Theor Appl Genet (2013) 126:1749–1761
DOI 10.1007/s00122-013-2089-6

ORIGINAL PAPER

Bayesian inference of mixed models in quantitative genetics of crop species

Fabyano Fonseca e Silva · José Marcelo Soriano Viana · Vinícius Ribeiro Faria · Marcos Deon Vilela de Resende

Received: 29 November 2012 / Accepted: 19 March 2013 / Published online: 20 April 2013

Abstract The objectives of this study were to implement a Bayesian framework for mixed models analysis in crop species breeding and to exploit alternatives for informative prior elicitation. Bayesian inference for genetic evaluation in annual crop breeding was illustrated with the first two half-sib selection cycles in a popcorn population. The Bayesian framework was based on the Just Another Gibbs Sampler software and the *R2jags* package. For the first cycle, a non-informative prior for the inverse of the variance components and an informative prior based on meta-analysis were used. For the second cycle, a non-informative prior and an informative prior defined as the posterior from the non-informative and informative analyses of the first cycle were used. Regarding the first cycle, the use of an informative prior from the meta-analysis provided clearly distinct results relative to the analysis with a non-informative prior only for the grain yield. Regarding the second cycle, the results for the expansion volume and grain yield showed differences among the three analyses. The differences between the non-informative and informative prior analyses were restricted to variance components and heritability. The correlations between the predicted breeding values from these analyses were almost perfect.

Communicated by M. Sillanpaa.

F. F. e Silva
Departamento de Estatística, Universidade Federal de Viçosa, 36570-000 Viçosa, MG, Brazil

J. M. S. Viana (✉) · V. R. Faria
Departamento de Biologia Geral, Universidade Federal de Viçosa, 36570-000 Viçosa, MG, Brazil
e-mail: jmsviana@ufv.br

M. D. V. de Resende
Departamento de Engenharia Florestal, Embrapa Florestas/ Universidade Federal de Viçosa, 36570-000 Viçosa, MG, Brazil

Introduction

The best linear unbiased prediction (BLUP) (Henderson 1974) has been widely used for genetic evaluation in animal and forestry breeding programs. A common method for estimating variance components has been the restricted maximum likelihood (REML) (Patterson and Thompson 1971). Bayesian prediction of genetic variances and breeding values has also been largely employed (Sorensen 2009; Blasco 2001). In fact, Bayesian inference has additional relevant applications in genetics and breeding, such as the prediction of breeding values using genome-wide dense marker maps (Meuwissen et al. 2001), quantitative trait loci mapping (Bink et al. 2008), analysis of population structure (Pritchard et al. 2000), association mapping (Marttinen and Corander 2010), and inferring levels of gene expression and regulation (Beaumont and Rannala 2004).

Only recently have annual crop breeders recognized the advantages of genetic evaluation by BLUP or Bayesian analysis, such as variance components estimation based on a superior method for unbalanced data, the use of pedigree information and historical data to increase the prediction accuracy, and the possibility of the inclusion of prior information about parameters to be estimated (Piepho et al. 2008; Bauer et al. 2009; Viana et al. 2012a). Bauer et al. (2006), Flachenecker et al. (2006), Oakey et al. (2007), Viana et al. (2010a, 2011a), and others, have demonstrated the efficacy of BLUP in recurrent intra- and interpopulation breeding programs and in the development of pure/inbred lines.

Studies on Bayesian inference of mixed models in annual crop breeding are scarce. Mathew et al. (2012)

observed that the Bayesian estimates of variance components were more accurate compared to the REML estimates for simulated data and as accurate as the REML estimates for barley field data. Furthermore, the accuracies of the Bayesian and BLUP predictions were equal. Bauer et al. (2009) analyzed field and simulated data from spring barley lines, taking into consideration genotype-by-environment interaction effects and pedigree information. In general, Bayesian inference and BLUP resulted in similar breeding value predictions when the heritability of the trait was high. However, the Bayesian approach was superior for traits with low heritability.

Fortunately, all Bayesian analyses for the genetic evaluation in animal and forestry breeding are suitable for annual crop breeding. Waldmann and Ericsson (2006) fitted a multi-trait individual model for partial diallel analyses of field and simulated data from Scots pine progeny. Differences were observed between REML and Gibbs sampling estimates in both data sets. The authors concluded that REML estimates are accurate and the mode of posterior distributions from the Gibbs sampling can be overestimated depending on the heritability. Using the same data sets, Waldmann et al. (2008) fitted an additive–dominance model based on transformations of the relationship matrices. With high dominance, the additive–dominance model had the best fit. With low dominance, an informative prior was necessary to avoid overestimation of the dominance variance. The REML and Gibbs sampling estimates agreed well and the Bayesian and BLUP predictions showed similar accuracies.

The Bayesian approach has some advantages compared to the BLUP analysis, such as flexibility in choosing the distributions for sample data and unknown parameters and the possibility of incorporating prior knowledge about parameters of the model (Sorensen 2009; Blasco 2001). Although this latter advantage is widely mentioned in the literature as a potentially attractive feature of Bayesian inference (Beaumont and Rannala 2004), it has been underexplored in practice in animal and plant breeding, perhaps because of a lack of situations in which this prior knowledge can be naturally incorporated. In our opinion, the incorporation of background information represents a special feature of Bayesian analysis in crop species breeding because the concept of selection cycles characterizes a natural mechanism for informative prior elicitation. This is because the posterior distribution for the parameters of interest from a given cycle, such as variance components, can be used as a prior distribution in the analysis of the next cycle, thus forming a knowledge update system.

In terms of the computational features of Bayesian inference of mixed models, statistical tools using Markov chain Monte Carlo (MCMC) algorithms, such as the Gibbs sampler, have been widely used, especially in animal breeding. Among these tools, featured software including MTGSAM (Van Tassell and Van Vleck 1996) and gibbsf90 (Misztal et al. 2002) can be used only for additive model with one vector of breeding values, such as the individual and half-sib family models. Furthermore, these softwares do not have flexibility in choosing the distributions for data and parameters, which prevents the use of non-normal data distributions and informative prior distributions. The R (R Development Core Team 2012) package *MCMCglmm* (Hadfield 2010), whose theoretical background was detailed by Hadfield and Nakagawa (Hadfield and Nakagaw 2010), is a more flexible tool. This package offers several options for data distribution, including uni- and multivariate discrete distributions, and allows changing hyperparameters of different classes of prior distributions. Additionally, it permits the inclusion of the additive relationship matrix by using the *pedigree* statement. However, similar to MTGSAM and gibbsf90, *MCMCglmm* is unable to address models that include dominance or more than one genetic random effect as the gametic model.

