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Bayesian prediction of crop performance modeling genotype by environment interaction with heterogeneous variances

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Bayesian prediction of crop performance modeling genotype by environment interaction with heterogeneous variances

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DEDICATION

I would like to dedicate this thesis to my parents Javier and Vicky, there are no words in English to express my gratitude, so I'll do it in Spanish when we are reunited again.

Thanks to my brother Ricardo and his family, Ximena, Antonia and Javiera. You have all inspired me and helped me to remain focused and finish my studies.

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CHAPTER 1. INTRODUCTION

In a breeding program the selection of the best performing cultivars is made considering the information provided by field trials conducted in several environments (multi-location, multi-year or both). A sample of promising genotypes are grown and screened considering multiple traits with the objective of identifying the presence of genotype-by-environments interactions (GEI). Crossa and Cornelius (2002) described the phenomenon as "inconsistent responses of some genotypes with respect to others due to the alteration of the ordering of the genotypes from one environment to another (GEI with rank change or crossover interaction) or as changes in the absolute differences between genotypes without rank change (GEI without range change or non-crossover interaction)".

Some authors see GEI as an obstacle to genetic improvement because it reduces the response to selection (Cooper and DeLacy, 1994; Kang and Magari, 1996; Epinat-Le Signor, 2001; Crossa et al., 2011), other authors consider it as an opportunity to select for specific environments choosing genotypes that show positive interaction with a specific location (exploitation of a specific adaptation) or genotypes that have low sensitivity to environmental stress (exploitation of yield stability) (Simmonds, 1991; Cecarelli, 1996).

The two-way fixed effects model proposed by Yates and Cochran (1938) was one of the early models used to analyze GEI, this model was later used by Finlay and Wilkinson (1963) and modified by Eberhart and Russell (1966) (Piepho, 1997; Crossa and Cornelius, 2002). In this model the error was considered normally distributed with mean zero and homogeneous variance (σ^2). Shukla (1972) dropped the assumption of homogeneous error variance and considered a separate variance by genotype (σ_i^2). The author proposed σ_i^2 as a stability measure.

Cooper and DeLacy (1994) grouped these and other approaches in three major areas and discussed the relationships between them, the groups were analysis of variance, indirect selection and pattern analysis. Among the last type of models, the Additive Main Effect and Multiplicative Interaction (AMMI) model gained popularity among breeders since it provides a measure of crop stability that allows the identification of genotypes that show a high performance across environments (broad usage) and also allows the identification of genotypes that are better adapted and perform well under specific conditions (specific usage).

The model uses principal component analysis (PCA) to summarize the patterns of the different genotypes across the environments. The use of PCA goes back to Williams (1952), Gollob (1968) and Mandel (1971) but their use for agricultural applications became popular under the name of AMMI proposed by Gauch (1992) who showed that the estimates produced by AMMI are more accurate than the estimates produced by ordinary least square. However the drawback of these models is that the assumptions behind them are unrealistic for the type of process that generates the data.

Crossa et al. (2006) stated that heterogeneous variance components are observed as the product of (i) variability on the within-location error variance caused by site-to-site difference between plots (ii) locations/years that show more genetic variation than others (iii) environmental factors such as soil type, temperature or precipitation, may affect the site in such way that some sites are more alike than others.

The initial work on heterogeneous variance can be found in the field of animal breeding. Hill (1984) showed that for a given intensity of mass selection, under normality, the differences in variance affect the proportion of individuals chosen from each testing environment, and therefore ignoring that difference will reduce response to selection. Foulley et al. (1992) and Gianola et al. (1992) are examples of early attempts to include variance heterogeneity with respect to some criterion of data classification in an analysis model. Foulley and Quaas (1995) proposed models of heterogeneity for both residual and other components of variance.

Among plant breeders, the use of mixed models has enabled the specification of heterogeneous variances; Smith et al. (2005) and Piepho et al. (2008) offer a detailed description and discussion of the use of mixed models in Plant Breeding. Piepho (1998) reviews different stability measures under the mixed model framework. Multiplicative Mixed Models also known as Factor Analytic Models, are the mixed model version of AMMI models (Piepho, 1997; Smith et al., 2001); in these models the variance structure for the GEI effects, known as Factor Analytic (FA) structure, can be defined to express the relationship between the genotypes and their environment, the model allows for heterogeneity of error variance.

Although the use of the Bayesian framework has been documented since the early nineties in animal breeding (Gianola et al., 1992; Sorensen and Waagepetersen, 2003), the adoption of this approach by plant breeders is a recent phenomenon. Viele and Srinivasan (2000) proposed the first Bayesian approach to estimate the multiplicative interaction using Gibbs sampling with embedded Metropolis-Hasting random walks. This model was later enhanced and used to fit data from multi-environment trials (Crossa et al., 2011; Perez-Elizalde et al., 2011). Theobald at al. (2002) proposed the use of Bayesian inference to study incomplete data sets in trials that considered genotype location year using a hierarchical model.

The flexibility of the Bayesian framework allows the use of models that define heterogeneous variance components (Edwards and Jannink, 2006). Cotes et al. (2006) presented a Bayesian approach to compute Shukla's (1972) stability variance. An alternate approach used pedigree information to estimate breeding values accounting for GEI (Bauer et al., 2009).

Bayesian inference is appealing because it promotes a common-sense interpretation of statistical conclusions. The analysis output is a posterior distribution, which instantly provides the ability of estimate intervals for an unknown parameter, or to calculate a probability of an event of interest. This direct quantification of uncertainty leads to the ability to fit complicated models with many parameters and multilayered probability specifications (Gelman et al. 2004).

Edwards and Jannink (2006), proposed a hierarchical model that considers heterogeneous genotype environment interaction and error variances. The form of the Bayesian estimator provided for the mean and variance in the experimental setup described for their analysis was provided by Leonard (1975) using a simple hierarchical model for heterogeneous treatment errors and its estimates. The analogous experiment in a plant breeding context would be a multi-environment yield trial with one replication in each environment, where m cultivars are observed in n environments (i.e., n replications per cultivar).

If we define y_{ij} as the yield observed for cultivar i in environment j, then the model specification is as follows

$$y_{ij} \sim N\left(\theta_i, \sigma_i^2\right)$$

$$\theta_i \sim N\left(0, \sigma_\theta^2\right),$$

where θ_i represents the mean of cultivar i across environments and σ_θ^2 is the variance of the cultivars under study.

Following the same approach of Shukla (1972), we can consider the variance σ_i^2 to represent the sum of both, the error and the GEI variance cultivar and define σ_i^2 such that $\ln\left(\sigma_i^2\right) = B\gamma = \alpha_i$, which means that we can assume a linear model for the logarithm of the error and GEI variance.

The notation presented above is useful, because allows us to define the prior for α_i as normal, with mean 0 and variance σ_α^2 (Leonard (1975) provides a detailed description of this derivation)

In this example, the variance component σ_i^2 is estimated as $e^{\tilde{\alpha}_i}$ and the posterior mean for α_i is given by

$$\tilde{\alpha}_i = \frac{\frac{1}{2} n_i \ln\left(S_i^2\right) + \frac{1}{\sigma_\alpha^2}\tilde{\alpha}}{\frac{1}{2} n_i + \frac{1}{\sigma_\alpha^2}} = \rho_{\alpha(i)} \ln\left(S_i^2\right) + \left(1 - \rho_{\alpha(i)}\right)\tilde{\alpha}, \tag{1.1}$$

where $S_i^2 = \dfrac{\sum\limits_{i=1}^{n_i}\left(y_{ij} - \tilde{\theta}_i\right)^2}{n_i}$ and $\tilde{\alpha} = \dfrac{\sum\limits_{i=1}^{n_i}\rho_{\alpha(i)}\ln\left(S_i^2\right)}{\sum\limits_{i=1}^{n_i}\rho_{\alpha(i)}}$ with $\rho_{\alpha(i)} = \frac{\frac{1}{2}n_i}{\frac{1}{2}n_i + \frac{1}{\sigma_\alpha^2}}$

The genotypic effects posterior mean is given by

$$\tilde{\theta}_i = \frac{\frac{n_i}{\sigma_i^2}\bar{y}_i + \frac{1}{\sigma_\theta^2}\tilde{\theta}}{\frac{n_i}{\sigma_i^2} + \frac{1}{\sigma_\theta^2}} = \rho_{\theta(i)}\bar{y}_i + \left(1 - \rho_{\theta(i)}\right)\tilde{\theta}, \tag{1.2}$$

where $\bar{y}_i$ represents the sample mean of cultivar i, and $\tilde{\theta} = \dfrac{\sum\limits_{i=1}^{n_i}\rho_{\theta(i)}\bar{y}_i}{\sum\limits_{i=1}^{n_i}\rho_{\theta(i)}}$ with $\rho_{\theta(i)} = \frac{\frac{n_i}{\sigma_i^2}}{\frac{n_i}{\sigma_i^2} + \frac{1}{\sigma_\theta^2}}$.

The estimators presented above are shrinkage estimators. This is a general term used to refer to a group of estimators that scale their estimated values according to the variability of the data. For example, if we re-write the formula for the weight to express its relationship with the repeatability $r = \frac{\sigma_\theta}{\sigma_\theta + \sigma_i}$, then $\rho_{\theta(i)} = \dfrac{n_i}{n_i + \frac{1-r_i}{r_i}}$.

The posterior mean of the genotypic effect ($\tilde{\theta}_i$) and the logarithm of the variance ($\tilde{\alpha}_i$) are weighted averages and represent a compromise between the prior and posterior distributions. The Bayes estimator will put more weight on the individual cultivar posterior means when the repeatability increases; if the repeatability is low, most of the weight will rely on the prior. For example, if the trials where performed in 3 locations with repeatability 30%, then 56% of the weight will be given to the individual cultivar sample mean and 44% will be given to the prior. However, if the repeatability was only 8% instead, then the weight of the individual cultivar sample mean would be only 20%.

The weight for the logarithm of the variance, $\rho_{\alpha(i)}$, considers the total number of observations of the individual cultivar and the variance of α, σ_α^2. For a cultivar with only 1 rep and 3

locations ($n_i = 3$), $\sigma^2_\alpha = 0.4$ then 38% of the weight is given to the individual cultivar posterior variance (S^2_i) and 62% of the weight would go to the prior ($\tilde{\alpha}_i$) (in this case the variance can be compared to a pooled variance). If the heterogeneity increases and $\sigma^2_\alpha = 1$ then 60% of the weight is given to the individual cultivar posterior variance and only 40% comes from the prior. If for the same heterogeneity ($\sigma^2_\alpha = 1$) the number of observations per cultivar increases to 5, then 71% of the weight is on the individual cultivar posterior variance. Therefore if the heterogeneity or the sample size increases, the Bayes estimator will favor the individual cultivar posterior component of variance estimate.

The estimators provided by the model proposed by Edwards and Jannink (2006) are more complex, but a completely analogous concept applies to unequally weighting means or observations from different environments if error variances or genotype-by-environment interaction variances differ among environments; a compromise variance estimator is obtained from each genotype at each environment and then is used to weight the means obtained from each genotypic effect.

The Bayesian estimator for the genotypic effect assigns differential weights by genotype taking into account their stability: the more unstable cultivars have greater GEI variances, and therefore they will have a reduced repeatability. For the case of multiple replications across locations, $r^2 = \frac{\sigma^2_\gamma}{\sigma^2_\gamma + \sigma^2_\delta + \sigma^2_{ij}}$; as the weights placed on the individual cultivar sample mean decrease, the combined estimator is "shrunk" towards the prior.

In the case of the log-variance estimates, the sample size or $G \times E$ effects per cultivar (given by the number of locations) largely determines whether there is sufficient information to differentiate among individual GEI variances. If there is a large enough sample size, or if the heterogeneity of the GEI variances is big enough, then the variance estimates are going to lead to a differential shrinkage (each cultivar will have their own estimate of GEI variance and this will affect the genotypic effect estimates).

The study conducted by Edwards and Jannink (2006) showed the presence of large amount of heterogeneity and also that when the heterogeneity of variances is considered in the model the obtained estimators for the variance components are more precise, suggesting that modeling heterogeneity may result in better estimated genotypic effects.

Two main questions motivated the work presented in this dissertation:

do corn yield trials exhibit enough heterogeneity to justify using a different model?

can we improve advancement decisions by modeling heterogeneity?

This dissertation is organized as follows. In chapter 2, we used a hierarchical model similar to the one proposed by Edwards and Jannink to study 11 years of data from the Iowa Crop Performance Test. We fitted the model using Bayesian tools and studied the heterogeneity of different subsets of data. In chapter 3 we simulated 33×3 datasets using different set of conditions using different level of number of observations, repeatability and level of heterogeneity, we focused on 2 main areas: (a) accuracy and precision of variance component estimates and (b) ability to predict performance. In each chapter we give an introduction of the problem and clearly state our objectives, describe the materials and methods used in the study, present the results with discussion of the implications for crop selection and finally we provide our conclusions. In chapter 4 a general conclusion is provided along with some recommendations for future work.

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CHAPTER 2. EVIDENCE OF HETEROGENEOUS VARIANCES ON MULTI-ENVIRONMENT YIELD TRIALS FOR CORN HYBRIDS

A paper to be submitted to Crop Science

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2.1 Abstract

Several statistical models have been proposed to assess genotype-by-environment interaction (GEI). Most of these models assume homogeneity of error and GEI variances. Our objective was to show that (i) Hierarchical models can be easily adapted to any experimental design; (ii) corn yield trials exhibit heterogeneity of error and genotype-by-environment interaction variances. A Bayesian approach was used to estimate variance components in a hierarchical model that allows for heterogeneous error and GEI variances applied to corn yield data from the Iowa Crop Performance Test carried out between 1995 and 2005. An average of 508 hybrids per year was tested with very little overlap between locations and years, which resulted in a very unbalanced data set. We divided the data into 16 subsets to study the effect of variability across locations and across years. All sub sets presented strong evidence of heterogeneity at both GEI and error variance levels.

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2.2 Introduction

Advancement decisions in plant breeding are driven by information obtained through multiple field trials conducted across years and locations. A great investment in research has been made to find appropriate statistical methods that summarize the main features of the data generated from these trials allowing the identification of genotypes that have both high yield and low sensitivity to adverse changes in their environmental condition. The presence of genotype-by-environment interaction (GEI) is a major concern; a cultivar's performance may vary widely when the GEI effect is large, making difficult to assess the differences between cultivars across location and therefore complicating the process of selection.

Multiple methods have been described to handle GEI, DeLacy et al. (1996) and Crossa et al. (2002) present a review of early approaches. Cooper and DeLacy (1994) grouped the approaches in three major areas and discussed the relationships between analysis of variance, indirect selection and pattern analysis. Among the last type of models, the Additive Main Effect and Multiplicative Interaction (AMMI) became widely used by plant breeders after Gauch (1992) suggested their use for yield trials. The use of biplots (Gabriel, 1971) is another feature of these models that has become very popular among plant breeders (Yan et al. 2007). However AMMI models have been criticized for their lack of flexibility and inferential statistics attached to the interaction parameters used to create the biplot (Yang et al. 2009).

Multiplicative Mixed Models are the mixed model version of AMMI models (Piepho, 1997; Smith et al., 2001); in these models the variance structure for the GEI effects can be defined to express the relationship between the genotypes and their environment and also allows for heterogeneity in the error variance.

There are several examples of applications of factor analytic mixed models in the literature, one of the first applications was provided by Smith et al (2001) where the authors presented an study on barley where the aim was to make varietal selections; different models were consid-

ered to accommodate spatial variation and heterogeneous error variances and for comparison they consider a model with homogeneous error structure; the estimates with spatial errors and heterogeneous error variance showed a better fit, the authors compared the ranks of the two models and found that the two models lead to different selected genotypes.

