobart, pp 141–144

Brooks SP, Gelman A (1998) Alternative methods for monitoring convergence of iterative simulations. J Comput Graph Stat 7:434–455

Browne WJ, Draper D (2006) A comparison of Bayesian and likelihood-based methods for fitting multilevel models. Bayesian Anal (in press)

Burch BD, Iyer HK (1997) Exact confidence intervals for a variance ratio (or heritability) in a mixed linear model. Biometrics 53:1318–1333

Chen M-H, Shao Q-M (1999) Monte Carlo estimation of Bayesian credible and HPD intervals. J Comput Graph Stat 8:69–92

Gelfand AE, Smith AFM (1990) Sampling-based approaches to calculating marginal densities. J Am Stat Assoc 85:398–409

Gelman A (2006) Prior distributions for variance parameters in hierarchical models. Bayesian Anal (in press)

Gelman A, Carlin JB, Stern HS, Rubin DB (2004) Bayesian data analysis, 2nd edn. Chapman & Hall, London

Geman S, Geman D (1984) Stochastic relaxation, Gibbs distributions and Bayesian restoration of images. IEEE Trans Pattern Anal Mach Intell 6:721–741

Gilmour AR, Thompson R, Cullis BR (1995) Average information: an efficient algorithm for variance parameter estimation in linear mixed models. Biometrics 51:1440–1450

Gilmour AR, Cullis BR, Welham SJ, Thompson R (2002) ASReml reference manual, 2nd edn., rel. 1.0. NSW Agricultural Biometrical Bulletin 3, NSW Agriculture, Locked Bag, Orange, Australia

Gwaze DP, Woolliams JA (2001) Making decisions about the optimal selection environment using Gibbs sampling. Theor Appl Genet 103:63–69

Haapanen M, Velling P, Annala M-L (1997) Progeny trial estimates of genetic parameters for growth and quality traits in Scots pine. Silva Fennica 31:3–12

Harville DA, Fenech AP (1985) Confidence intervals for a variance ratio, or for heritability, in an unbalanced mixed linear model. Biometrics 41:137–152

Henderson CR (1986) Recent developments in variance and covariance estimation. J Anim Sci 63:208–216

Henderson CR, Quaas RL (1976) Multiple trait evaluation using relatives' records. J Anim Sci 43:1188–1197

Hohls T (1996) Setting confidence limits to genetic parameters estimated by restricted maximum likelihood analysis of North Carolina design II experiments. Heredity 77:476–487

Jensen J, Wang CS, Sorensen D, 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 44:193–201

Jensen J, Mäntysaari EA, Madsen P, Thompson R (1996) Residual maximum likelihood estimation of (co)variance components in multivariate mixed linear models using average information. J Indian Soc Agric Stat 49:215–236

Kempthorne O, Curnow RN (1961) The partial diallel cross. Biometrics 17:229–250

Kendall M, Stuart A (1977) The advanced theory of statistics, vol 1. Distribution theory, 4th edn. Macmillan, New York

Lin EC, Berger PJ (2001) Comparison of (co)variance component estimates in control populations of red flour beetle (*Tribolium castaneum*) using restricted maximum likelihood and Gibbs sampling. J Anim Breed Genet 118: 21–36

Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer, Sunderland

Meyer K (1991) Estimating variances and covariances for multivariate animal models by restricted maximum likelihood. Genet Sel Evol 23:67–83

Meyer K, Thompson R (1986) Sequential estimation of genetic and phenotypic parameters in multitrait mixed model analysis. J Dairy Sci 69:2696–2703

Misztal I, Perez-Encisco M (1993) Sparse matrix inversion for restricted maximum likelihood estimation of variance components by expectation maximization. J Dairy Sci 76:1479–1483

Misztal I, Tsuruta S, Strabel T, Auvray B, Druet T, Lee DH (2002) BLUPF90 and related programs (BGF90). In: Proc. seventh world congress Gen. Appl. Livest. Prod., Montpellier, France. CD-ROM communication 28:07. http://www.nce.ads.uga.edu/~ignacy/programs.html

Patterson HD, Thompson R (1971) Recovery of inter-block information when block sizes are unequal. Biometrika 58:545–554

Schenkel FS, Schaeffer LR, Boettcher PJ (2002) Comparison between estimation of breeding values and fixed effects using Bayesian and empirical BLUP estimation under selection on parents and missing pedigree information. Genet Sel Evol 34:41–59

Shoemaker JS, Painter IS, Weir BS (1999) Bayesian statistics in genetics: a guide for the uninitiated. Trends Genet 15:354–358

Sorensen D, Gianola D (2002) Likelihood, Bayesian and MCMC methods in quantitative genetics. Springer, Berlin Heidelberg New York

Sorensen DA, Kennedy BW (1984) Estimation of genetic variances from unselected and selected populations. J Anim Sci 59:1213–1233

Sorensen DA, Wang CS, Jensen J, Gianola D (1994) Bayesian analysis of genetic change due to selection using Gibbs sampling. Genet Sel Evol 26:333–360

Soria F, Basurco F, Toval G, Silió L, Rodriguez MC, Toro M (1998) An application of Bayesian techniques to the genetic evaluation of growth traits in Eucalyptus globules. Can J For Res 28:1286–1294

van Tassel 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 74:2586–2597

van Tassel CP, Casella G, Pollak EJ (1995) Effects of selection on estimates of variance components using Gibbs sampling and restricted maximum likelihood. J Dairy Sci 78:678–692

Waldmann P, Garcia-Gil MR, Sillanpää MJ (2005) Comparing Bayesian estimates of genetic differentiation of molecular markers and quantitative traits: an application to *Pinus sylvestris*. Heredity 94:623–629

Wand MP, Jones MC (1995) Kernel smoothing. Chapman & Hall, London

Wang CS, Rutledge JJ, Gianola D (1993) Marginal inference about variance components in a mixed linear model using Gibbs sampling. Genet Sel Evol 21:41–62

Xu S (2003) Advanced statistical methods for estimating genetic variances in plants. Plant Breed Rev 22:113–163

Zeng W, Gosh S, Li B (2004) A blocking Gibbs sampling method to detect major genes with phenotypic data from a diallel mating. Genet Res 83:143–154