One attractive solution to this problem is using the software WinBUGS (Lunn et al. 2009), which is a general Bayesian programming environment. It is highly flexible in relation to the previously mentioned models and distributions, and only requires specifications of the data listing, likelihood function, and prior distributions. Damgaard (2007), Waldmann (2009), and Hallander et al. (2010) implemented mixed models analysis in this software on animal and forestry breeding data. The method proposed by Hallander et al. (2010) is a very flexible Bayesian analysis that allows inferences in linear mixed models with a large number of genetic parameters. Additionally, their approach reduces the computational demand of large pedigrees. Although the flexibility of WinBUGS is indisputable, it does not allow direct handling of incidence and relationship matrices. These limitations make it necessary to use indirect methods based on algebraic notations, making the codes complex and unfavorable for many users. One interesting alternative is the Just Another Gibbs Sampler (JAGS) software (Plummer 2012), which has the same flexibility and facilities of WinBUGS but has the advantage of allowing matrix language programming.

The objectives of the present study were to implement a Bayesian framework for mixed models analysis in crop species breeding and to exploit alternatives for informative prior elicitation.

Materials and methods

Experimental data

The Bayesian inference in annual crop breeding was illustrated with the first two half-sib selection cycles of the

Viçosa popcorn population. The two trials composed of 196 progeny were designed as a 14 × 14 simple lattice and performed in the experimental station of the Federal University of Viçosa at Coimbra, Minas Gerais state, Brazil, in the 1999/2000 and 2001/2002 growing seasons. Each plot corresponded to a 5 m row with 25 plants (ideal stand). The traits analyzed were the expansion volume (EV) and the grain yield.

Model and Bayesian inference

The mixed model fitted (half-sib family model) was

$$y = X\beta + Z_1 u_1 + Z_2 u_2 + e \quad (1)$$

where **y** is the vector of phenotypic values; **X** and **β** are, respectively, the incidence matrix and the correspondent vector of fixed effects (population mean and replication effects); Z_1 and Z_2 are the incidence matrices of the random effects; u_1 is the vector of half of the additive genetic values of the common parents; u_2 is the vector of block within replication effects; and **e** is the residuals vector.

Assuming $e|\sigma_e^2 \sim N(0, I\sigma_e^2)$, the distribution of the observed data (likelihood function) is

$$y|\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_{u_2}, \sigma^2_e \sim N(X\beta + Z_1 u_1 + Z_2 u_2, I\sigma^2_e) \quad (1.1)$$

where $\sigma^2_{u_1} = (1/4)\sigma^2_A$ and σ^2_A is the additive genetic variance.

The prior distributions for the location parameters (fixed and random effects) were given by

$$\beta|\mu_\beta, I_\beta\sigma^2_\beta \sim \mathrm{N}(\mu_\beta, I_\beta\sigma^2_\beta) \quad (1.2)$$

$$u_1|A\sigma^2_{u_1} \sim \mathrm{N}(0, A\sigma^2_{u_1}) \quad (1.3)$$

$$u_2|I_b\sigma^2_{u_2} \sim \mathrm{N}(0, I_b\sigma^2_{u_2}) \quad (1.4)$$

where μ_β and σ^2_β are the known parameters (hyperparameters) of a multivariate normal distribution with the covariance matrix given by $I_\beta\sigma^2_\beta$; $\mathbf{A} = \{2r_{ij}\}$ is the additive relationship matrix and r_{ij} is the coefficient of coancestry between the common parents of progeny i and j. The prior distributions for the variance components $\sigma^2_{u_1}$, $\sigma^2_{u_2}$, and σ^2_e were the following scaled inverted Chi-squared distributions,

$$\sigma^2_{u_1}|\nu_{u1}, S_{u1} \sim \nu_{u1}S_{u1}\chi^{-2}_{\nu_{u1}} \quad (1.5)$$

$$\sigma^2_{u_2}|\nu_{u2}, S_{u2} \sim \nu_{u2}S_{u2}\chi^{-2}_{\nu_{u2}} \quad (1.6)$$

$$\sigma^2_e|\nu_e, S_e \sim \nu_e S_e \chi^{-2}_{\nu_e} \quad (1.7)$$

where ν_{u1}, S_{u1}, ν_{u2}, S_{u2}, ν_e, and S_e are free parameters, called hyperparameters.

Under Bayes' Theorem, the joint posterior distribution of all unknown parameters ($\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_{u_2}$ and σ^2_e) is proportional to the product of the likelihood function (Eq. 1.1) and the prior distributions (Eqs. 1.2–1.7). Thus, the general formulation of this theorem is

$$\begin{aligned}
\mathrm{P}\left(\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_{u_2}, \sigma^2_e|y\right) &\propto \mathrm{P}\left(y|\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_{u_2}, \sigma^2_e\right) \\
&\times \mathrm{P}\left(\beta|\mu_\beta, \sigma^2_\beta\right) \times \mathrm{P}\left(u_1|A\sigma^2_{u_1}\right) \\
&\times \mathrm{P}\left(\sigma^2_{u_1}|\nu_{u1}, S_{u1}\right) \times \mathrm{P}\left(u_2|I_b\sigma^2_{u_2}\right) \times \mathrm{P}\left(\sigma^2_{u_2}|\nu_{u2}, S_{u2}\right) \\
&\times \mathrm{P}\left(\sigma^2_e|\nu_e, S_e\right)
\end{aligned}$$

Using the respective probability density of these prior distributions, the formula of the joint posterior distribution can be obtained as

$$\begin{aligned}
\mathrm{P}\left(\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_{u_2}, \sigma^2_e|y\right) &\propto \left(\sigma^2_e\right)^{-\mathrm{N}/2}\exp \\
&\times \left\{-\frac{[y - (X\beta + Z_1u_1 + Z_2u_2)]'[y - (X\beta + Z_1u_1 + Z_2u_2)]}{2\sigma^2_e}\right\} \\
&\times \left(\sigma^2_\beta\right)^{(-n_\beta/2)}\exp\left[-\frac{(\beta-\mu_\beta)'(\beta-\mu_\beta)}{2\sigma^2_\beta}\right] \\
&\times \left(\sigma^2_{u_1}\right)^{(-n_{u_1}/2)}\exp\left(-\frac{u_1' A u_1}{2\sigma^2_{u_1}}\right) \\
&\times \left(\sigma^2_{u_1}\right)^{-\left(\frac{\nu_{u1}}{2}+1\right)}\exp\left(-\frac{\nu_{u1}S_{u1}}{2\sigma^2_{u_1}}\right) \\
&\times \left(\sigma^2_{u_2}\right)^{(-n_{u_2}/2)}\exp\left(-\frac{u_2' u_2}{2\sigma^2_{u_2}}\right) \\
&\times \left(\sigma^2_{u_2}\right)^{-\left(\frac{\nu_{u2}}{2}+1\right)}\exp\left(-\frac{\nu_{u2}S_{u2}}{2\sigma^2_{u_2}}\right) \times \left(\sigma^2_e\right)^{-\left(\frac{N}{2}+1\right)}\exp\left(-\frac{\nu_e S_e}{2\sigma^2_e}\right)
\end{aligned} \quad (2)$$