Oakey et al. (2007) extended the model proposed by Smith (2001) to consider pedigree information, the model is fitted to 253 lines of wheat in advanced stage that were grown in 14 locations in 2004; the pedigree model was superior, with more accurate estimators. However the authors observed a high correlation between the estimated genotypic values obtained under the pedigree and standard model, 80% of the top 20 ranking lines matched exactly under both models.

Beeck et al. (2010) fitted a factor analytic mixed model to a trial conducted in two years and 19 locations with Australian canola incorporating the pedigree information of 578 entries out of a total of 647 lines. The overlap of lines across year and locations was very high (almost all entries en common within a year and approx. 80% entries in common between years). The model used by the researchers incorporated ideas from the previous work mentioned above and modify them to improve the modeling of the spatial terms and to differentiate between entries in the pedigree that are present in the data set and entries in the pedigree but were not evaluated in a given location and therefore are not present in the data.

The results of Beeck et al. (2010) and Oakey et al. (2006) are consistent suggesting that pedigree information should be included on the analysis of early generation yield trials. They also noted that highly heritable traits showed a high proportion of additive variance while the degree of heteroscedasticity was relatively small. On the other hand, for traits with low heritability, the proportion of additive variance was smaller while the heterogeneity of the variances was higher.

Kelly et al. (2009) compared the performance of factor analytic models using different

degrees of genetic information in their pedigree matrices. A dataset with observations for two years of trials of barley lines planted in 14 locations was used to fit the competing models. Heterogeneity of the genetic and error variance components was observed across years and locations.

The identification of the source of GEI and its quantification are crucial to select for stability or make any recommendation in case of narrowed targeted cultivars (Epinat-Le Signor et al., 2001; Ceccarelli, 1996). Although in many of the studies mentioned above heterogeneity was measured and accounted for, examples of studies that focused on quantifying heterogeneity of GEI and/or error variances in corn for a large series of years are scarce (van Eeuwijk, 1995; Epinat-Le Signor et al., 2001).

So and Edwards (2009) studied the amount of GEI and error variance heterogeneity fitting a variety of mixed models to 11 years of corn data, the scope of their study was restricted to balanced subsets in a single year basis; the results of this study suggested that the error variance components were heterogeneous. In a second work using the same data but this time combining 2 years of data (with a total of 51 datasets), the authors compared linear mixed models with 12 different types of variance-covariance structure representing the variation of hybrid performance across environments; their list considered nine factor analytic models and also included univariate models where the simplest case was the classical univariate linear model with homogeneous GEI and error variances. The authors found that simpler and more parsimonious models produced better predictors. Fitting a model that allowed for heterogeneous error variances improved the predictions in 63% of the studied data sets, whereas specifying heterogeneous genotypic variance-covariance structure had small impact in improving their predicted values.

Edwards and Jannink (2006), proposed a univariate Bayesian approach using a hierarchical model that considered heterogeneous error and genotype-by-environment interaction variances. In that work the authors analyzed oat data from the Iowa State University Variety Trial for

years 1997 to 2003. They found evidence of heterogeneity at both levels: error and genotype-by-environment interaction variances. The analysis results showed that the heterogeneous model gives a more precise estimation of the variance components, suggesting that this model may be advantageous for predicting future cultivar performance.

The Bayesian methodology uses a probability concept that is easy to grasp, it gives solutions with common sense interpretation and it may be applied to complex, richly structured problems, fairly inaccessible to traditional statistical methods, for example, it can easily handle datasets that are highly unbalanced. Bayesian computation often requires sophisticated integration procedures. However with new computational methods developed in the early 1990s, its use has been widely extended.

Herein, we report the use of Bayesian inference to quantify the heterogeneity in a corn yield trial that was conducted over 11 years in the state of Iowa. Our objective was to show that (i) Hierarchical models can be easily adapted to commonly used field plot designs; (ii) corn yield trials exhibit heterogeneity of error and genotype-by-environment interaction variances.

2.3 Materials and Methods

2.3.1 Data

The data sets used in our analysis were taken from Iowa Crop Performance Test from 1995 to 2005. In this program the state of Iowa was divided into seven districts and each district had three locations. Table 2.1 shows the number of hybrids evaluated per year. The data set is highly unbalanced; the hybrids tested in a district were the same for all three locations in a given district, however the entries tested across districts varied (see Table 2.2). Most of the hybrids were tested only one year within a same district (69%), whereas only a 12% were tested for more than 2 years with a maximum of 10 years (Table 2.3). Finally, Table 2.4 shows the distribution of the hybrids among districts by year, for example, in 2004 none of the hybrids

were evaluated at all 7 districts simultaneously; only 4 hybrids were tested in 6 districts, and 18 hybrids were tested in 5 districts. On the other hand, 180 hybrids were tested in only one district. An average of 30% of the total entries were tested in 3 or more districts. The experimental design also varied over the years; from 1995 to 2003 the design of choice was the α-lattice whereas for the last two years the experiment was conducted in a row-column design; 4 replications were used across all trials. We created 16 subsets using different selection criteria with the objective of studying the effects of different factors on the variability of the data and its effects on the inference drawn from them (Table 2.4).

Table 2.1 Total number of hybrids evaluated by year.

Years	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
Hybrids Tested	714	610	500	466	533	529	495	484	440	452	361

Table 2.2 Number of hybrids evaluated by year at each district.

District id	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
1	196	169	144	156	156	144	144	121	110	121	100
2	196	169	132	132	144	132	110	110	110	110	119
3	256	240	196	196	210	210	169	156	144	156	139
4	196	169	144	156	182	182	144	132	132	132	108
5	256	225	182	169	196	196	169	156	144	156	118
6	210	182	144	121	169	169	144	156	132	132	95
7	182	169	144	144	156	156	132	132	132	132	90
Avg.	213	189	155	153	173	170	145	138	129	134	110

Table 2.3 Number of years that hybrids were tested at a given district

Number of years tested	Frequency	Percent	Cumulative Frequency	Cumulative Percent
1	5435	68.68	5435	68.68
2	1525	19.27	6960	87.96
3	573	7.24	7533	95.20
4	228	2.88	7761	98.08
5	95	1.20	7856	99.28
6	35	0.44	7891	99.72
7	15	0.19	7906	99.91
8	6	0.08	7912	99.99
10	1	0.01	7913	100.00

Table 2.4 Number of hybrids evaluated by number of districts and year

Number of Districts	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
1	293	256	214	170	197	198	213	246	190	180	140
2	211	161	121	129	159	148	149	114	120	145	106
3	111	90	80	82	78	95	70	54	73	65	71
4	62	59	51	40	55	47	38	35	35	40	26
5	28	29	24	34	28	30	15	25	18	18	13
6	7	11	4	7	8	5	6	8	3	4	0
7	2	4	6	4	8	6	4	2	1	0	5

Table 2.5 Data subsets from the Iowa Crop Performance Test for corn used for this paper. The identification columns indicate which districts and years are considered in each subset.

Identification			Number of		
Set	Districts	Years	Hybrids	Environments	GEI
1	1	96-97	253	6	933
2	3	99-00	346	6	1236
3	5	03-04	249	6	900
4	5	95-97	466	9	1983
5	4, 5	2000	252	6	1134
6	6, 7	2003	181	6	777
7	4, 5	99-00	408	11	2067
8	1-7	95-97	1259	60	1187
9	1-7	96-98	1079	60	9927
10	1-7	97-99	1072	59	9402
11	1-7	98-00	1120	58	9573
12	1-7	99-01	1140	60	9687
13	1-7	00-02	1122	61	9167
14	1-7	01-03	1055	62	8442
15	1-7	02-04	1037	60	7951
16	1-7	03-05	953	59	7263

2.3.2 Model Specification

We defined the following hierarchical model

$$y_{ijk}|\theta_{k(j)},\beta_{l(jk)},\gamma_i,\delta_{ij},\sigma^2_{ij} \sim N\left(\theta_{k(j)}+\beta_{l(jk)}+\gamma_i+\delta_{ij},\sigma^2_{ij}\right), \tag{2.1}$$

where,

$$\begin{aligned}
y_{ijk} &= \text{Yield of genotype } i, \text{ replication } k \text{ in environment } j.\\
\beta_{l(jk)} &= \text{Effect of lattice block } l \text{ within replication } k \text{ at envronment } j.\\
\theta_{k(j)} &= \text{Effect of replication } k \text{ within envronment } j.\\
\gamma_i &= \text{Effect of genotype } i.\\
\delta_{ij} &= \text{interaction of genotype } i \text{ and the environment } j.\\
\sigma^2_{ij} &= \text{Error variance for genotype } i \text{ and the environment } j.
\end{aligned}$$

.

The second level of the hierarchy consists of the prior for the replication effects and of the population distributions for the exchangeable parameters. These are specified as follows:

$$\begin{aligned}
\theta_{k(j)}|\sigma^2_\theta &\sim N(0,10^7)\\
\beta_{l(jk)}|\sigma^2_\beta &\sim N(0,\sigma^2_\beta)\\
\gamma_i|\sigma^2_\gamma &\sim N(0,\sigma^2_\gamma)\\
\delta_{ij}|\sigma^2_{\delta_{ij}} &\sim N(0,\sigma^2_{\delta_{ij}}).
\end{aligned} \tag{2.2}$$

The third level of the hierarchy proposes the hyper-prior distributions for the variance components and was given by

$$\begin{aligned}
\sigma^2_\beta &\sim IG(0.001,0.001)\\
\sigma^2_\gamma &\sim IG(0.001,0.001).
\end{aligned} \tag{2.3}$$

We expressed the GEI variances as $\sigma^2_{\delta_{ij}} = \exp(b_0 + b_{1i} + b_{2j})$, where b_0 is a term for the average of the genotype-by-environment variances, b_{1i} represents the effect of genotype i on the genotype-by-environment variance and b_{2j} represents the effect of environment j on the

genotype-by-environment variance. For the heterogeneous model we specified the distribution for b_0, b_{1i} and b_{2j} as

$$\begin{aligned} b_0|\sigma_{b_0} &\sim N(0, 10^7) \\ b_{1i}|\sigma^2_{b_1} &\sim N(0, \sigma^2_{b_1}) \\ b_{2j}|\sigma^2_{b_2} &\sim N(0, \sigma^2_{b_2}), \end{aligned} \tag{2.4}$$

and

$$\begin{aligned} \sigma^2_{b_1} &\sim IG(0.001, 0.001) \\ \sigma^2_{b_2} &\sim IG(0.001, 0.001). \end{aligned} \tag{2.5}$$

Similarly, the error variance was expressed as $\sigma^2_{ij} = \exp(a_0 + a_{1i} + a_{2j})$, where a_0 is the intercept, a_{1i} represents the genotypic effect on the residual variances and a_{2j} represents the environment effect on the residual variances.

We also defined

$$\begin{aligned} a_0|\sigma_{a_0} &\sim N(0, 10^7) \\ a_{1i}|\sigma^2_{a_1} &\sim N(0, \sigma^2_{a_1}) \\ a_{2j}|\sigma^2_{a_2} &\sim N(0, \sigma^2_{a_2}) \end{aligned} \tag{2.6}$$

$$\begin{aligned} \sigma^2_{a_1} &\sim IG(0.001, 0.001) \\ \sigma^2_{a_2} &\sim IG(0.001, 0.001) \end{aligned}$$

If we choose $b_{1i} = b_{2j} = a_{1i} = a_{2j} = 0$, the model defined by equation 2.1 has homogeneous GEI and error variances and the GEI and error variance can be written as $\sigma^2_\delta = \exp(b_0)$ and $\sigma^2 = \exp(a_0)$, respectively.

Finally, to complete the model specification we defined

$$\begin{aligned} \sigma^2_\delta &\sim IG(0.001, 0.001) \\ \sigma^2 &\sim IG(0.001, 0.001). \end{aligned} \tag{2.7}$$

2.4 Results and Discussion

In Figure 2.1 we show the posterior distribution of σ^2_{b1}, σ^2_{b2}, σ^2_{a1} and σ^2_{a2} for all the subsets considered in this study. All the distributions presented in Figure 1 show nearly zero probability in the proximity of zero, suggesting that the variance components are variable, i.e. the components of variance for a specific set exhibit different values by cultivar and environment; and the amount of variability differs across sets. The first seven sets present bigger variability than the rest of the sets. Sets 1 to 7 included less than 500 entries and only between 6 and 11 environments whereas sets 8 to 16 included more than 950 entries and 58 environments or more which resulted in more precise estimates for the last group of sets as consequence of the larger number of observations. On the other hand districts were balanced within a year but not across districts or years, therefore sets with data coming from different districts and across several years were more unbalanced.

To provide a better understanding on how the parameters mentioned above affect the resulting GEI and error variances, we picked 3 sets from Table 2.5: Set 3 has observations for 249 hybrids tested in only one district across two years; Set 5 includes 252 hybrids evaluated in two districts for only one year and finally, Set 12 included 1140 hybrids evaluated in all the seven districts over three years. To provide a clear visualization of the results, we randomly selected 15 genotypes and 6 environments per set and drew boxplots of the posterior distribution of the GEI and error variances by individual genotype and environment shown in Figures 2.2 to 2.4 where the red dashed line represents the homogeneous variance posterior mean.

To examine the genotype effect on the GEI variance we calculated $ln(\sigma^2_{\delta_{i.}}) = b_0 + b_{1i}$ (Figures 2.2 a, 2.3 a, 2.4 a). We also calculated $ln = (\sigma^2_{\delta_{.j}}) = b_0 + b_{2j}$ which reflects the environmental effect on the GEI variance (Figures 2.2 b, 2.3 b, 2.4 b). All three sets showed evidence of heterogeneity at the GEI level. Posterior means for the GEI standard deviation across genotypes for set 3, ranged from 3.32 to 12.18 with an average of 5.87; for set 5 the range for the same parameter had a minimum equal to 1.91 and a maximum equal to 8.55, the average was 3.92.

In the case of set 12 the range of the posterior mean for the GEI standard deviation had a minimum equal to 3.76 and a maximum equal to 7.94, the average across genotypes was 5.25 (Table 2.6).

We also calculated the genotypic and environmental effect on the error variances (Figures 2.2 c, 2.3 c, 2.4 c and 2.2 d, 2.3 d, 2.4 d, respectively). The error standard deviation for sets 3, 5 and 12 also showed evidence of heterogeneity. We present the summary for the posterior means of the error standard deviation in Table 2.7. Given the different conditions for each dataset, it is difficult to compare the selected data sets, but in general we can say that the GEI and error variance posterior distributions for set 12 were less variable than the posteriors for the other sets as expected from Figure 2.1.

Set 3 has higher GEI and error variance than set 5; this indicates that the variability across locations in a same year is less than the variability across years for the same location, this was also observed by So and Edwards (2011), who reported that in general, correlations among locations within a year were higher than correlations between two years in the same location.

Finally, all three sets showed that the genotypic effect was one of the sources of variance heterogeneity, suggesting the possibility of selecting for genotypes that show lower environmental sensitivity.

The model used in this study provides weighted estimates of performance. The component of variance estimators are weighted proportionally to different amounts of sample size and heterogeneity (in our example, heterogeneity is controlled by σ^2_{b1}, σ^2_{b2}, σ^2_{a1} and σ^2_{a2}); if the sample size or heterogeneity increases, more weight is given to the individual estimates of variance whereas if the sample size or amount of heterogeneity decreases, more weight would be given to the pooled variance estimator (Edwards and Jannink, 2006).