The statistical inference on the parameters from Eq. 2 is based on the posterior marginal distributions, P(.|y), for each of the parameters. The necessary integrals to obtain these distributions are intractable, implying the use of numerical evaluation by specialized algorithms as those from the MCMC class. In summary, these algorithms generate random samples from the posterior marginal distributions indirectly from the full conditional posterior distributions (f.c.p.d.), which are the posterior distribution for a given parameter conditional on the data and the remaining parameters. In general terms, defining $\theta = [\theta_1, \theta_2, \ldots, \theta_p]$ as the full set of p parameters, the f.c.p.d. for a particular parameter θ_k is denoted by

P $(\theta_k|\theta_1, \ldots, \theta_{k-1}, \theta_{k+1}, \ldots, \theta_p, y)$. Once these f.c.p.d. are characterized as known families of probability distributions, therefore presenting closed forms, the Gibbs sampler algorithm can be used.

The Gibbs sampler begins with $\boldsymbol{\theta}^{(0)}$, the starting values for the considered parameters, where $\boldsymbol{\theta}^{(t)}$ represents the values generated at the tth iteration of this algorithm, which are obtained by collecting the draws from each of the f.c.p.d., such that $\theta_k^{(t)} \sim \theta_k|\theta_1^{(t)}, \ldots, \theta_{k-1}^{(t)}, \theta_{k+1}^{(t-1)}, \ldots, \theta_p^{(t-1)}, y$ and $\theta^{(t)} = \left[\theta_1^{(t)}, \theta_2^{(t)}, \ldots, \theta_p^{(t)}\right]$. Thus, defining T as the total number of iterations, if $T \to \infty$, the Markov chain property ensures that after discarding some initial iterations (burn-in period), the values generated for a given parameter, θ_k, are characterized as samples from its marginal posterior distribution, $P(\theta_k|y)$.

Computational features

Obtaining the f.c.p.d. is a key point in Bayesian inference. Assuming normal distributions for the data and location parameters as well as scaled inverted Chi-squared distributions for the variance components, García-Cortés and Sorensen (1996) and Sorensen and Gianola (2002) employed a detailed mathematical handling of Eq. 2 to derive general classes of f.c.p.d. for some mixed models with one and two random effects. These distributions have been used in animal breeding software such as MTGSAM and gibbsf90. Thus, using these special model structures, obtaining the f.c.p.d. is required to apply MCMC algorithms, but obtaining the f.c.p.d. can prove to be an arduous task for many animal and plant breeders. To address this problem, flexible and easy software has been developed.

The JAGS software (Plummer 2012) has the same flexibility and facilities of WinBUGS but has the advantage of working under a full matrix approach, allowing direct handling of incidence and relationship matrices. Thus, the distributions for the data and unknown parameters can be specified in accordance with the theory, as shown in detail in the appendix. Note the alternative code defining the Student-t distribution for the data, a reparameterization of the genetic and error variances in terms of heritability and phenotypic variance, and a uniform prior distribution for the standard deviation of variance components. Another interesting feature of JAGS is its special link to the R software through the *R2jags* package (Su and Yajima 2012). This package has featured capability for data reading (phenotypic values, incidence and relationship matrices, and initial values) through the *read.table* function. This function avoids working with the *list* statement of WinBUGS, which is impracticable with larger data sets. Another advantage of *R2jags* is the possibility of using R packages directly for MCMC convergence diagnostics and for obtaining highest probability density (HPD) intervals of the posterior distributions, such as *boa* (Smith 2007) and *coda* (Plummer et al. 2012). A detailed code for *R2jags* using the fitted model is shown in the appendix.

In relation to the prior distributions for the variance components ($\sigma^2_{u_1}, \sigma^2_{u2}$ and σ^2_e) in the appendix, note that a reparameterization of the original scaled inverted Chi-squared (Scale χ^{-2}) distribution (Eqs. 1.5–1.7) is being used because the JAGS package does not work directly with this distribution. This distribution is a special case of the inverse gamma distribution (inv Gamma). Thus, assuming that $\sigma^2 \sim \text{Scale}\chi^{-2}(v, \text{S})$, where $S = \nu\sigma^{2^*}$ and σ^{2^*} is the prior most likely value to σ^2, one equivalent distribution is $\sigma^2 \sim \text{inv Gamma}(v/2, \text{S}/2)$ (Sorensen and Gianola 2002, p. 85), which allows using $\tau = 1/\sigma^2 \sim \text{Gamma}(v/2, \text{S}/2)$.

Informative prior distributions

To perform analyses involving different prior distributions, for the first cycle non-informative priors were initially used for the inverse of the variance components, defined by $\tau = 1/\sigma^2 \sim \text{Gamma}(0.001, 0.001)$. As the same population and phenotypes were analyzed by ANOVA/BLUE (best linear unbiased estimation) or REML/BLUP (Viana et al. 2010b, 2011b), an informative prior based on meta-analysis was used as well. In order to validate the inclusion of these two studies in the meta-analysis, a homogeneity test based on the Q statistics (Hedges and Olkin 1985) was employed using the *epi.smd* (fixed-effect meta-analysis of continuous outcomes) function of the R software. This test was applied independently to each one of the four sets of values (genetic and residual variances for EV and grain yield), and the p values ranged from 0.39 to 0.82, indicating homogeneity of these independent studies and, consequently, the adequacy to combine the results from them into a single measure.

For this, the inverse of the average value of a given variance component ($\bar{\tau} = 1/\bar{\sigma}^2$) and its respective variance ($S^2_{\bar{\tau}}$) were calculated from a set of values reported in these studies and equalized to the expectation and variance of a gamma (α, β) distribution: $\bar{\tau} = \frac{\alpha}{\beta}$ and $S^2_{\bar{\tau}} = \frac{\alpha}{\beta^2}$. Thus, it was possible to define $\alpha = \frac{\bar{\tau}}{S^2_{\bar{\tau}}}$ and $\beta = \frac{\bar{\tau}^2}{S^2_{\bar{\tau}}}$, resulting in $\tau = 1/\sigma^2 \sim \text{Gamma}(\alpha, \beta)$, which is an informative prior, such that its expectation and variance are coincident with the mean and variance, respectively, of the data set containing the reported values in the referenced papers. A similar procedure was used by Pérez et al. (2010) to choose

hyperparameters for prior distributions in a Bayesian regression model applied to genomic selection.

This same system of equality was used to exploit the results of the first cycle as prior information for the second cycle. For this, the mean and variance of the marginal posterior distributions for the inverse of the variance components obtained from the analysis with or without an informative prior were equalized to the expectation and variance of a gamma distribution, from which the values of α and β were calculated. Thus, the expectation and variance of these gamma distributions are coincident with the mean and variance, respectively, of the posterior distributions from the first cycle, characterizing an incorporation of prior knowledge coming from the previous cycle. It is worth noting that the prior information was only exploited for the genetic and error variances.

Bayesian analysis

Based on previous analyses of some MCMC chains, we decided to use one chain of 70,000 iterations per trait. We set the burn-in to 20,000 iterations and thinned every fifth iteration, resulting in a total sample of 10,000 iterations for both traits. In each chain, we analyzed the posterior mean, standard deviation, 95 % HPD interval, and convergence criterion statistics (Geweke 1992; Raftery and Lewis 1992) for the additive, blocks within replication and error variances, heritability, and breeding values. The heritability at the half-sib family level is $(1/4)\sigma_A^2/\left((\sigma^2/r)+(1/4)\sigma_A^2\right)$, where σ^2 is the error variance and r is the number of replications.

Results

For all parameters, the absolute values of Geweke's *Z* statistics were below 1.96 and the dependence factor of Raftery and Lewis were below 5.0, indicating that convergence was reached (Tables 1, 2). Regarding the first cycle, the analyses of the EV showed that the use of an informative prior from a meta-analysis did not provided clearly distinct results relative to the analysis with a non-informative prior (Table 1). The estimates and precision of the additive genetic variance and heritability were equivalent because the values of the standard deviation and the 95 % HPD intervals were similar. However, for the grain yield, both analyses provided distinct results. For the additive genetic variance and heritability, the analysis with informative prior provided estimates 1.7 times higher than those found when the non-informative prior was used. There was also an increase in precision because the coefficient of variation for the additive genetic variance and heritability decreased from 58.9 to 33.1 % and from 52.3 to 26.4 %, respectively. The differences between the two analyses are highlighted by the posterior densities of the genetic and non-genetic parameters (Fig. 1). For the EV, there was a tendency toward overlap between the densities, indicating little influence from informative prior on posterior distributions. However, for the grain yield, differences are evident between the posterior densities, mainly because the informative prior resulted in a more narrow and symmetric distribution, confirming the increase in precision.

For the second cycle, the results for both traits showed the effectiveness of the prior information in increasing the precision of the genetic parameters (Table 2). For the EV,

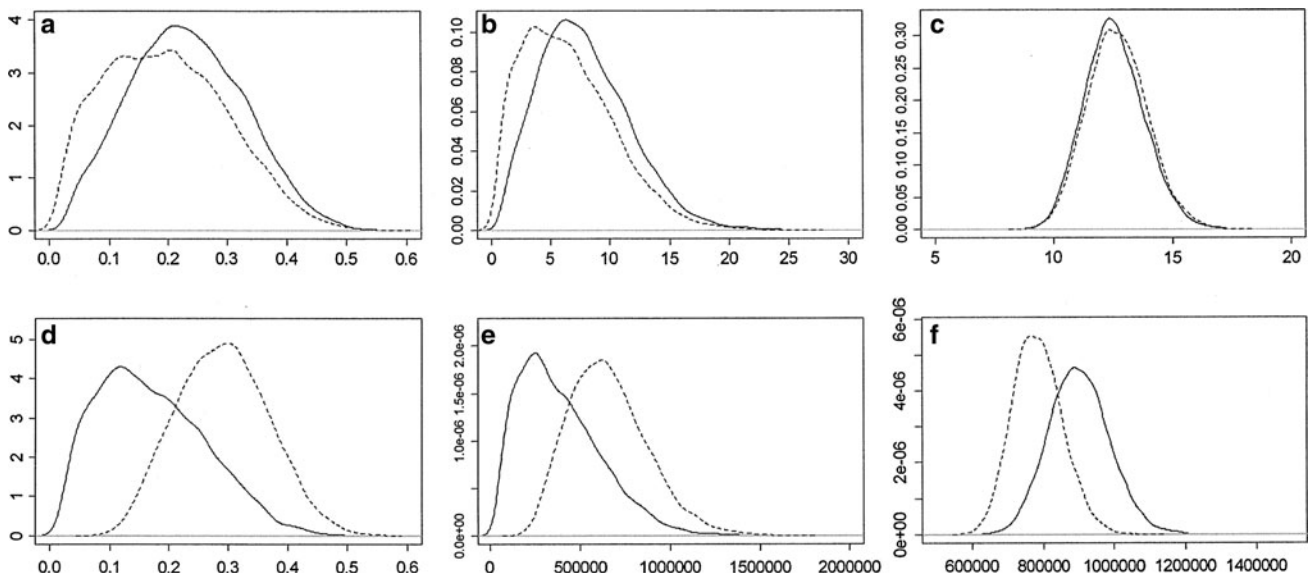

Fig. 1 Posterior distributions of genetic parameters and error variance of the first cycle. **a** Heritability for EV; **b** additive genetic variance for EV; **c** error variance for EV; **d** heritability for grain yield; **e** additive genetic variance for grain yield; **f** error variance for grain yield. *Continuous line indicates* non-informative prior, *dashed line* indicates informative prior (meta-analysis)

Table 1 Mean, 95 % highest probability density interval and standard deviation (SD) of the posterior densities of the genetic and non-genetic parameters for expansion volume (EV; ml g^{-1}) and grain yield (kg ha^{-1}) relative to the first cycle, statistics of convergence[†] and REML estimates, 95 % confidence intervals and BLUP predictions[‡]