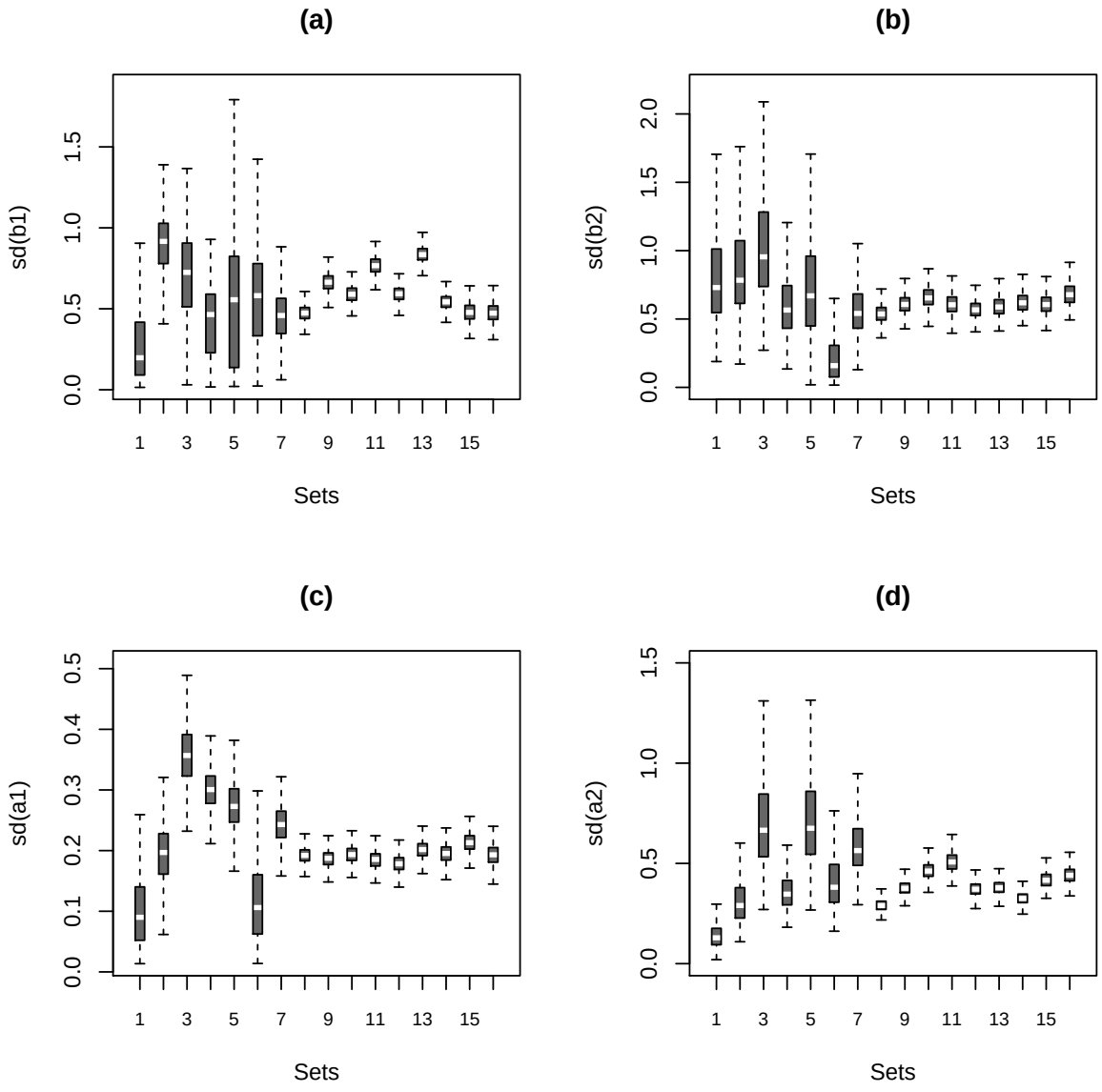

Figure 2.1 Posterior distribution of heterogeneity parameters (a) σ^2_{b1} , (b) σ^2_{b2}, (c) σ^2_{a1} and (d) σ^2_{a2} for the 16 sets considered in the analysis.

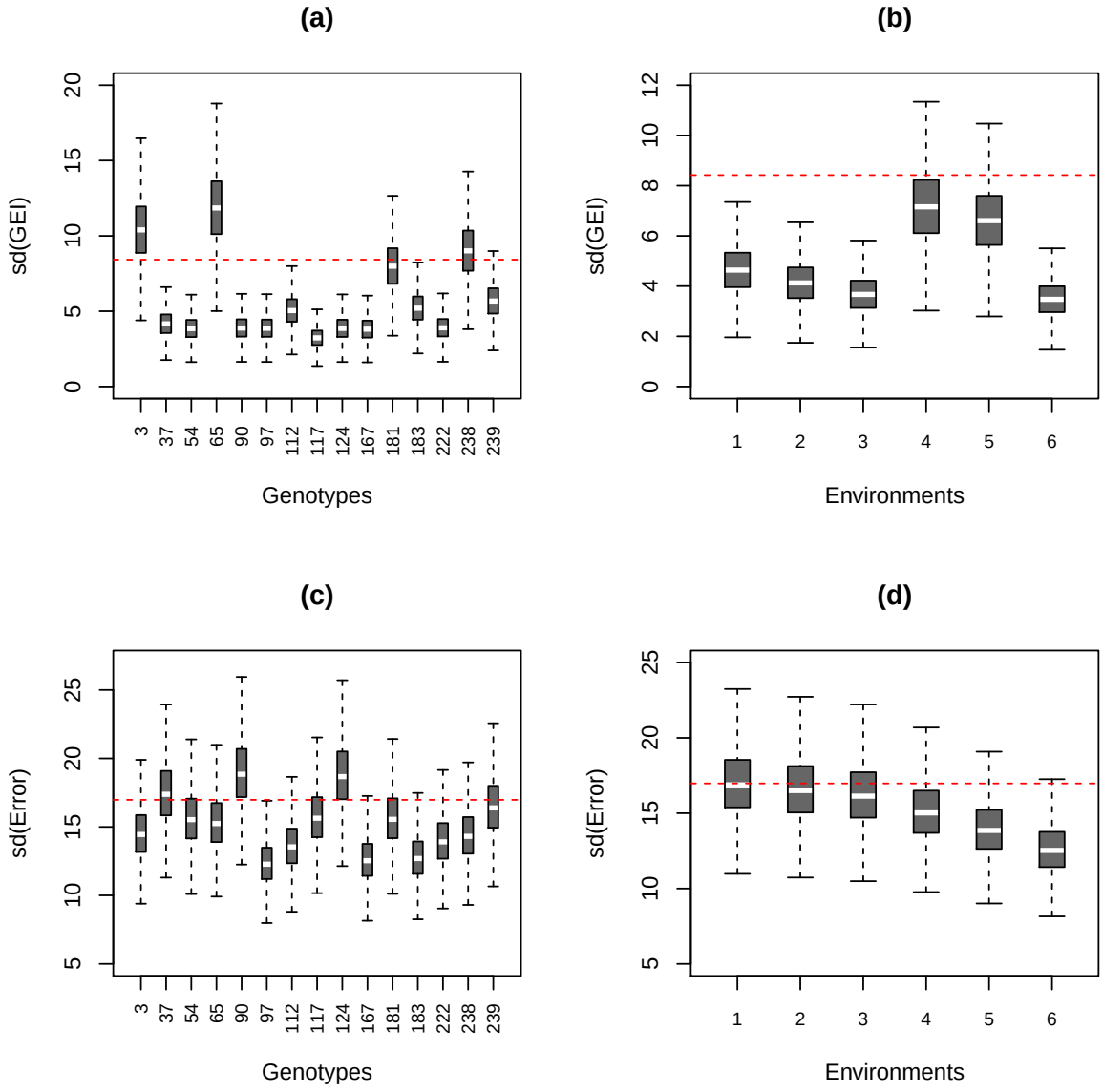

Figure 2.2 Variance estimates for set 3: (a) standard deviation of the GEI ($\sigma_{\delta_{i\cdot}}$) across selected genotypes, (b) standard deviation of the GEI ($\sigma_{\delta_{\cdot j}}$) across selected environments, (c) standard deviation of the error ($\sigma_{i\cdot}$) across selected genotypes, (d) standard deviation of the error ($\sigma_{\cdot j}$) across selected environments. The dashed line represents the estimate obtained by the homogeneous model.

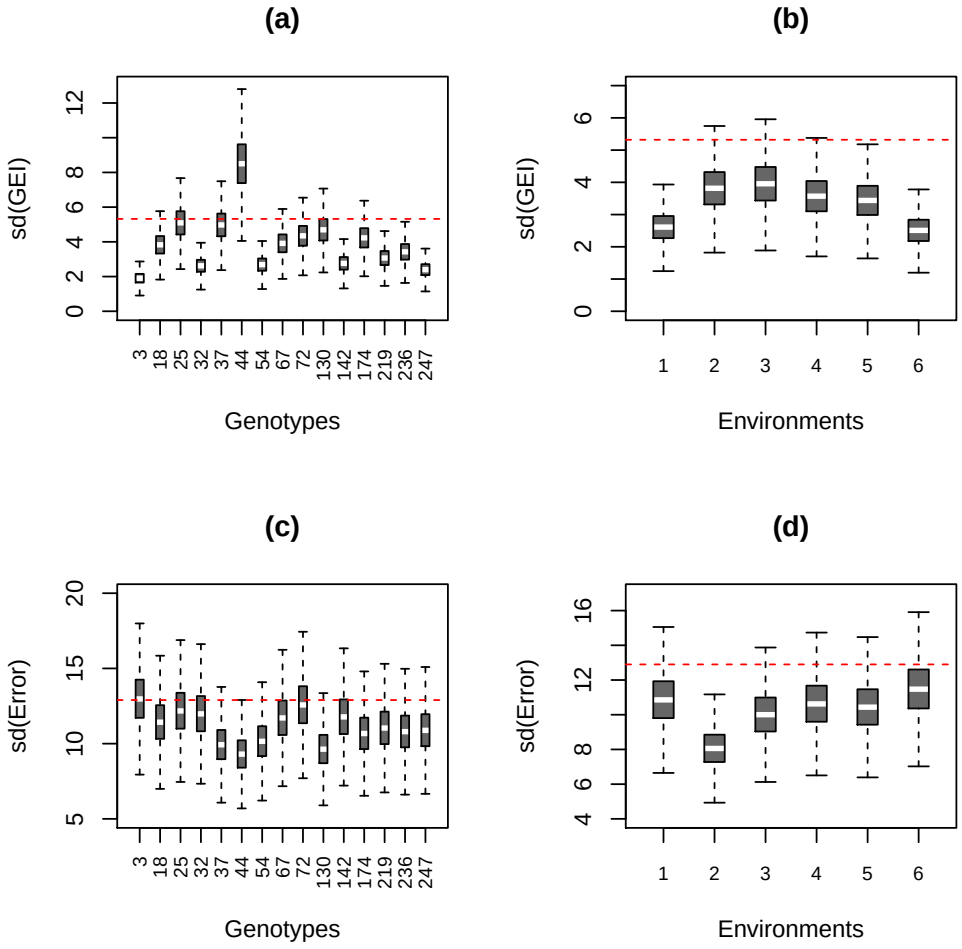

Figure 2.3 Variance estimates for set 5: (a) standard deviation of the GEI ($\sigma_{\delta_{i.}}$) across selected genotypes, (b) standard deviation of the GEI ($\sigma_{\delta_{.j}}$) across selected environments, (c) standard deviation of the error ($\sigma_{i.}$) across selected genotypes, (d) standard deviation of the error ($\sigma_{.j}$) across selected environments. The dashed line represents the estimate obtained by the homogeneous model.

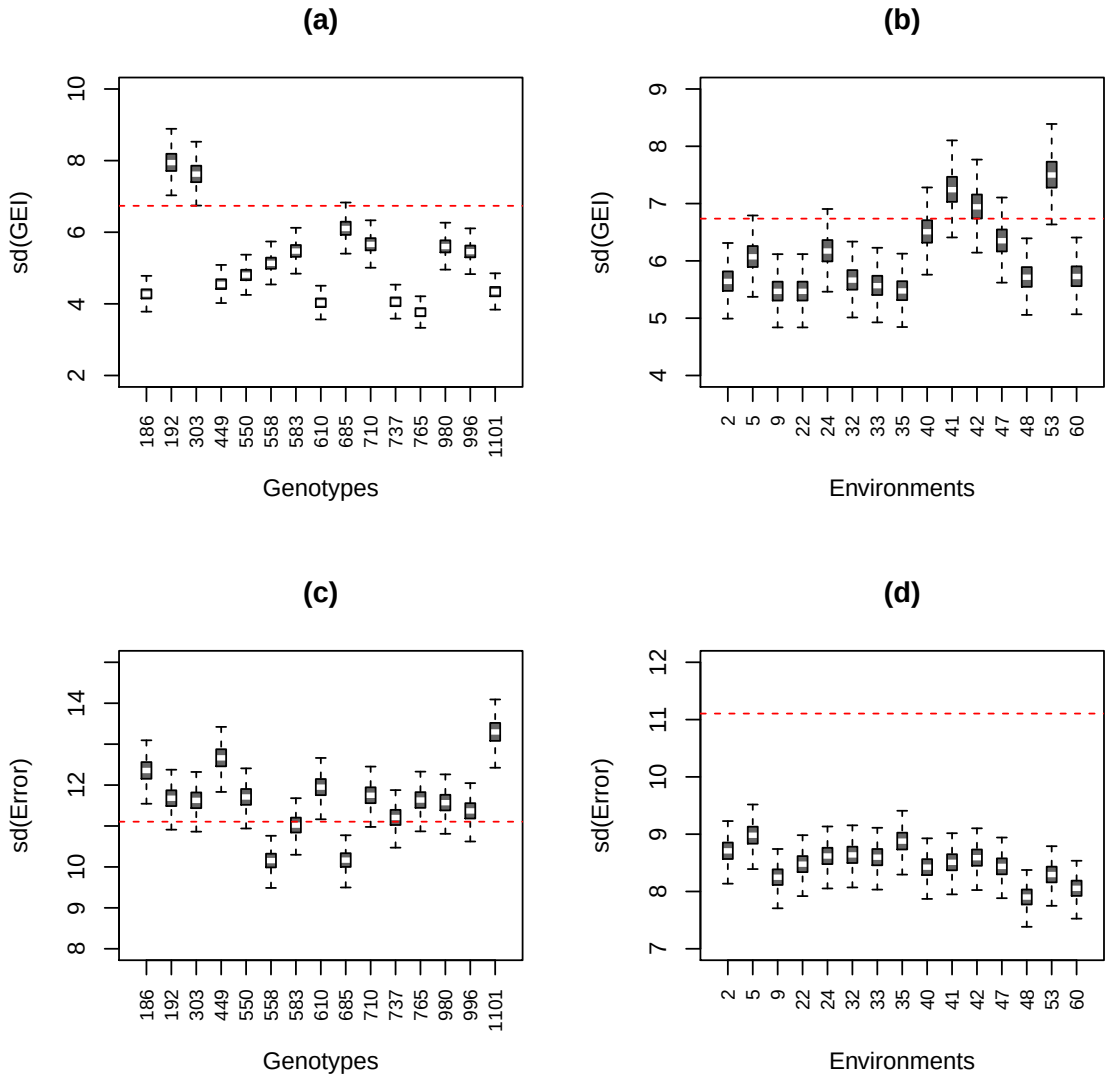

Figure 2.4 Variance estimates for set 12: (a) standard deviation of the GEI ($\sigma_{\delta_{i.}}$) across selected genotypes, (b) standard deviation of the GEI ($\sigma_{\delta_{.j}}$) across selected environments, (c) standard deviation of the error ($\sigma_{i.}$) across selected genotypes, (d) standard deviation of the error ($\sigma_{.j}$) across selected environments. The dashed line represents the estimate obtained by the homogeneous model.

Table 2.6 GEI Standard deviation: Posterior mean summary across genotypes and environments for selected sets

Summary on the	Across Genotypes			Across Environments		
Posterior Means	set 3	set 5	set 12	set 3	set 5	set 12
Minimum	3.32	1.91	3.76	3.57	2.52	5.47
Average	5.87	3.92	5.25	5.08	3.34	6.1
Maximum	12.18	8.55	7.94	7.36	3.98	7.5

Table 2.7 Error Standard deviation: Posterior mean summary across genotypes and environments for selected sets

Summary on the	Across Genotypes			Across Environments		
Posterior Means	set 3	set 5	set 12	set 3	set 5	set 12
Minimum	12.45	9.4	10.15	12.71	8.14	7.9
Average	15.34	11.25	11.61	15.37	10.35	8.49
Maximum	19.11	13.11	13.3	17.12	11.59	8.98

Unstable genotypes will have a bigger shrinkage towards the mean, so for example if an unstable hybrid performed extremely well in some environments, the estimated genotypic value will be "penalized" and brought down towards the mean which may result in changes on the rankings of the genotypes, where the rankings not only take into account the average performance of the genotype across environments but also the variability of the performance across environments.

2.5 Conclusions

We fitted two hierarchical model to study the level of heterogeneity in a corn yield trial conduct in the state of Iowa. We found very strong evidence of heterogeneity on both GEI and error variances. The next step is to assess the properties of the model proposed by Edwards and Jannink (2006). We plan to conduct an extensive simulation study to investigate the impact of modeling heterogeneous variances on the breeder's ability to select the best cultivars.

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CHAPTER 3. EFFECT OF EXPERIMENTAL CONDITIONS ON ADVANCEMENT DECISIONS WHEN MODELING WITH GENOTYPE BY ENVIRONMENT HETEROGENEOUS VARIANCES: A BAYESIAN APPROACH

A paper to be submitted to Crop Science

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3.1 Abstract

Multiple tools are available to assist plant breeders in their efforts to identify cultivars that show high and stable yield performance across environments. Yield trials data are essential to the process as they provide information regarding the performance of the genetic material being tested across multiple locations and seasons. The usefulness of the data depends on the accuracy and precision of the statistical methods used to predict the performance of the selected material to move onto the next stage of the breeding program. The analysis is complicated by the presence of genotype-by-environment interaction (GEI). Edwards and Jannink (2006), showed that using a model that allowed for heterogeneous genotype-by-environment and error variances the obtained estimates were more precise. The Bayesian estimator "penalizes" the more unreliable observations and puts more weight on environments with higher quality data.

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We simulated data under 33 different conditions of repeatability (5%, 13% and 21%), sample size (Nenv=5, 10, 30) and level of heterogeneity ($\sigma_{b(1)} = 0.4, 0.8, 1.2$) including 6 data sets simulated from a model that had no heterogeneity (homogeneous model); we considered these sets our control. The objective of this work was to determine if there are any set of conditions where (i) selections made under the heterogeneous model lead to bigger increments in yield in comparison with the homogeneous model (ii) the heterogeneous model provides "better" parameters, in terms of accuracy and precision (iii) the heterogeneous model leads to select more stable cultivars.

The heterogeneous model was able to pick up the lack of variability of the data from the control sets, and performed very similarly to the homogeneous model suggesting a broader use of the model even when the heterogeneity is not detectable. In the case of data simulated from the heterogeneous model, the estimates of the component of variance where more accurate when using the heterogeneous model, we observed a very large improvement on the estimates of GEI variances, which in our study was the only term truly heterogeneous. The Bayesian estimator penalizes the more unstable genotypes bringing their average towards the overall mean, leading to selection of more stable cultivars. The genetic gain differential after selection using the heterogeneous model was small, however consistently showed and advantage in favor of the heterogeneous model suggesting that selections made under the heterogeneous model will lead to bigger increments in yield in comparison with the homogeneous model.

3.2 Introduction

Yield trials data are essential to the process as they provide information regarding the performance of the genetic material being tested across multiple locations and seasons. The usefulness of the data depends on the accuracy and precision of the statistical methods used to predict the performance of the selected material to move onto the next stage of the breeding program. The analysis is complicated by the presence of genotype-by-environment interaction (GEI), which in practical terms means that genotypes present differential performance across environments, the variation can be expressed as a change on the mean difference between specific genotypes, or a change in the genotypes ranks which may result in a reduced response to selection (Piepho, 1996; Cooper and DeLacy, 1994; Crossa, 2002).

Among the long list of methods proposed to analyze GEI, Additive Main Effect and Multiplicative Interaction (AMMI) model (Gauch, 1992) gained popularity among breeders since it provides a measure of crop stability that allows the identification of genotypes that show a high performance across environments and could be targeted for a broader usage; and also allows the identification of genotypes that are better adapted and perform well under specific conditions suggesting a more specific usage. These models also provide a visualization tool through the use of biplots (Gabriel, 1971). The drawback of these models is that their applications consider fixed effects where the genetic effect is assumed to be independent from the environmental effect and the error variances are assumed homogeneous which is rather unrealistic (Crossa et al., 2006, Edwards and Jannink, 2006).

In a classical context, mixed models provide a way to tackle the shortcomings of AMMI models allowing enough flexibility to model heterogeneous variances taking into account possible correlations among the effects present in the model (Piepho, 1997; Smith et al., 2001). Extensions of these models consider the use of pedigree information, which have been found useful to obtain more precise estimators (Oakey et al., 2007; Kelly et al.. 2009; Beeck et al., 2010)

In recent years there has been a growing interest in the adoption of the Bayesian framework in crop studies (Theobald at al., 2002; Edwards and Jannink, 2006; Cotes et al.. 2006; Bauer et al., 2009; Crossa et al., 2011; Perez-Elizalde et al., 2011). The Bayesian approach has the ability to handle datasets that are highly unbalanced, using all the available data to improve the estimates, as result of this the Bayesian estimated values will be shrunk towards the mean. With the use of new computational methods and improvement of computational speed, a broader adoption of Bayesian tools has been possible.

The Gibbs sampler (Gelfand and Smith, 1990; Geman and Geman 1984) is a MCMC technique that allows the specification of complex models without the need of closed forms; by using their conditional distributions the Gibbs sampler draws values of the parameters of interest and then uses sample averages to approximate their expectations; a chain with these values is constructed after several iterations to produce its marginal posterior distribution (Gilks et al. 1996).

Edwards and Jannink (2006) discussed the properties of the Bayesian estimator obtained from a model that considered heterogeneous GEI and error variances. The Bayesian estimator is a weighted average, where the weights are given by functions of the sample size and the repeatability. For locations with large sample size and/or repeatability, the estimator will put more weight on the mean for that location showing that this location is more "reliable". If the sample size or repeatability decrease the estimator will put more weight on the prior, in absence of a informative prior the weight will be placed on the overall mean, the authors refer to this as a "penalty" to cultivar instability.

There is evidence that modeling GEI and error heterogeneity lead to improved genetic gain (Smith and Cullis, 2001b; Beeck et al., 2010), however the conditions where accounting for a differential stability will have a direct impact on rankings are still unclear. A study under known conditions would allow us to determine under what parameter values and sample sizes the heterogeneous model outperforms the homogeneous model.

In this work we used the approach proposed by Edwards and Jannink (2006) to evaluate a model that considered heterogeneity only on the GEI variance components and compared it to the homogeneous model. We made the comparison under different conditions of repeatability, number of environments and degree of heterogeneity with the objective of determining if there are any set of conditions where (i) selections made under the heterogeneous model lead to bigger increments in yield in comparison with the homogeneous model (ii) the heterogeneous model provides "better" parameters, in terms of accuracy and precision (iii) the heterogeneous model leads to select more stable cultivars.

3.3 Materials and Methods

3.3.1 Model

We defined the following hierarchical model

$$y_{ijk}|\theta_{k(j)}, \gamma_i, \delta_{ij}, \sigma^2 \sim N\left(\theta_{k(j)} + \gamma_i + \delta_{ij}, \sigma^2\right), \tag{3.1}$$

where

$$\begin{aligned} y_{ijk} &= \text{Yield of genotype } i\text{, replication } k \text{ at the environment } j. \\ \theta_{k(j)} &= \text{Effect of replication } k \text{ within environment } j. \\ \gamma_i &= \text{Effect of genotype } i. \\ \delta_{ij} &= \text{interaction of genotype } i \text{ and the environment } j. \\ \sigma^2 &= \text{Error variance.} \end{aligned}$$

The second level of the hierarchy consists of the prior for the replication effects and of the population distributions for the exchangeable parameters. These are specified as follows:

$$\begin{aligned} \theta_{k(j)}|\sigma^2_\theta &\sim N(0, 10^7) \\ \gamma_i|\sigma^2_\gamma &\sim N(0, \sigma^2_\gamma) \\ \delta_{ij}|\sigma^2_{\delta_{ij}} &\sim N(0, \sigma^2_{\delta_i}). \end{aligned} \tag{3.2}$$

The third level of the hierarchy proposes the hyper-prior distributions for the variance components and was given by

$$\sigma^2_\gamma \sim IG(0.001, 0.001). \tag{3.3}$$

We expressed the GEI variances as $\sigma^2_{\delta_{ij}} = \exp(b_0 + b_{1i})$, where $b_0 \sim N(0, 10^7)$; b_0 represents the average of the genotype-by-environment variances, while b_{1i} represents the effect of genotype i on the genotype-by-environment variance.

The error variance was expressed as $\sigma^2 = \exp(a_0)$, where a_0 represents the average of the error variance and $a_0 \sim N(0, 10^7)$.

To fit a model with heterogeneous GEI variances we specified the distribution for b_{1i} as

$$\begin{aligned} b_{1i}|\sigma^2_{b_1} &\sim N(0, \sigma^2_{b_1}) \\ \sigma^2_{b_1} &\sim IG(0.001, 0.001). \end{aligned} \tag{3.4}$$

To specify a model with homogeneous GEI variances we dropped b_{1i} and fitted $\sigma^2_{\delta_{ij}} = \exp(b_0)$.

3.3.2 Simulated Data

Thirty-three datasets were simulated from the model specified in the previous section. The datasets obtained from simulations that considered homogeneous GEI and error variances were deemed as control data sets. Six sets were simulated under the homogeneous model, each one coming from the combination of two levels of plot-basis repeatability (5 and 13%) and three levels of number of environments (5, 10 and 30).

We calculated the genotypic repeatability on a plot-basis as

$$r_{ij}^2 = \frac{\sigma_\gamma^2}{\sigma_\gamma^2 + \sigma_{\delta_{ij}}^2 + \sigma_{ij}^2}. \tag{3.5}$$

To get the desired repeatability we varied the values used to simulate the genotypic variance and the hyper parameters b_0 and a_0 used to simulate the GEI and error variances, respectively (see tables 3.1 and 3.2).

Table 3.1 Parameter values used to simulate sets from the homogeneous model (Control).

ID	r^2	Nenv	a_0	b_0	σ_γ
C1	0.05	5	6.0	4.5	5.3
C2	0.05	10	6.0	4.5	5.3
C3	0.05	30	6.0	4.5	5.3
C4	0.13	5	5.2	4.0	6.0
C5	0.13	10	5.2	4.0	6.0
C6	0.13	30	5.2	4.0	6.0

To generate data from a model that allows for heterogeneous GEI variance we used three factors, each with three different levels to simulate the data, therefore we had 3^3 set of conditions for the heterogeneous model. Table 3.2 shows the parameter values used to simulate the 27 datasets from the heterogeneous model.

Each set of conditions was used to generate data 3 times, producing a total of 27 $\times$ 3 datasets under the conditions specified in tables 3.1 and 3.2. After generating all the data set used in this study, we fit and summarized our data using MCMC techniques, namely the Gibbs sampler (Gelfand and Smith, 1990; Geman and Geman 1984).

Table 3.2 Parameter values used to simulate sets from the heterogeneous model.

Data	r^2	Nenv	a_0	b_0	σ_{b1}	σ_γ
1	0.05	5	6	4.5	0.4	5.3
2	0.05	5	6	4.5	0.8	5.3
3	0.05	5	6	4.5	1.2	5.3
4	0.05	10	6	4.5	0.4	5.3
5	0.05	10	6	4.5	0.8	5.3
6	0.05	10	6	4.5	1.2	5.3
7	0.05	30	6	4.5	0.4	5.3
8	0.05	30	6	4.5	0.8	5.3
9	0.05	30	6	4.5	1.2	5.3
10	0.13	5	5.2	4.0	0.4	6.0
11	0.13	5	5.2	4.0	0.8	6.0
12	0.13	5	5.2	4.0	1.2	6.0
13	0.13	10	5.2	4.0	0.4	6.0
14	0.13	10	5.2	4.0	0.8	6.0
15	0.13	10	5.2	4.0	1.2	6.0
16	0.13	30	5.2	4.0	0.4	6.0
17	0.13	30	5.2	4.0	0.8	6.0
18	0.13	30	5.2	4.0	1.2	6.0
19	0.21	5	4.5	3.8	0.4	6.0
20	0.21	5	4.5	3.8	0.8	6.0
21	0.21	5	4.5	3.8	1.2	6.0
22	0.21	10	4.5	3.8	0.4	6.0
23	0.21	10	4.5	3.8	0.8	6.0
24	0.21	10	4.5	3.8	1.2	6.0
25	0.21	30	4.5	3.8	0.4	6.0
26	0.21	30	4.5	3.8	0.8	6.0
27	0.21	30	4.5	3.8	1.2	6.0

We implemented our simulations using OpenBUGS. To run the analysis, a model and initial values need to be provided besides the data. Two MCMC chains were generated allowing for a "burn-in" period of 500,000 after which 1000 MCMC draws were taken from each chain and to ensure independence between the values drawn from the MCMC chain we used a thinning value of 60. Once the algorithm converged, inferential summaries were obtained by using the empirical distribution of the simulation as an estimate of the posterior distribution.

3.3.3 Demonstration with Real Data

In order to illustrate the application of the methodologies discussed in the next sections, data were taken from the Iowa Crop Performance Test for years 2000 and 2001. The trial divided the state of Iowa into seven districts and each district had three locations. The dataset is highly unbalanced; although the hybrids tested in a district were the same for all three locations in a given district, the entries tested across districts not necessarily matched. For the purposes of this paper we balanced the data in such way that we considered only hybrids that were tested in both years regardless the number of locations where they were tested.

3.3.4 Posterior Inferences

For each simulated replicate and for the corn data, point and interval estimates of posterior distribution where obtained. In the summaries we focused on two types of measures: (a) accuracy and precision of variance component estimates (b) ability to predict performance. As a measure of accuracy we used the deviations between estimators and the true value. To determine precision of the GEI variance we used the Mean Squared Error (MSE) defined as $E_\theta\left(\hat{\theta}-\theta\right)^2$. In practice we compared the estimated variance component to the true value, and took the squared difference defining the following discrepancy measure

$$D_{\delta\cdot} = \frac{1}{n}\sum_{j=1}^{n}\left(\hat{\sigma}^2_{\delta_i} - \sigma^2_{\delta_i}\right)^2 \tag{3.6}$$

The methods described next were used to measure the ability of the proposed models to predict performance of genotypes.