Trait	Parameter	REML estimates	Non-informative prior				Informative prior (meta-analysis)			
			Mean	SD	Z-Gewek	DFRL	Mean	SD	Z-Gewek	DFRL
EV	Additive var.	8.5440 (0–17.1015)	7.8387 (0.9802–14.6581)	3.7674	0.74	0.98	6.4737 (0.5050–13.5140)	3.8308	−0.76	1.03
	Bl.lRep. var.	2.3565	2.6342 (0.9128–4.8569)	1.0740	−1.46	0.97	2.6066 (0.8997–4.6551)	1.0565	0.97	0.99
	Error var.	12.2483	12.5642 (10.1622–14.9576)	1.2419	0.59	0.98	12.6878 (10.2474–15.1336)	1.2546	0.02	0.98
	Heritability	0.2477	0.2318 (0.0511–0.4085)	0.0952	0.47	0.99	0.1966 (0.0183–0.3747)	0.1018	−0.74	1.01
	Add. value[§]	−4.0; 3.5	−3.6; 3.2	2.4582	–	–	−3.0; 2.6	2.2832	–	–
Grain yield	Additive var.	448,080 (0–1,072,938)	386,745 (38,121–822,410)	227,780	0.489	1.03	656,679 (254,778–1,069,416)	217,637	−0.45	1.02
	Bl.lRep. var.	12,121	75,908 (16,635–153,991)	41,858	2.21	1.00	80,989 (18,179–161,467)	43,668	0.94	0.99
	Error var.	927,171	900,829 (733,565–1,062,399)	84,614	−0.71	1.02	784,676 (650,397–919,638)	69,568	0.13	0.98
	Heritability	0.1881	0.1718 (0.0248–0.3392)	0.0898	0.56	0.99	0.2906 (0.1403–0.4329)	0.0768	−0.42	1.01
	Add. value[§]	−819; 1,204	−646; 1,086	564	–	–	−1,078; 1,818	1,368	–	–

[†] Z-Geweke: z-score of the Geweke test; DFRL: Dependence Factor of Raftery and Lewis

[‡] From Viana et al. (2011b)

[§] Minimum and maximum additive value and average SD

the coefficient of variation of the additive genetic variance decreased from 51.1 %, using non-informative prior, to 35.8 and 46.7 % using informative prior from posterior of the first cycle. For the grain yield, the coefficient of variation of the additive genetic variance decreased from 42.5 % to 32.3 and 18.6 %. The precision of the heritability also increased for both traits. With one exception, the increases in precision were higher with the posterior from cycle 1 with meta-analysis. The gain in precision from the use of informative prior was accompanied by a reduction in the additive genetic variance and heritability estimates, with one exception. For the grain yield, compared with the analysis using a non-informative prior, there was a relevant decrease (42.0 %) in the estimate of the additive genetic variance with an informative prior and posterior from cycle 1 and a significant increase (59.6 %) with an informative prior and posterior from cycle 1 with meta-analysis. It is clear that the narrowest densities for posterior distributions were obtained from informative prior distributions (Fig. 2). Furthermore, the displacements of the densities are more visible in the second cycle than the first cycle, highlighting the larger differences between additive genetic variance and heritability estimates observed in the second cycle.

For the EV, the breeding values obtained from the analyses with an informative prior showed higher precision (Tables 1, 2). Higher precision was also observed for the grain yield but only in the analysis of the second cycle with an informative prior as the posterior from cycle 1. The differences between the analyses with informative and non-informative priors were restricted to variance components and heritability. For the EV and grain yield, the correlations between the breeding values obtained by Bayesian (mean of the estimated posterior distribution) and BLUP analysis were almost perfect (0.99), yielding a coincidence between the 20 superior parents of at least 90 %.

Discussion

We must not try to establish that Bayesian inference is the breeder's best choice for genetic evaluation in crop species improvement. However, we should try to demonstrate that with an adequate statistical tool, it is possible, although not necessarily easy, to use Bayesian inference for genetic evaluation in crop species breeding, as has been done using REML/BLUP (Bauer et al. 2006; Flachenecker et al. 2006; Oakey et al. 2007; Viana et al. 2010a, 2011a), using the ASReml software (Gilmour et al. 2009) and the procedure Mixed of the SAS software (Littell et al. 2006) [free of charge software as WOMBAT (Meyer 2007) and BLUPF90 (Misztal et al. 2002) has not been used in plant breeding]. Many theoretical and applied studies have compared ANOVA/BLUE (best linear unbiased estimation),

Table 2 Mean, 95 % highest probability density interval and standard deviation (SD) of the posterior densities of the genetic and non-genetic parameters for expansion volume (EV; ml g^{-1}) and grain yield (GY; kg ha^{-1}) relative to the second cycle, statistics of convergence[†] and REML estimates, 95 % confidence intervals and BLUP predictions[‡]

Trait	Parameter	REML estimates	Non-informative prior				Informative prior (posterior from cycle 1)				Informative prior (posterior from cycle 1 with meta-analysis)			
			Mean	SD	Z-Gewek	DFRL	Mean	SD	Z-Gewek	DFRL	Mean	SD	Z-Gewek	DFRL
EV	Additive var.	2.3014 (0–7.9619)	4.5306 (0.4882–8.8265)	2.3166	−0.98	1.01	3.8331 (1.6314–6.5953)	1.3739	0.55	1.03	2.6920 (0.7119–5.1734)	1.2568	−0.20	0.99
	Bl.lRep. var.	1.3463	1.3862 (0.4324–2.4974)	0.5779	−0.90	0.98	1.8636 (1.0163–2.8905)	0.5100	−0.57	0.98	1.7340 (0.9094–2.6872)	0.4858	1.29	0.97
	Error var.	8.3030	7.7155 (6.2800–9.2592)	0.7720	1.76	0.98	9.6341 (8.4841–10.7829)	0.5994	−2.23	1.01	9.7512 (8.5847–10.9617)	0.6080	0.85	0.99
	Heritability	0.0834	0.2209 (0.0364–0.3963)	0.0967	−1.15	0.99	0.1639 (0.0774–0.2636)	0.0501	0.77	0.99	0.1194 (0.0403–0.2198)	0.0493	−0.19	0.99
	Add. value[§]	−1.4; 1.3	−2.9; 2.4	0.9400	–	–	−2.2; 1.8	0.8982	–	–	−1.6; 1.3	0.7696	–	–
Grain yield	Additive var.	145,642 (0–1,072,938)	166,435 (34,755–300,017)	70,756	0.56	0.95	96,487 (43,236–156,879)	31,187	0.19	0.95	265,653 (172,664–362,333)	49,301	0.56	1.01
	Bl.lRep. var.	80,022	103,093 (40,595–180,718)	39,204	−0.01	1.03	65,475 (29,149–116,513)	24,073	−1.43	1.00	67,160 (29,551–115,966)	23,945	0.89	0.95
	Error var.	205,564	196,555 (157,157–237,749)	20,904	0.35	0.99	487,976 (434,601–547,013)	29,007	1.27	0.98	458,476 (404,618–509,766)	26,964	3.12	0.96
	Heritability	0.1590	0.2903 (0.0805–0.4693)	0.1023	0.39	0.96	0.0894 (0.0418–0.1397)	0.0263	0.19	0.95	0.2237 (0.1603–0.2887)	0.0332	−0.30	0.99
	Add. value[§]	−532; 476	−590; 560	173	–	–	−180; 170	148	–	–	−436; 420	228	–	–

[†] Z-Geweke: z-score of the Geweke test; DFRL: Dependence Factor of Raftery and Lewis

[‡] From Viana et al. (2011b)