3.3.5 Ranking Methods

We were interested in measuring the ability of the models to estimate the genotypic effect, therefore rather than focusing on the mean given by $\mu_i = \theta + \gamma_i + \delta_i$ we focused on the posterior distribution of the genotypic effect (γ_i). Plant breeders are interested in selecting top performing candidates, since in this study we were evaluating performance on yield we focused on genotypes that exhibited high yield values. To rank the genotypes we used the approach that calculates the probability of a given genotype of being among the K top performers noted in this paper as $Pr(TOP - k)$ (Besag and Higdon, 1999; Miaou and Song, 2005; Cotes et al. 2006). The probability of a genotype of being at rank k was computed as the number of times the genotype had rank k in the MCMC chains.

3.3.6 Posterior Probability Ranking Plots

We generated posterior probability ranking plots in which the probability of a cultivar being among the best k performers is plotted on the y-axis versus the rank position k on the x-axis. This is a graphical representation of the $Pr(TOP - k)$ ranking technique(Schmidt et al., unpublished). Instead of looking at the probability of a given genotype ranked at a specific position this plot allows the simultaneous comparison of a range of posterior probabilities, e. g. $\{Pr(TOP - 1), Pr(TOP - 1), \ldots, Pr(TOP - 50)\}$.

3.3.7 True Selection Differential

We defined the "true" selection differential as the deviation of the average genetic effect computed for the selected genotypes from the average genetic effect computed for all the simulated genotypes. We selected the top 5% ($i = 2.063$) individuals for each dataset, to select we used rankings obtained from the homogeneous and heterogeneous model and then instead of comparing the averages of the simulated values we took the average of the true genotypic value used to simulate the data.

$$S = \bar{\gamma}_{Selected} - \bar{\gamma}_{All} \tag{3.7}$$

The statistic shown in equation 3.6 differs from the selection differential not only because it considers the true genetic value, but also because it does not include the effect of genotype-by-environment interaction. Gauch (2006) pointed out that the genotypic effect gives us information about broad adaptations while GEI is related to narrow adaptations. In our objectives we stated that we were focusing not only on

high performing genotypes, but also that we were interested in the ability of selecting stable genotypes, thus rather than looking at the combination of G and GEI, we decided to look only to the estimates of G, in this paper represented by γ and compared the true selection differential of the two competing models to determine which model achieved a higher true selection pressure.

3.4 Results and Discussion

3.4.1 Control Set

The posterior distribution of each variance component was obtained from the heterogeneous and homogeneous model. The parameter of heterogeneity, σ_{b1}, and the genotypic variance, σ_γ, are unique per set, but for the heterogeneous model each set had multiple GEI and error variances estimators. Instead of considering all estimators, we used their marginal variance given by $\sigma^2_{\delta_\cdot} = \exp(b_0)$ and $\sigma^2_\cdot = \exp(a_0)$, obtaining only one posterior distribution by variance component across genotypes and environments, herein we refer to the distribution of $\sigma^2_{\delta_\cdot}$ and $\sigma^2_\cdot$ as the "marginal" posterior for the GEI and error variance respectively.

In Table 3.3 we report the credible set for the posterior distribution of the component of variance σ_{b1}, σ_γ and the marginal variances, $\sigma^2_{\delta_\cdot}$ and $\sigma^2_\cdot$ for the 6 sets with data simulated from the homogeneous model, our control cases. The heterogeneous model captures some heterogeneity from the data and this is reflected on the values obtained for σ_{b1}, the parameter that determines the variability of the GEI variance; the posterior densities of this parameter in all cases are rather small, with posterior means that go from 0.12 to 0.28, the highest estimated value was obtained from the sets that had repeatability 5% and considered only 5 environments.

The true values and posterior means for the genotypic, GEI and error variances are presented in Table 3.4. We compared the deviations between the models estimates $\hat{\sigma}^2_\gamma$, $\hat{\sigma}^2_\cdot$ and $\hat{\sigma}^2_{\delta_\cdot}$ respectively, and their true values (figures 3.1 to 3.3). In these figures the effect of the level of heterogeneity is shown in the plot on the bottom right; sd.b1=0 corresponds to our control cases. Both models perform very similarly, with estimates that are close to the true value used to simulate the data.

Table 3.3 Control sets. Credible sets for the posterior distribution of the heterogeneity parameter (σ_{b1}), genetic variance (σ_γ), GEI variance ($\sigma^2_{\delta.}$) and error variance ($\sigma^2_{\cdot}$), for the heterogeneous and homogeneous model.

set details	parameters	model	mean	2.5%	50%	97.5%
$C1$	σ_{b1}	hetero	0.28	0.04	0.22	0.80
	σ_γ	hetero	22.10	8.88	22.12	44.44
		homo	23.09	9.05	23.53	45.34
$r^2 = 0.05$	$\sigma^2_{\delta.}$	hetero	100.02	60.76	100.42	138.94
		homo	104.77	70.75	105.24	142.19
Nenv=5	$\sigma^2_{\cdot}$	hetero	402.12	367.23	401.58	439.14
		homo	401.72	367.63	401.90	438.97
$C2$	σ_{b1}	hetero	0.18	0.03	0.13	0.52
	σ_γ	hetero	24.44	14.99	24.39	36.74
		homo	24.44	14.67	24.40	36.66
$r^2 = 0.05$	$\sigma^2_{\delta.}$	hetero	95.54	71.97	95.48	119.60
		homo	97.11	74.57	97.48	120.45
Nenv=10	$\sigma^2_{\cdot}$	hetero	394.84	371.13	394.72	420.10
		hetero	394.89	370.72	394.58	420.42
$C3$	σ_{b1}	hetero	0.17	0.03	0.16	0.41
	σ_γ	hetero	26.49	20.11	26.31	34.63
		homo	26.51	20.17	26.37	34.71
$r^2 = 0.05$	$\sigma^2_{\delta.}$	hetero	93.57	79.57	93.78	107.47
		homo	95.32	82.21	95.53	108.31
Nenv=30	$\sigma^2_{\cdot}$	hetero	404.93	391.07	404.83	419.30
		homo	405.18	391.27	405.25	419.60
$C4$	σ_{b1}	hetero	0.16	0.02	0.12	0.53
	σ_γ	hetero	43.31	30.16	43.16	59.78
		homo	43.26	30.11	43.05	59.44
$r^2 = 0.13$	$\sigma^2_{\delta.}$	hetero	52.63	35.47	52.44	70.16
		homo	54.03	38.00	54.20	71.38
Nenv=5	$\sigma^2_{\cdot}$	hetero	180.38	165.00	180.10	197.60
		homo	179.85	164.72	179.77	196.97
$C5$	σ_{b1}	hetero	0.23	0.03	0.20	0.59
	σ_γ	hetero	33.68	25.14	33.54	44.62
		homo	33.89	25.26	33.67	44.50
$r^2 = 0.13$	$\sigma^2_{\delta.}$	hetero	53.48	40.74	53.44	66.04
		homo	55.50	44.47	55.63	66.95
Nenv=10	$\sigma^2_{\cdot}$	hetero	182.61	171.70	182.50	194.43
		homo	182.52	171.45	182.45	194.07
$C6$	σ_{b1}	hetero	0.12	0.03	0.10	0.29
	σ_γ	hetero	36.32	29.17	36.17	45.24
		homo	36.26	29.10	36.04	45.18
$r^2 = 0.13$	$\sigma^2_{\delta.}$	hetero	54.29	48.01	54.29	60.47
		homo	54.72	48.49	54.78	60.84
Nenv=30	$\sigma^2_{\cdot}$	hetero	178.86	172.60	178.80	185.27
		homo	178.93	172.75	178.94	185.42

In general, for all the variance components, the precision decreases as the number of environments (Nenv) and repeatability (r^2) decrease, this can be seen also in Table 3.3; the credible sets become wider as the two quantities mentioned before get smaller, for example, under conditions of high levels of heterogeneity the width of the credible set for the genetic variance when Nenv=30 and $r^2 = 13\%$ is 16.1 for both models; the width of the credible set for the genetic variance when Nenv=5 and $r^2 = 5\%$ is 35.6 for the heterogeneous model and 36.3 for the homogeneous model.

To determine the effect of fitting the heterogeneous model in conditions of very small or non-variability on advancement decisions, we calculated the true selection differential (Table 3.8). For comparison purposes, after obtaining the true selection differential the ratio between heterogeneous and homogeneous model was also computed. The true selection differential was very similar across all sets generated from the homogeneous model, with ratios that ranged from 1 to 1.15.

3.4.2 Simulated Sets Assuming Variance Heterogeneity

The posterior means for σ_{b1}, σ_{γ}, $\sigma^2_{\delta\cdot}$ and $\sigma^2_{\cdot}$ obtained using the heterogeneous and homogeneous model and their respective true value for all sets generated under the heterogeneous model are shown in Table 3.4. As described earlier, we report the posterior mean of the marginal GEI and error variances. We present the deviations between estimates and the true values of GEI, genetic and error variances in figures 3.1, 3.2 and 3.3, respectively. The estimates between models are very similar for genotypic and error variance. In the case of GEI variances, the heterogeneous model provides estimates that are more accurate than the estimates provided by the homogeneous model; when the variability increases, the homogeneous model increasingly overestimates the GEI variance (Figure 3.1, plots at the bottom). Similarly to what Edwards and Jannink (2006) observed, with increasing heterogeneity, the heterogeneous model had a slightly higher estimated repeatability than the model with homogeneous variances (Table 3.4), this difference is explained by the homogeneous model overestimating the GEI (and possibly the error variance when they are heterogeneous).

We also calculated the mean-squared error of the GEI variance and summarized our results using the discrepancy measure D(G×E) defined in equation 3.6. The effect of number of environments, repeatability and level of heterogeneity on the precision of the GEI variance is shown in Figure 3.4. Increasing repeatability improves the precision and accuracy of the estimates. For a given repeatability,

Table 3.4 True parameter values and estimates per test set: Parameter of heterogeneity (σ_{b1}), genetic variance (σ^2_γ), GEI marginal variance ($\sigma^2_{\delta.}$) and error marginal variance ($\sigma^2_.$), for the heterogeneous and homogeneous model.

		σ_{b1}		$\sigma^2_{\delta.}$			$\sigma^2_.$			σ_γ			$r^2_.$		
set	n.env	true	hetero	true	hetero	homo	true	hetero	homo	true	hetero	homo	true	hetero	homo
C1	5	0	0	90.0	97.8	104.8	403.4	401.6	401.7	28	22.1	23.1	0.05	0.04	0.05
1	5	0.4	0.3	90.0	84.8	90.0	403.4	401.4	400.7	28	26.5	27.3	0.05	0.05	0.05
2	5	0.8	0.5	90.0	114.8	134.2	403.4	392.4	393.1	28	23.3	19.3	0.05	0.05	0.04
3	5	1.2	1.1	90.0	105.5	182.1	403.4	396.3	396.4	28	28.7	42.5	0.05	0.05	0.07
C2	10	0	0	90.0	94.7	97.1	403.4	394.7	394.9	28	24.4	24.4	0.05	0.05	0.05
4	10	0.4	0.2	90.0	94.0	96.1	403.4	410.0	409.8	28	29.1	29.2	0.05	0.06	0.06
5	10	0.8	0.7	90.0	98.4	128.4	403.4	410.5	411.3	28	29.7	29.4	0.05	0.05	0.05
6	10	1.2	1.2	90.0	79.4	150.1	403.4	409.3	409.0	28	31.5	29.7	0.05	0.06	0.05
C3	30	0	0	90.0	93.3	95.3	403.4	404.8	405.2	28	26.5	26.5	0.05	0.05	0.05
7	30	0.4	0.4	90.0	90.0	96.5	403.4	404.0	404.2	28	29.6	29.7	0.05	0.06	0.06
8	30	0.8	0.8	90.0	88.8	122.4	403.4	402.1	402.6	28	28.0	28.1	0.05	0.05	0.05
9	30	1.2	1.3	90.0	89.1	197.0	403.4	394.5	395.0	28	27.5	29.3	0.05	0.05	0.05
C4	5	0	0	54.6	52.6	54.0	181.3	180.4	179.8	36	43.3	43.3	0.13	0.16	0.16
10	5	0.4	0.3	54.6	55.0	59.5	181.3	182.1	181.7	36	38.7	38.6	0.13	0.14	0.14
11	5	0.8	0.8	54.6	52.4	73.4	181.3	181.1	180.3	36	28.0	28.4	0.13	0.11	0.10
C5	10	0	0	54.6	53.5	55.5	181.3	182.6	182.5	36	33.7	33.9	0.13	0.12	0.12
13	10	0.4	0.2	54.6	53.4	55.0	181.3	185.4	185.2	36	34.3	34.5	0.13	0.13	0.13
14	10	0.8	0.7	54.6	56.2	71.3	181.3	180.8	180.9	36	36.3	36.6	0.13	0.13	0.13
15	10	1.2	1.2	54.6	60.9	122.1	181.3	178.6	178.6	36	33.9	33.1	0.13	0.11	0.10
C6	30	0	0	54.6	54.3	54.7	181.3	178.9	178.9	36	36.3	36.3	0.13	0.14	0.13
16	30	0.4	0.4	54.6	55.6	60.1	181.3	182.8	182.8	36	37.2	37.1	0.13	0.13	0.13
17	30	0.8	0.8	54.6	58.6	76.7	181.3	180.8	181.3	36	39.1	39.1	0.13	0.14	0.13
18	30	1.2	1.2	54.6	51.6	114.9	181.3	182.0	181.9	36	36.1	35.0	0.13	0.12	0.11
12	5	1.2	1.3	54.6	51.4	121.2	181.3	190.1	190.3	36	45.5	39.3	0.13	0.15	0.11
19	5	0.4	0.3	44.7	41.9	44.4	90.0	95.0	94.8	36	39.2	39.6	0.21	0.22	0.22
20	5	0.8	0.6	44.7	51.1	61.3	90.0	91.9	91.7	36	30.3	30.0	0.21	0.17	0.16
21	5	1.2	1.2	44.7	47.4	95.7	90.0	86.3	86.1	36	34.9	36.8	0.21	0.18	0.17
22	10	0.4	0.3	44.7	42.6	45.6	90.0	90.0	90.0	36	33.4	33.6	0.21	0.20	0.20
23	10	0.8	0.9	44.7	39.3	55.9	90.0	88.0	88.0	36	40.8	41.0	0.21	0.23	0.22
24	10	1.2	1.2	44.7	46.0	90.9	90.0	91.2	91.3	36	40.3	39.5	0.21	0.21	0.18
25	30	0.4	0.4	44.7	44.1	47.4	90.0	91.2	91.3	36	37.9	38.0	0.21	0.22	0.21
26	30	0.8	0.8	44.7	45.3	60.4	90.0	90.0	90.1	36	32.8	32.9	0.21	0.19	0.18
27	30	1.2	1.2	44.7	42.9	89.7	90.0	90.6	90.5	36	33.5	33.6	0.21	0.18	0.16

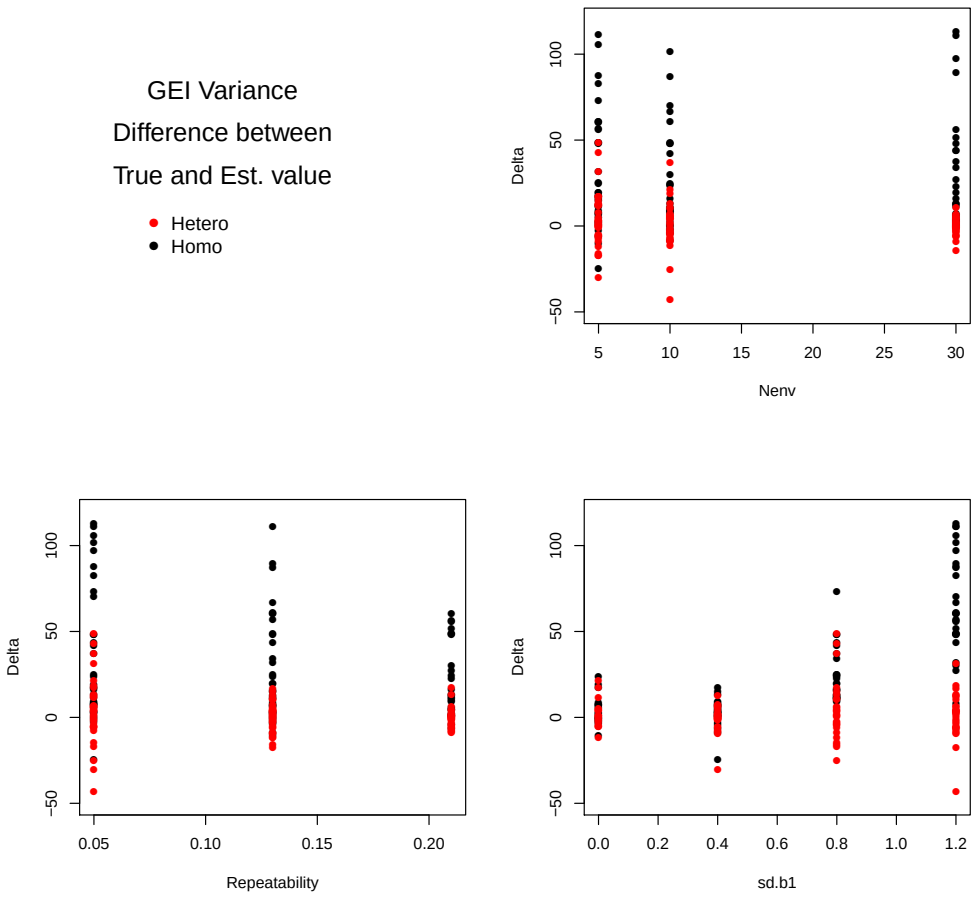

Figure 3.1 GEI variance: Discrepancy between estimates and true value by different levels of number of environments, repeatability and heterogeneity. Red dots represent differences computed for the heterogeneous model, black dots represent differences computed for the homogeneous mode

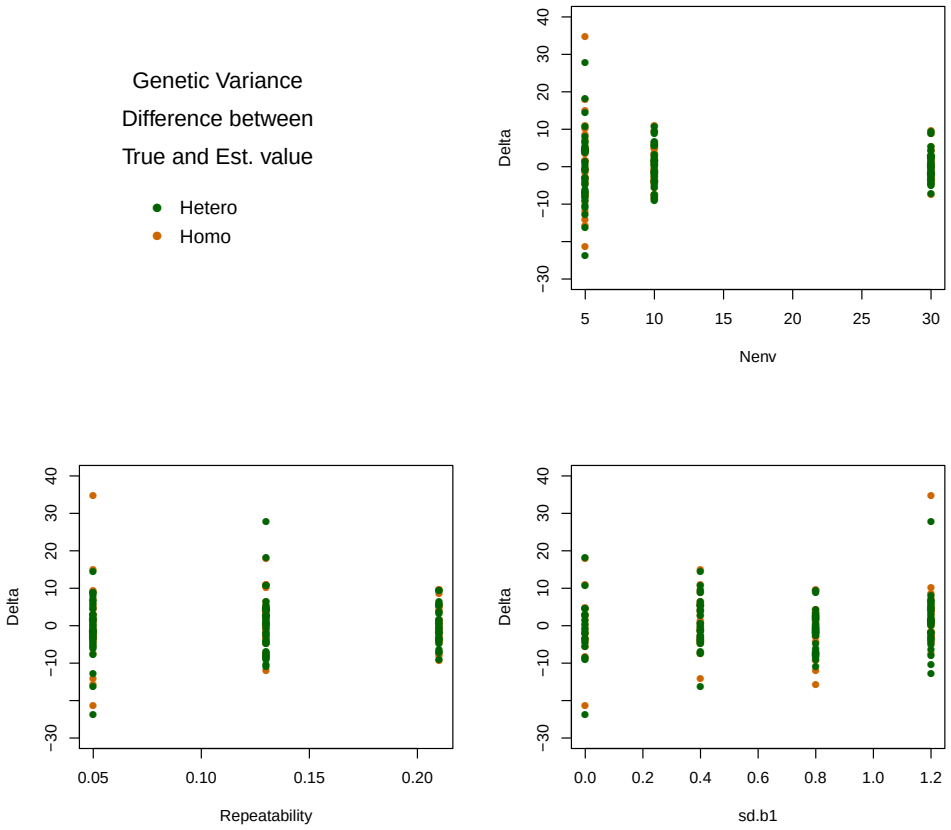

Figure 3.2 Genetic variance: Discrepancy between estimates and true value by different levels of number of environments, repeatability and heterogeneity. Green dots represent differences computed for the heterogeneous model, brown dots represent differences computed for the homogeneous mode

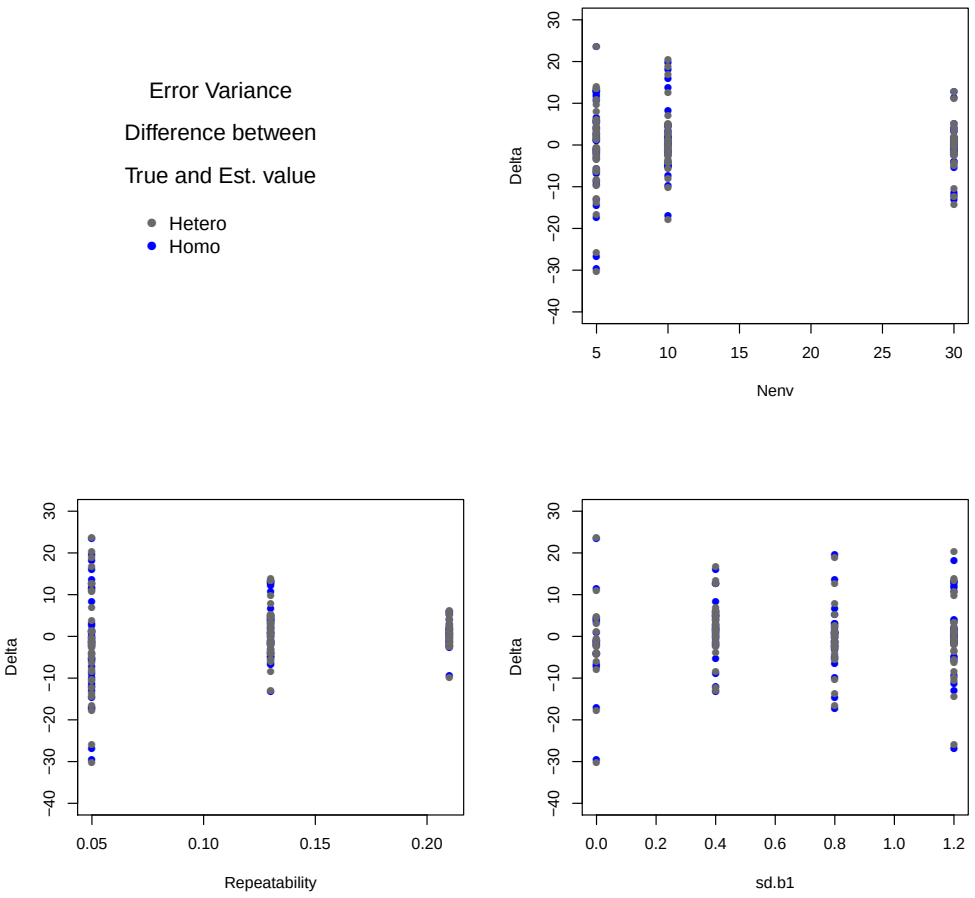

Figure 3.3 Error variance: Discrepancy between estimates and true value by different levels of number of environments, repeatability and heterogeneity. Blue dots represent differences computed for the heterogeneous model, grey dots represent differences computed for the homogeneous mode

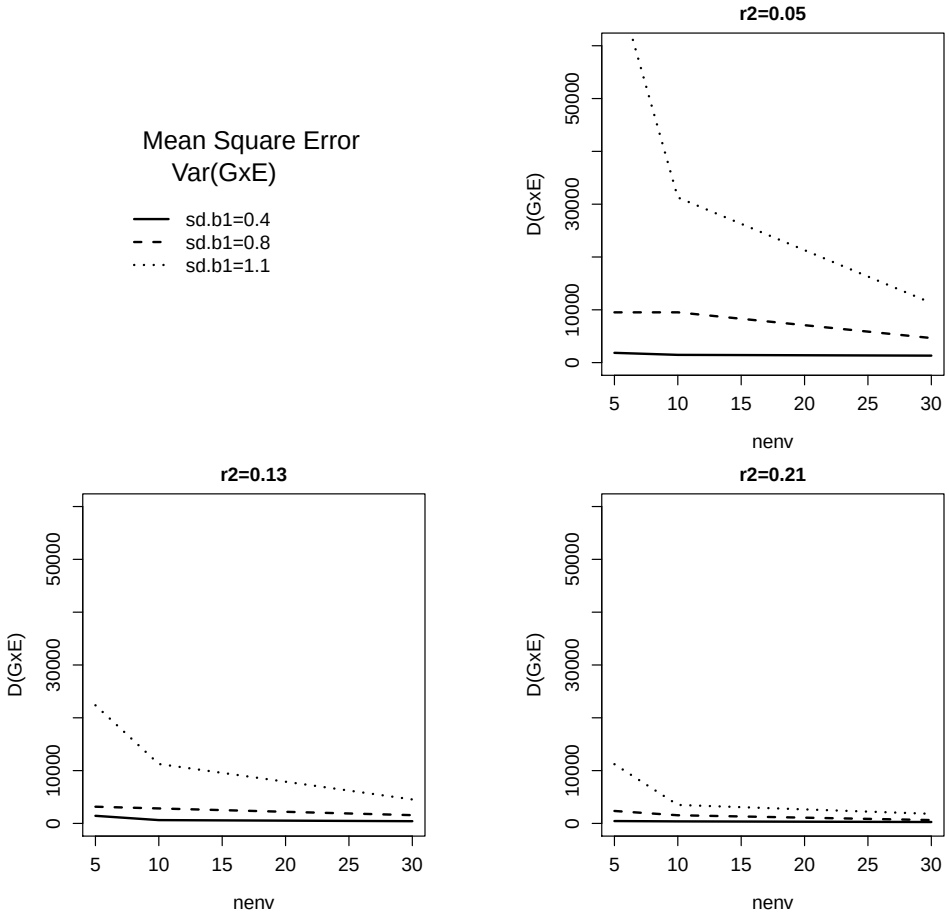

Figure 3.4 Discrepancy assessment for the GEI variance components: Effect of repeatability (r^2), number of environments (Nenv) and level of heterogeneity ($\sigma^2_{\delta_i}$).

increasing the number of environments reduced the mean-squared error. Edwards and Jannink (2006) explained the relationship between these factors using the example provided by Leonard (1975). The Bayesian estimator for the GEI variance is a weighted average that represents a compromise between the prior (in this case it can be thought as a pooled variance) and the data or "likelihood" in Bayesian jargon (in this case it represents an estimate of the variance of an individual cultivar).

In our study, the weight for the logarithm of the GEI variance for an individual genotype, $\ln\left(\sigma^2_{\delta_i}\right)$, considers the total number of observations of cultivar i and the variance of b_{1i}, σ^2_{b1}. When the sample size (Nenv) or the level of heterogeneity (σ_{b1}) increase, the Bayesian estimator will assign more weight to the individual cultivar variance estimator; if the GEI variance components exhibit low variability (i.e., if variances are homogeneous), then the Bayes estimator will assign more weight to the pooled variance.

The Bayes estimator for the genotypic effect (γ) is also a weighted average; when the repeatability increases, more weight will be put on the individual cultivar posterior means. Therefore, cultivars with large GEI variance will have differential variance estimates that in turn will affect their genotypic effects estimates.

In Figure 3.5 we compare the precision of the two models used in this paper. The continuous line represents the homogeneous model and the dashed line represents the heterogeneous model, plots from left to right have lower repeatability, whereas plots from top to bottom have smaller number of environments. In all cases, the heterogeneous model provides estimates that are closer to the true value. Although there is an effect of repeatability and sample size, the main differences are found when the heterogeneity of the data gets larger (σ_{b1} =1.2). Table 3.5 presents the credible sets for the marginal GEI variance for both homogeneous and heterogeneous models, note that the quantity displayed in Table 3.5 correspond to an estimation of the overall GEI (we obtained a value per set and model), while the quantity displayed in figures 3.4 and 3.5 denoted by D(G×E) was calculated at the GEI level (we obtained 200 values and took the average of those values per model and set).

The credible sets for the posterior distribution of the GEI variance analyzed using the heterogeneous model are wider, the width absolute differences go from 0.4 to 11. The estimates for the marginal error variance component are very similar between models. The credible sets width for the error variance estimates are also very similar for both models (Table 3.6), the differences in width go from 0.02 to 1.93.

In the case of the genetic variance (σ_γ) we also calculated the mean-squared error obtaining a value per each replicated set. The estimates for genetic variance showed the same trend than the GEI variance components, their accuracy increased as repeatability and number of environments increased, however the variation of the estimates in this case was smaller, the mean-squared error for the genetic variance ranged from 0.003 to 1197 (data non-shown).

The largest average difference between the true value and the estimated genotypic variance was 14.5 (Table 3.4). When comparing the performance of the two competing models, the estimates were very similar (Figure 3.2); the width of the credible sets were very similar for both models in all the sets (Table 3.7).