[§] Minimum and maximum additive value and average SD

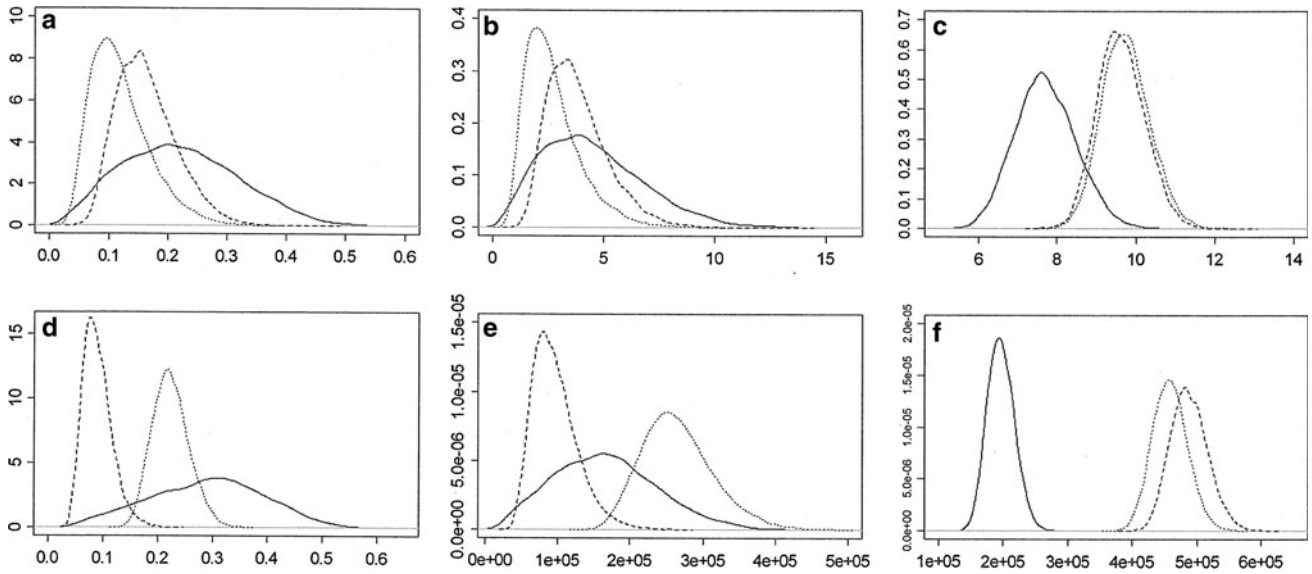

Fig. 2 Posterior distributions of genetic parameters and error variance of the second cycle. **a** Heritability for EV; **b** additive genetic variance for EV; **c** error variance for EV; **d** heritability for grain yield; **e** additive genetic variance for grain yield; **f** error variance for grain yield. *Continuous line indicates* non-informative prior, *dotted line* indicates informative prior (posterior from cycle 1), *dashed line indicates* informative prior (posterior from cycle 1 with meta-analysis)

REML/BLUP and Bayesian inference for the estimation or prediction of genetic parameters. In general, no single statistical approach can be considered superior in all situations. As stated by Blasco (2001), both Bayesian and frequentist schools of inference are well established, neither of them has, in general, operational difficulties, and there is software available to analyze a large variety of problems from both points of view. For this author, the choice should be based on possible statistical approaches to solve the problem, facility to solve the problem, and confidence of the scientist to establish inferences, if the possible analyses are equally efficient.

There are four important advantages of the Bayesian approach compared to the BLUP analysis. First, Bayesian inference allows using informative priors about parameters of the model (Beaumont and Rannala 2004). When the prior distribution is informative, the credibility intervals are narrower than the confidence intervals. When the parameters of the mixed model are assigned non-informative distributions, Bayesian inference and BLUP should be equivalent (Sorensen and Gianola 2002). Second, uncertainties in the parameters are fully acknowledged throughout the inference process using Bayesian MCMC methods (location and scale parameters are jointly inferred) (Sorensen 2009). In the BLUP procedure, variance components are first estimated and the obtained point estimates are then used as true values to obtain breeding values, thus ignoring uncertainty in the variance parameters. It should be emphasized, however, that the quality of Bayesian inferences depends on the efficacy of the MCMC method to generate good samples from the posterior distributions (Sorensen 2009).

Third, credibility intervals are directly obtained from the inferred posterior distributions without making any further assumptions, whereas in the BLUP approach asymptotic assumptions are made to derive the confidence intervals (Blasco 2001). Finally, MCMC methods integrate over the parameter space instead of trying to maximize the likelihood (Sorensen 2009; Blasco 2001). The maximization of a function can become problematic in some cases. For large randomized trials, the likelihood function will most likely be unimodal with a sharp peak meaning that maximization will most likely succeed. However, for small pedigree sizes, and/or if the model consists of multiple, correlated random terms, the likelihood function could become bimodal or very flat, making maximization problematic. No convergence, however, is not restricted to the BLUP approach. With MCMC methods, it is necessary to ensure that the chain has reached its stationary state and run it for sufficient iterations.

Mathew et al. (2012) showed that Bayesian inference is superior to BLUP when the posterior distribution of a variance component is bimodal. Their adaptive MCMC algorithm was able to detect different modes in the posterior distribution. The estimates of variance components using Gibbs sampling and REML were very similar in the studies of Van Tassell and Van Vleck (1996) and Van Tassell et al. (1995), especially for traits with high heritability. However, the mean squared error tended to be smaller for the estimators based on Gibbs sampling, especially for the low heritability scenario. Mathew et al. (2012), Waldmann et al. (2008), Schenkel et al. (2002), and Harville and Carriquiry (1992) did not find relevant differences between the breeding

values predicted by BLUP or Bayesian approach. Schenkel et al. (2002) also observed that the breeding values presented the same bias and accuracy. Our results relative to the non-informative analyses and the results of the REML/BLUP analyses presented by Viana et al. (2011b) are equivalent for some components of variance and heritability and for breeding values. For both the EV and grain yield, the correlations between breeding values predicted by Bayesian inference and BLUP ranged from 0.89 to 0.99. However, the standard error prediction was lower than the standard deviation of the Bayesian prediction. The 95 % HPD intervals for the additive genetic variances and breeding values were narrower than the correspondent 95 % confidence intervals, as observed by Waldmann and Ericsson (2006).

In recurrent intra- and interpopulation breeding programs and in the development of pure/inbred lines, the prior information for a given selection cycle can be based on meta-analysis or on the posterior distributions of the parameters from the previous cycle. Waldmann et al. (2008) showed that an informative prior was necessary to avoid overestimation of the dominance variance. Wang et al. (1993) showed that the parameter estimates were more precise when using higher levels of prior information. However, in a study by Rodriguez et al. (1996) the results of the analyses that assigned a greater weight to external information were identical to those obtained with flat priors. For Van Tassell et al. (1995), the use of improper priors, including flat priors, for variance components created difficulty in the application of Gibbs sampling approach because the use of these priors resulted in improper posterior densities of the variance components. These authors also noted that the effect of the prior distribution decreases as the heritability or the amount of information increases.

Using the scale parameters of the prior distributions from a meta-analysis or from the posterior distributions from the previous cycle has some limitations. Actually, given a trait, using estimates of additive and error variances from distinct populations and experiments can provide biased estimates of the mean and variance of the scale parameters because all genetic parameters are associated with a base population and its estimates were obtained under different experimental conditions. We used ANOVA and REML estimates from the same population, which were obtained in distinct trials with non-inbred and inbred progeny. However, this option reduces the available data for the meta-analysis. An interesting alternative would be a reparameterization for heritability and phenotypic variance (García-Cortés et al. 2001). Although heritability is also a population parameters under a given experimental condition, heritability values are more consistent. The breeders know that for some traits the heritability is regularly low, but for other traits the values are consistently high. Furthermore, selection can have a more relevant effect on additive genetic variance than it can on heritability. Fortunately, JAGS allows modeling heritability and phenotypic variance in place of the additive and error variances (see the appendix). However, phenotypic variance is also required, which also depends on genetic and non-genetic components, that is, population and experimental conditions.

A limitation of prior information from the posterior distribution of a previous cycle is that the estimate of the additive genetic variance tends to be more biased as the selection process is more effective. Assuming an infinitesimal model, the expected reduction in the additive genetic variance would be of 10 % with half-sib selection (Bulmer, 1980). Additional changes can be attributable to within-family selection and linkage disequilibrium. Assuming that the intensity of within-family selection is 10 % and that the average phenotypic variance within a family is twice the error variance, the additional reduction in the additive genetic variance would be 9 %. Assuming an additive model and that selection changes the phenotypic variance by a constant proportion of the genotypic variance, Bulmer (1980) demonstrated that the linkage disequilibrium can reduce the genotypic variance by up to 80 %. Hallander and Waldmann (2007) showed that the number of loci and non-additive genetic effects greatly influenced the change in additive genetic variance in populations that were subjected to selection. Assuming the same magnitude for dominance and epistatic variance, they observed that additive-by-additive epistasis induced a greater increase in additive genetic variance than dominance variance. Furthermore, they also observed an influence of the initial gene frequencies and the number of individuals under selection. In general, it is difficult to assess the change in the additive genetic variance in a population undergoing directional truncation selection because the additive genetic variance is influenced by many complex factors as genetic control of the trait (number of genes, magnitude, number and sign of dominance and epistatic effects), linkage, gene frequencies in the population, effective population size, and selection efficacy. Assuming only additive effects, the additive genetic variance will decrease under selection (Hallander and Waldmann 2007).

According to Waldmann (2009), one challenge that limits the use of Bayesian inference in quantitative genetics is the lack of user-friendly software that researchers can use without having extensive statistical knowledge. Waldmann (2009) presented a "flexible and easy" way to implement Bayesian analysis using the WinBUGS software. However, this software is limited by the fact that it does not allow direct matrix operations. Thus, the ability to directly program models involving matrix operations is the greatest advantage of the JAGS software. Furthermore, there is the advantage of working in the R interface through

the *R2Jags* package, which has a simple and easily implementable routine. The JAGS software also allows for all chains of the Gibbs sampler and its iterations to be saved. This feature allows for the use of such iterations in convergence analysis, which is easy to perform and interpret using the R package *boa*.

With respect to computational speed, general-purpose software such as JAGS and WinBUGS show inferior performance in relation to specific software for animal breeding, such as gibbsf90. However, this is the price paid for high flexibility. For our data set, the average processing time using an Intel(R) i7-2600 (3.4 GHz) processor with 4 GB of RAM was 1 h and 43 min, corresponding to approximately 0.08 s for each MCMC iteration. Although this performance can be considered plausible, improvements can be obtained using the conditional decompositions proposed by Hallander et al. (2010), but the algebraic notation originally implemented by the authors in WinBUGS must be translated to matrix notation in JAGS.

Lastly, based on the presented code, it is straightforward to fit the individual model in non inbred and inbred populations (Viana et al. 2010a, 2012b), the full-sib family model, the gametic model and the inbred family model (Viana et al. 2010a, 2012a), as well as the models for testcross (Viana et al. 2011a) and diallel analyses (Viana et al. 2011c). The adequate models for interpopulation half- and full-sib progeny include one [general combining ability (gca) effects] and three (gca effects of populations A and B and specific combining ability effects) random genetic vectors (Viana et al. 2013), respectively.

Acknowledgments We thank the anonymous reviewer for the relevant comments and the Foundation for Research Support of Minas Gerais State (Fapemig), the Brazilian Federal Agency for Support and Evaluation of Graduate Education (Capes) and the National Council for Scientific and Technological Development (CNPq) for financial support.

Appendix

(1) Code for JAGS

```
model
{
#likelihoodfunction
Y ~dmnorm(mu[1:N,1],I[1:N,1:N]*tau_e)
```

$y|\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_{u_2}, \sigma^2_e \sim N(\mu, I\sigma^2_e)$ Eq.(1.1)

```
#Y ~dt(mu[1:N,1],I[1:N,1:N]*tau_e,v)
```

$y|\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_{u_2}, \sigma^2_e, v \sim$ Student - $t(\mu, I\sigma^2_e, v)$ (assuming the Student - t distribution for the data)

```
#Y ~dmnorm(mu[1:N,1],I[1:N,1:N]*(1-h^2)*tau_p)
```

$y|\beta, u_1, u_2, \sigma^2_{u_1}, \sigma^2_p, h^2 \sim N(\mu, I(1-h^2)\sigma^2_p)$ (assuming a reparameterization in terms of h^2 and σ^2_p)

```
mu[1:N,1] <- X[1:N,1:nbeta]%*%beta[1:nbeta,1]+Z1[1:N,1:nu1]%*%u1[1:nu1,1]+Z2[1:N,1:nu2]%*%u2[1:nu2,1]
```

$\mu = X\beta + Z_1u_1 + Z_2u_2$

```
#priordistributionforfixedeffects
beta[1:nbeta,1] ~dmnorm (mean_beta[1:nbeta,1], Ibeta[1:nbeta,1:nbeta]*0.00001)
```

$\beta|\mu_\beta, I_\beta\sigma^2_\beta \sim N(\mu_\beta, I_\beta\sigma^2_\beta)$ Eq.(1.2)

```
#priordistributionsforrandomeffects
u1[1:nu1,1] ~dmnorm (mean_u1[1:nu1,1], A[1:nu1,1:nu1]*tau_u1)
```