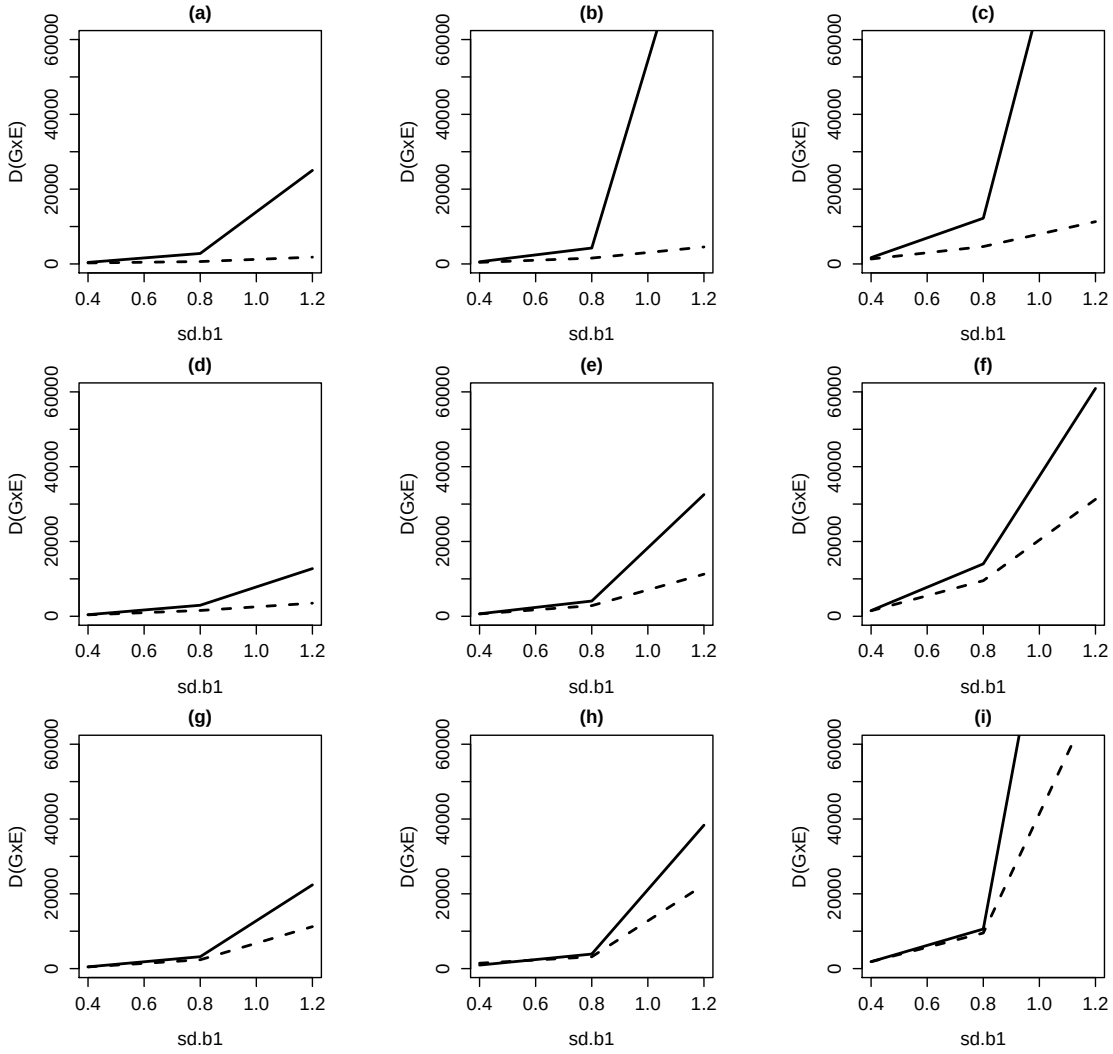

Figure 3.5 Level of GEI variance discrepancy measured in 9 sets generated using the heterogeneous model. Conditions: (a) $r^2 = 21\%$, Nenv = 30, (b) $r^2 = 13\%$, Nenv = 30, (c) $r^2 = 5\%$, Nenv = 30, (d) $r^2 = 21\%$, Nenv = 10, (e) $r^2 13\%$, Nenv = 10, (f) $r^2 = 5\%$, Nenv = 10, (g) $r^2 = 21\%$, Nenv = 5, (h) $r^2 = 13\%$, Nenv = 5, (i) $r^2 = 5\%$, Nenv = 5. Solid lines represent the homogeneous model; dashed lines represent the heterogeneous model.

Table 3.5 Credible sets for the posterior distributions of $\sigma^2_{\delta\cdot}$.

				heterogeneous model				homogeneous model			
Set	nenv	r2	sdb1	Mean	2.50%	50%	97.50%	Mean	2.50%	50%	97.50%
1	5	0.05	0.4	84.81	46.77	84.85	123.48	90.05	57.30	90.63	126.43
2	5	0.05	0.8	114.76	71.87	114.59	160.03	134.21	96.85	134.46	175.67
3	5	0.05	1.2	105.54	60.70	104.45	158.61	182.10	141.98	182.01	227.24
4	10	0.05	0.4	94.01	69.09	94.20	118.90	96.08	73.22	96.41	120.60
5	10	0.05	0.8	98.37	67.63	97.77	129.47	128.37	103.35	128.64	154.65
6	10	0.05	1.2	79.43	50.22	79.10	113.01	150.13	123.69	150.27	177.22
7	30	0.05	0.4	90.03	73.91	90.13	105.33	96.55	83.52	96.71	110.09
8	30	0.05	0.8	88.78	69.64	89.01	106.88	122.42	108.81	122.62	136.46
9	30	0.05	1.2	89.06	65.45	89.33	112.84	197.02	181.24	197.09	213.22
10	5	0.13	0.4	55.02	34.46	55.12	74.29	59.55	43.23	59.69	77.43
11	5	0.13	0.8	52.37	30.47	52.31	75.64	73.39	56.29	73.39	92.79
12	5	0.13	1.2	51.38	29.22	50.62	76.38	121.23	99.07	121.32	145.82
13	10	0.13	0.4	53.36	40.84	53.53	65.29	54.97	43.88	54.99	66.62
14	10	0.13	0.8	56.20	41.87	56.30	71.00	71.30	59.58	71.39	83.72
15	10	0.13	1.2	60.86	42.54	60.53	80.75	122.08	107.50	122.02	137.49
16	30	0.13	0.4	58.55	46.29	58.66	70.02	60.14	53.90	60.15	66.74
17	30	0.13	0.8	58.55	48.92	58.51	68.55	76.72	69.99	76.79	83.76
18	30	0.13	1.2	51.56	39.83	51.42	64.36	114.95	106.90	114.93	123.47
19	5	0.21	0.4	41.91	30.18	41.88	53.15	44.45	34.85	44.47	55.13
20	5	0.21	0.8	51.08	37.04	50.90	65.37	61.30	50.33	61.28	73.19
21	5	0.21	1.2	47.44	32.00	47.14	64.45	95.74	82.41	95.60	110.63
22	10	0.21	0.4	42.64	35.13	42.65	50.38	45.57	39.20	45.59	52.43
23	10	0.21	0.8	39.30	30.32	39.25	48.15	55.94	48.92	55.96	63.24
24	10	0.21	1.2	45.99	33.84	45.88	58.49	90.92	81.48	90.91	100.61
25	30	0.21	0.4	44.13	39.45	44.12	48.79	47.38	43.64	47.40	51.28
26	30	0.21	0.8	45.32	39.11	45.23	52.01	60.42	56.31	60.40	64.72
27	30	0.21	1.2	42.90	34.43	42.71	52.29	89.70	84.63	89.64	94.97

Table 3.6 Credible sets for the posterior distributions of σ^2.

				heterogeneous model				homogeneous model			
Set	nenv	r2	sdb1	Mean	2.50%	50%	97.50%	Mean	2.50%	50%	97.50%
1	5	0.05	0.4	401.41	366.90	401.13	437.87	400.67	366.60	400.41	437.94
2	5	0.05	0.8	392.39	358.93	391.90	427.83	393.11	359.77	392.74	430.07
3	5	0.05	1.2	396.31	362.37	396.18	431.50	396.42	363.06	396.16	432.41
4	10	0.05	0.4	410.04	386.00	409.73	436.17	409.76	385.12	409.57	436.44
5	10	0.05	0.8	410.50	385.73	410.43	435.87	411.29	386.47	410.97	438.17
6	10	0.05	1.2	409.33	385.47	409.07	435.37	409.02	384.20	409.03	436.03
7	30	0.05	0.4	404.02	389.83	404.00	419.07	404.18	389.99	404.07	418.82
8	30	0.05	0.8	402.14	388.17	401.93	416.34	402.60	388.62	402.54	416.85
9	30	0.05	1.2	394.46	380.93	394.40	408.64	395.01	381.31	395.10	409.14
10	5	0.13	0.4	182.09	166.50	181.83	198.63	181.69	166.47	181.59	198.52
11	5	0.13	0.8	181.08	165.57	180.90	198.03	180.27	165.25	180.14	197.17
12	5	0.13	1.2	190.14	173.97	189.87	207.44	190.26	174.34	190.09	207.67
13	10	0.13	0.4	185.38	173.93	185.37	196.83	185.15	173.89	184.96	197.41
14	10	0.13	0.8	180.76	169.77	180.63	192.13	180.92	169.88	180.65	192.86
15	10	0.13	1.2	178.56	167.80	178.47	189.97	178.61	167.88	178.50	190.27
16	30	0.13	0.4	182.80	176.33	182.77	189.33	182.79	176.46	182.80	189.44
17	30	0.13	0.8	180.78	174.53	180.80	187.07	181.33	175.21	181.35	188.06
18	30	0.13	1.2	182.04	175.83	182.02	188.40	181.90	175.66	181.90	188.43
19	5	0.21	0.4	95.00	86.95	94.88	103.77	94.77	86.78	94.67	103.37
20	5	0.21	0.8	91.89	84.31	91.74	100.35	91.72	83.86	91.66	100.14
21	5	0.21	1.2	86.29	79.10	86.11	94.12	86.14	78.90	86.10	94.04
22	10	0.21	0.4	90.00	84.53	89.95	95.70	89.99	84.53	89.98	95.87
23	10	0.21	0.8	87.95	82.68	87.87	93.59	88.05	82.76	87.97	93.70
24	10	0.21	1.2	91.18	85.79	91.15	96.92	91.31	85.75	91.26	97.31
25	30	0.21	0.4	91.22	87.99	91.22	94.51	91.26	88.04	91.25	94.52
26	30	0.21	0.8	89.97	86.89	89.93	93.26	90.11	87.03	90.08	93.38
27	30	0.21	1.2	90.61	87.39	90.62	93.89	90.51	87.31	90.51	93.73

Table 3.7 Credible sets for the posterior distributions of σ^2_γ.

				heterogeneous model				homogeneous model			
Set	nenv	r2	sdb1	Mean	2.50%	50%	97.50%	Mean	2.50%	50%	97.50%
1	5	0.05	0.4	26.48	10.82	27.83	49.31	27.27	11.35	28.01	48.96
2	5	0.05	0.8	23.33	3.60	24.85	47.36	19.32	3.06	21.79	45.77
3	5	0.05	1.2	28.65	8.96	30.22	56.59	42.50	19.05	42.83	70.64
4	10	0.05	0.4	29.07	18.82	28.91	42.54	29.19	18.59	29.11	42.62
5	10	0.05	0.8	29.72	18.64	29.59	44.02	29.41	18.23	29.41	43.48
6	10	0.05	1.2	31.51	20.08	31.47	45.91	29.67	17.93	29.70	44.69
7	30	0.05	0.4	29.65	22.69	29.52	38.76	29.75	22.70	29.59	38.51
8	30	0.05	0.8	27.99	21.08	27.83	36.62	28.10	21.16	28.04	36.53
9	30	0.05	1.2	27.45	20.59	27.30	36.36	29.32	22.00	29.15	38.54
10	5	0.13	0.4	38.73	26.34	38.61	54.41	38.63	26.33	38.52	54.41
11	5	0.13	0.8	27.99	17.04	28.02	42.53	28.45	17.07	28.52	42.16
12	5	0.13	1.2	45.55	30.46	45.48	63.85	39.28	23.67	39.24	58.48
13	10	0.13	0.4	34.33	25.87	34.18	44.93	34.47	25.45	34.38	45.53
14	10	0.13	0.8	36.29	27.14	36.09	47.98	36.55	27.12	36.46	48.29
15	10	0.13	1.2	33.85	24.73	33.69	45.50	33.10	23.54	33.01	45.46
16	30	0.13	0.4	37.17	29.76	37.01	46.43	37.09	29.77	36.85	46.24
17	30	0.13	0.8	39.11	31.25	38.93	49.34	39.08	31.33	38.86	49.02
18	30	0.13	1.2	36.05	28.81	35.86	45.48	35.03	27.91	34.85	44.09
19	5	0.21	0.4	39.19	28.84	39.15	52.09	39.59	29.24	39.43	52.89
20	5	0.21	0.8	30.26	20.93	30.19	41.87	30.00	20.67	29.87	41.39
21	5	0.21	1.2	34.91	24.00	34.86	48.44	36.82	25.28	36.77	51.34
22	10	0.21	0.4	33.36	25.88	33.23	42.70	33.55	26.10	33.42	42.89
23	10	0.21	0.8	40.79	31.90	40.58	52.26	40.99	31.80	40.78	52.28
24	10	0.21	1.2	40.29	31.34	40.11	51.82	39.51	29.95	39.32	51.33
25	30	0.21	0.4	37.88	30.59	37.71	47.03	37.99	30.94	37.75	47.05
26	30	0.21	0.8	32.78	26.39	32.53	40.87	32.87	26.65	32.70	40.96
27	30	0.21	1.2	33.46	26.86	33.28	41.80	33.63	27.13	33.48	41.83

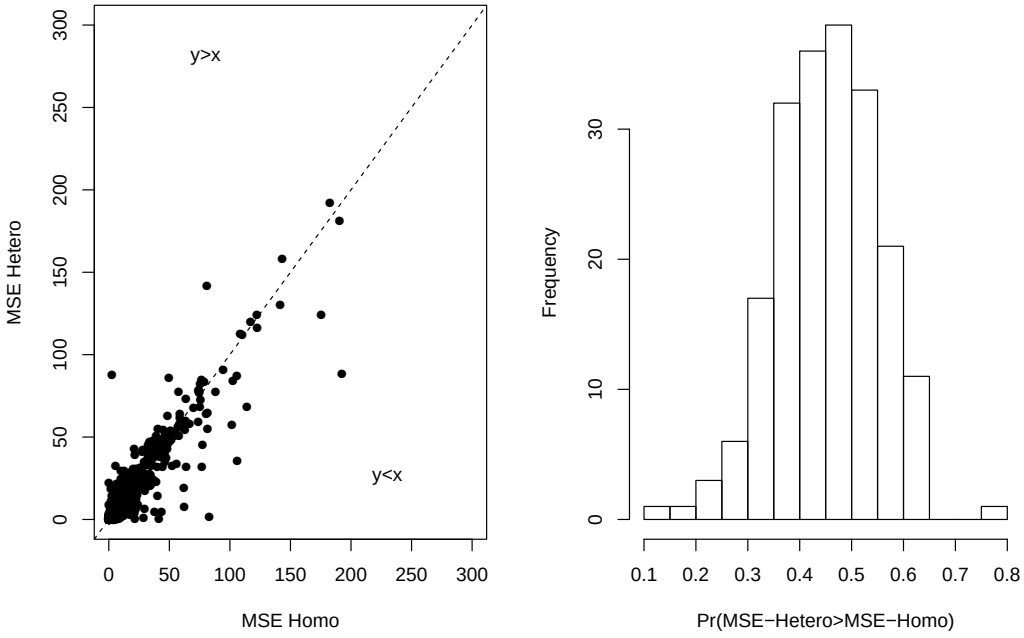

Figure 3.6 Left: Genotypic effect MSE, for set 3 (Nenv $= 5$, $r^2 = 5\%$, $\sigma_{b1} = 1.2$). Right: Probability of $MSE(Gen_{hetero}) < MSE(Gen_{homo})$.

Besides studying the accuracy and precision of estimates of variance components we were also interested in the ability of the models to predict performance. We used the discrepancy measure defined in equation 3.6 to evaluate the accuracy of the genotypic effect estimates under both, the heterogeneous and homogeneous model. We obtained all the values from the MCMC chains and calculated the mean-squared error using the true value for the genotypic effect (γ); we did this for the two competing models. A comparison of mean-squared error for the homogeneous and heterogeneous models is shown in Figure 3.6, the homogeneous model seems to generate more estimates that depart from the true value. Under the Bayesian framework it is possible to calculate the probability of $MSE(Gen_{hetero}) < MSE(Gen_{homo})$ counting the number of times that the mean-squared error of the genotypic effect calculated fitting the heterogeneous model was less than the same quantity calculated under the homogeneous model. Most of the genotypes (83%) showed a probability between 0.5 and 0.6, therefore we conclude that for the data used in the example, the heterogeneous model does not show a clear advantage on precision compared to the genotypic effect estimates provided by the homogeneous model.

In Figure 3.7 we compare two sets that only differ on the level of heterogeneity ($\sigma_{b1} = 0.8, 1.2$) showing how the Bayes estimator is a shrinkage estimator which is a common term used to indicate that for

datasets with conditions of high variability (such as low repeatability, or lower number of environments) the estimated value will be pushed closer to the mean. As the observed data becomes more "reliable", this is, with smaller error and/or GEI variances, and/or more environments tested, the Bayesian estimator will put more weight on the individual cultivar means. In most of the cases the competing models have similar posteriors and are very close to the true distribution, however when the variability increases the heterogeneous model produces values that are closer to the mean. In other words, the more unstable cultivars will be "penalized" and the Bayes estimator will rely less on the data coming from these individuals.