$u_1|A\sigma^2_{u_1} \sim N(0, A\sigma^2_{u_1})$ Eq.(1.3)

```
#u1[1:nu1,1] ~dmnorm (mean_u1[1:nu1,1], A[1:nu1,1:nu1]*h2*tau_p)
```

$u_1|A\sigma^2_{u_1} \sim N(0, Ah^2\sigma^2_p)$ (assuming a reparametrization in terms of h^2 and σ^2_p)

```
u2[1:nu2,1] ~dmnorm (mean_u2[1:nu2,1], Ib[1:nu2,1:nu2]*tau_u2)
```

$u_2|I_b\sigma^2_{u_2} \sim N(0, I_b\sigma^2_{u_2})$ Eq.(1.4)

#priordistributionsfortheinverseofvariancecomponents

$\underbrace{\text{tau\_u1}} \sim \text{dgamma(vu1/2, Su1/2)}$

$\sigma^2_{u1}|\nu_{u1}, S_{u1} \sim \nu_{u1} S_{u1} \chi^{-2}_{\nu_{u1}}$ Eq.(1.5)

$\underbrace{\text{tau\_u2}} \sim \text{dgamma(vu2/2, Su2/2)}$

$\sigma^2_{u2}|\nu_{u2}, S_{u2} \sim \nu_{u2} S_{u2} \chi^{-2}_{\nu_{u2}}$ Eq.(1.6)

$\underbrace{\text{tau\_e}} \sim \text{dgamma(ve/2, Se/2)}$

$\sigma^2_e|\nu_e, S_e \sim \nu_e S_e \chi^{-2}_{\nu_e}$ Eq.(1.7)

$\#\ \text{sd\_p} \sim \text{dunif (a, b)}$

$\underbrace{\#\text{tau\_p} < -\text{sd\_p} * \text{sd\_p}}$

$\sigma_p|a,b \sim U[a,b]$ (assuming a uniform prior for the phenotypic standard deviation)

$\underbrace{\#}\ \text{h2} \sim \text{dbeta(c,d)}$

$h^2|c,d \sim \text{Beta}[c,d]$ (assuming a Beta prior for h^2)

$\underbrace{\#}\ \text{v} \sim \text{dunif(e,f)}$

$v|e,f \sim U[e,f]$ (assuming a uniform prior for degrees of freedom when using a Student - t for the data)

#definitionofvariancecomponents

$\text{sigma2\_e} < -1/\text{tau\_e}$

$\text{sigma2\_u1} < -1/\text{tau\_u1}$

$\text{sigma2\_u2} < -1/\text{tau\_u2}$

$\text{sigma2\_a} < -4 * \text{sigma2\_u1}$

$\text{h2} < -\text{sigma2\_u1}/(\text{sigma2\_u1} + \text{sigma2\_e}/2)$

#assumingareparametrizationintermsofh^2 and σ^2_p

$\#\text{sigma2\_p} < -1/\text{tau\_p}$

$\#\text{sigma2\_u1} < -\ \text{sigma2\_p} * \text{h2}$

}

where Y is the phenotypic values vector; X, Z1, and Z2 are, respectively, incidence matrices for **β**, $\mathbf{u}_1$, and $\mathbf{u}_2$; N, nbeta, nu1, and nu2 are, respectively, the numbers of observations, of fixed effects, of families and of blocks; mean_beta, mean_u1, and mean_u2 are, respectively, the mean vectors of prior distributions for **β**, $\mathbf{u}_1$, and $\mathbf{u}_2$; I, Ibeta, A, Ib are, respectively, matrices related with covariance of prior distributions for **e**, **β**, $\mathbf{u}_1$, and $\mathbf{u}_2$; and ν. and S. are the hyperparameters for the inverse of the variance components.

(2) Code for *R2jags*

```
Y = as.matrix(read.table("Yp1.txt")) #reading phenotypic observations (Y)
X = as.matrix(read.table("X.txt")) #reading incidence matrix of β
Z1 = as.matrix(read.table("Z.txt")) #reading incidence matrix of u1
Z2 = as.matrix(read.table("Jp.txt")) #reading incidence matrix of u2
```

#specifying dimensions

```
N = nrow(Y) # number of observations in Y
nbeta = ncol(X) # number of fixed effects (β)
nu1 = ncol(Z1) # number of families (u1)
nu2 = ncol(Z2) # number of blocks (u2)
```

#mean vectors of prior distributions for location parameters

```
mean_beta = matrix(100,nbeta,1) # μβ in Eq. 1.2
mean_u1 = matrix(0,nu1,1) # 0 in Eq. 1.3
mean_u2 = matrix(0,nu2,1) # 0 in Eq. 1.4
```

#matrices related with covariance of prior distributions for location parameters

```
I = diag(N) # I in Eq. 1.1
Ibeta = diag(nbeta) # Iβin Eq. 1.2
A = as.matrix(read.table("A.txt")) # A in Eq. 1.3
Ib = diag(nu2) # Ib in Eq. 1.4
```

#specifying hyperparameters for the inverse of variance components (non-informative prior)

```
v1 = 0.001; v2 = 0.001; ve = 0.001; S1 = v1*1; S2 = v2*1; Se = ve*1;
```

```
library(R2jags) #loading R2jags package
#listing JAGS input
jags.data = list("Y","X","Z1","Z2","N","nbeta","nu1","nu2","mean_beta", "mean_u1","mean_u2", "Ibeta", "A", "Ib", "I","v1","v2","ve","S1","S2","Se")
```

#listing JAGS output

```
jags.params = c("beta","u1","u2","sigma2_u1", "sigma2_a","sigma2_u2", "sigma2_e","h2")
```

#listing initial values for MCMC simulation

```
jags.inits = function() {
list("beta" = structure(.Data = c(4500,100,300),.Dim = c(nbeta, 1)), "u1" = structure(.Data = mean_u1,.Dim = c(nu1, 1)),
"u2" = structure(.Data = mean_u2,.Dim = c(nu2, 1)),
"tau_u1" = c(0.0001), "tau_u2" = c(0.001), "tau_e" = c(0.00001))}
```

#calling jags function of R2jags package

```
bayes = jags(data = jags.data, jags.params, inits = jags.inits, n.chains = 1, n.iter = 70000, n.burnin = 20000,
```

n.thin = 5, model.file = "bayes_model.txt") **# "bayes_model.txt" is txt file containing model specified in Code for JAGS**

#saving MCMC output

write.table(as.mcmc(bayes),
"prod_noninf.txt",row.names = FALSE,quote = FALSE)

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