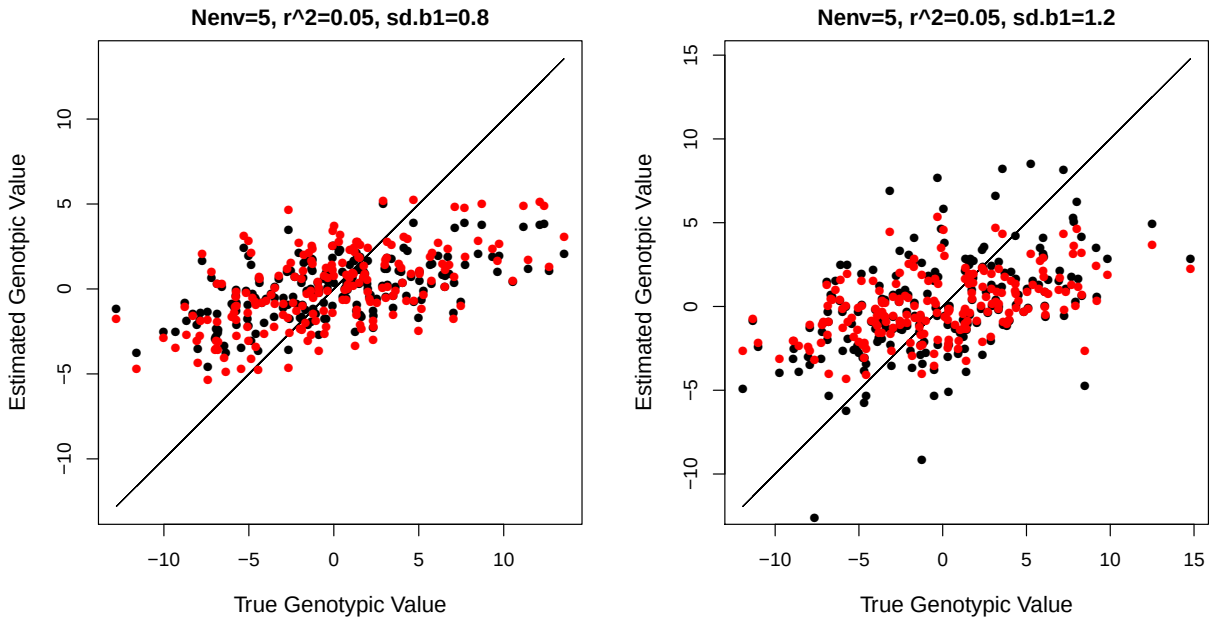

Figure 3.7 Scatter plot of the genotypic effects estimated under the homogeneous (black dots) and the heterogeneous (red dots) model.

Table 3.8 True selection differential for sets simulated under different conditions of repeatability (r^2), level of heterogeneity (σ_{b1}), and number of environments (Nenv). The selection was conducted using estimates from the heterogeneous and homogeneous model, after obtaining the true selection differential, the ratio between heterogeneous and homogeneous model was computed to compare the two quantities.

				Sel Diff		
Set	r^2	σ_{b1}	Nenv	homo	het	ratio
C1	0.05	0	5	2.20	2.22	1.01
1	0.05	0.4	5	7.03	7.19	1.02
2	0.05	0.8	5	6.70	6.60	0.98
3	0.05	1.2	5	4.56	5.17	1.13
C2	0.05	0	10	8.36	8.34	1.00
4	0.05	0.4	10	8.21	8.04	0.98
5	0.05	0.8	10	7.07	7.24	1.02
6	0.05	1.2	10	5.68	5.96	1.05
C3	0.05	0	30	8.87	8.87	1.00
7	0.05	0.4	30	9.02	8.99	1.00
8	0.05	0.8	30	9.54	9.57	1.00
9	0.05	1.2	30	8.34	8.48	1.02
C4	0.13	0	5	3.89	4.47	1.15
10	0.13	0.4	5	10.13	10.13	1.00
11	0.13	0.8	5	7.69	7.85	1.02
12	0.13	1.2	5	7.17	7.76	1.08
C5	0.13	0	10	10.09	10.34	1.03
13	0.13	0.4	10	11.72	11.72	1.00
14	0.13	0.8	10	9.87	10.25	1.04
15	0.13	1.2	10	12.27	12.35	1.01
C6	0.13	0	30	11.04	11.04	1.00
16	0.13	0.4	30	11.13	11.19	1.01
17	0.13	0.8	30	11.65	11.64	1.00
18	0.13	1.2	30	10.24	10.39	1.01
19	0.21	0.4	5	9.07	9.10	1.00
20	0.21	0.8	5	9.84	10.15	1.03
21	0.21	1.2	5	9.78	10.07	1.03
22	0.21	0.4	10	11.41	11.38	1.00
23	0.21	0.8	10	10.48	10.96	1.05
24	0.21	1.2	10	11.07	11.07	1.00
25	0.21	0.4	30	11.25	11.24	1.00
26	0.21	0.8	30	11.05	11.14	1.01
27	0.21	1.2	30	9.35	9.49	1.02

Table 3.9 Genotypic effect (γ_i) and GEI variance (δ_i) true values and their respective estimates ($\hat{\gamma}_i$ and $\hat{\delta}_i$) for the heterogeneous and homogeneous model. Simulated set for 5 environments, 21% repeatability and highest heterogeneity level ($\sigma^2_{b1} = 1.2$).

	true value		heterogeneous			homogeneous		
Genotype	γ_i	δ_i	$\hat{\gamma}_i$	Ranking	$\hat{\delta}_i$	$\hat{\gamma}_i$	Ranking	$\hat{\delta}_i$
g[131]	24.83	211.86	7.34	6	377.25	14.23	1	100.60
g[81]	-0.18	496.14	5.37	13	472.83	11.91	2	100.60
g[110]	9.24	54.13	10.91	1	50.85	9.88	5	100.60
g[153]	8.37	84.08	8.88	3	116.08	9.45	6	100.60
g[186]	10.15	33.48	9.80	2	65.60	9.13	7	100.60
g[88]	14.63	2.40	7.89	4	86.97	7.97	8	100.60
g[58]	12.82	180.69	7.79	5	55.28	7.01	10	100.60
g[157]	15.39	14.48	7.50	7	62.86	6.99	11	100.60
g[167]	16.42	15.73	7.72	8	41.81	6.68	12	100.60
g[25]	12.01	6.17	7.21	9	34.33	5.93	13	100.60

We wanted to assess if having differential estimates of GEI variance had an impact on the decisions made based on the rankings of the genotypic effects. We calculated the true selection differential selecting the top 5% of the population based on the rankings obtained under each model (Table 3.8); 58% of the selected sets under the heterogeneous model presented a higher genotypic effect differential after selection in comparison to the homogeneous model, this means that the use of the heterogeneous model led to select different individuals in comparison to the homogeneous model, and the decisions resulted in an improved genetic gain; 36% of the selected sets had 100% concordance between models, therefore, the true selection differential was the same and only 6% of the selected sets had a higher true selection differential when selecting under the homogeneous model.

To show how the Bayesian estimator works, we chose one of the sets that was generated considering 5 environments, high level of heterogeneity ($\sigma_{b1} = 1.2$) and high repeatability ($r^2 = 21\%$). True values, genotypic effect, GEI variance and rankings estimates for 10 genotypes are shown in Table 3.9 for both heterogeneous and homogeneous model.

This example clearly shows how the heterogeneous model ranks is not only considering the genotypic effect estimates but also the cultivar stability through their GEI estimates; unstable cultivars will have larger GEI variance estimates and for this reason their genotypic effects estimates will be "penalized" and pushed towards the mean. For example, g[131] has a true GEI variance equal to 211.9, the GEI variance obtained for the homogenous model is 100.6 and 377.3 for the heterogeneous model. The true

genotypic effect of this genotype is 24.8; the genotypic effect estimate provided by the homogeneous model is 14.2 whereas the estimate for the heterogeneous model is only 7.3. Therefore the estimate of stability, given by the GEI variance estimate, provided an automatic penalty to the unstable genotype pushing the estimate towards zero, the overall mean.

The posterior probability ranking plot is a graphical representation of Table 3.9, it not only allows the visualization and comparison of several ranking lists at a glance, but also provides information regarding the stability of the genotypes on the plot. For example, in Figure 3.8 the homogeneous model places g[131] and g[81] as the two top performer genotypes, whereas the heterogeneous model rank them as 6 and 13, respectively, this is clearly shown on the plots, where for the heterogeneous model, g[131] and g[81] exhibit a flat slope.

3.4.3 Application: Iowa Crop Performance Test from 2000 - 2001

The data for this example comes from the Iowa Crop Performance test for years 2000 and 2001. There were a total of 184 hybrids that were present in both years. We fitted the two models and calculated the rankings. In the case of the heterogeneous model we used the $Pr(TOP-k)$ ranking method previously described; for the homogeneous model, we ranked the posterior means. The advantage of using the $Pr(TOP-k)$ approach is that it provides a visualization method for many ranking list at a time. In Figure 3.9 we present some selected genotypes. Genotypes 174, 109, 128 and 35 and 49 showed the highest performance in 2000, they quickly reach a high probability of being among the $TOP-20$ hybrids. However, there are some other genotypes that increase their probability slowly, like genotype 11; these genotypes have a higher probability of being ranked at lower positions, and this probability is even higher than the probability for the other genotypes that initially had a high probability of being ranked among the first few top performers (compare genotypes 11 and 49 at position 20), other genotypes that present this behavior are 28, 151 and 105. The rankings obtained for the top 10 genotypes in 2000 an 2001 are shown in Table 3.10; small numbers indicate better performance.

The homogeneous model selects different genotypes than the heterogeneous model. For example, the homogeneous model assigned higher ranking scores to genotypes 74 and 57 than the heterogeneous model. Under our criteria of selecting only the $TOP-10$, these two genotypes would have been included on the

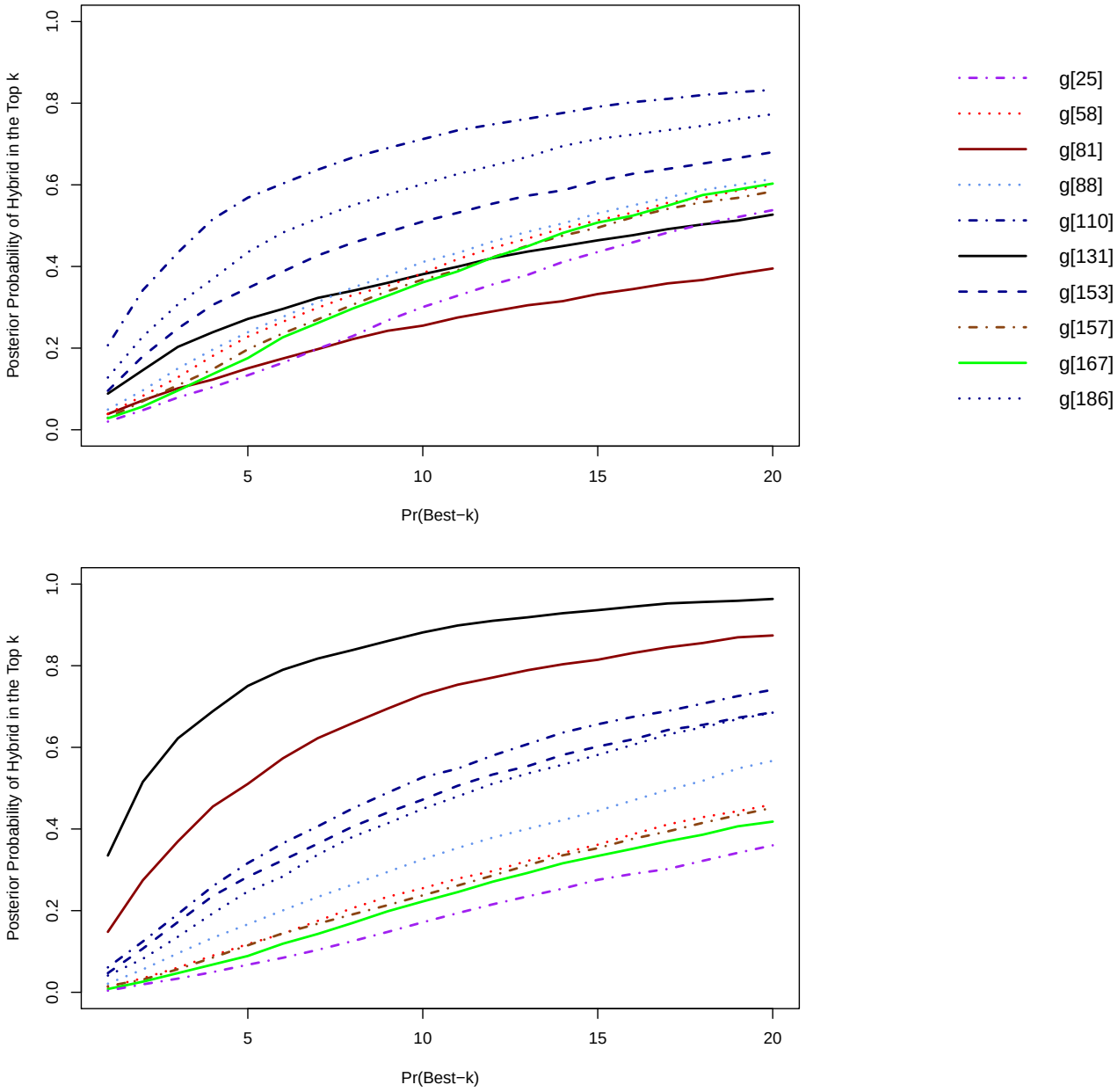

Figure 3.8 Posterior probability ranking plots for 10 genotypes (top: Heterogeneous, bottom: Homogeneous). Chosen set was generated under following criteria: 5 environments, high level of heterogeneity ($\sigma_{b1} = 1.2$) and high repeatability ($r^2 = 21\%$).

list generated by the homogeneous model leaving out genotype 151. In 2001 genotype 151 was among the $TOP-10$ performers and genotypes 74 and 57 were ranked as 71 and 35 respectively; by looking only at the posterior means we would disregard promising genotypes because we are not taking into account their stability and in some cases we may be selecting cultivars that exhibit a high performance but also are highly unstable as we showed for the simulated data in the previous section. The heterogeneous model incorporates a measure of stability by taking into account the differential estimates of GEI variance (fig. 3.10); the genotypes that perform extremely well under some specific conditions, and thus have high GEI variance, will have lower weight placed on them in the estimation of average genotypic values, this feature of the Bayes estimator is desirable for breeders and growers looking for high performing genotypes for a broader target region; the adoption of the posterior probability ranking plots in earlier stages of a breeding program can be a powerful tool to discard material that shows no potential.

Table 3.10 Conditions for sets simulated from the Heterogeneous model.

	2000		2001	
Genotype	HOMO	HETERO	HETERO	HOMO
174	1	1	6	5
109	2	2	20	21
128	3	3	10	7
35	5	4	95	94
49	6	5	5	11
11	7	6	152	157
94	8	7	46	47
151	11	8	4	4
28	10	9	45	54
125	13	11	26	20
74	4	12	71	64
54	47	17	2	2
57	9	19	35	37
133	44	30	3	3
145	53	49	16	19
183	94	68	7	6
90	87	71	1	1
135	104	103	8	8
139	159	146	9	12

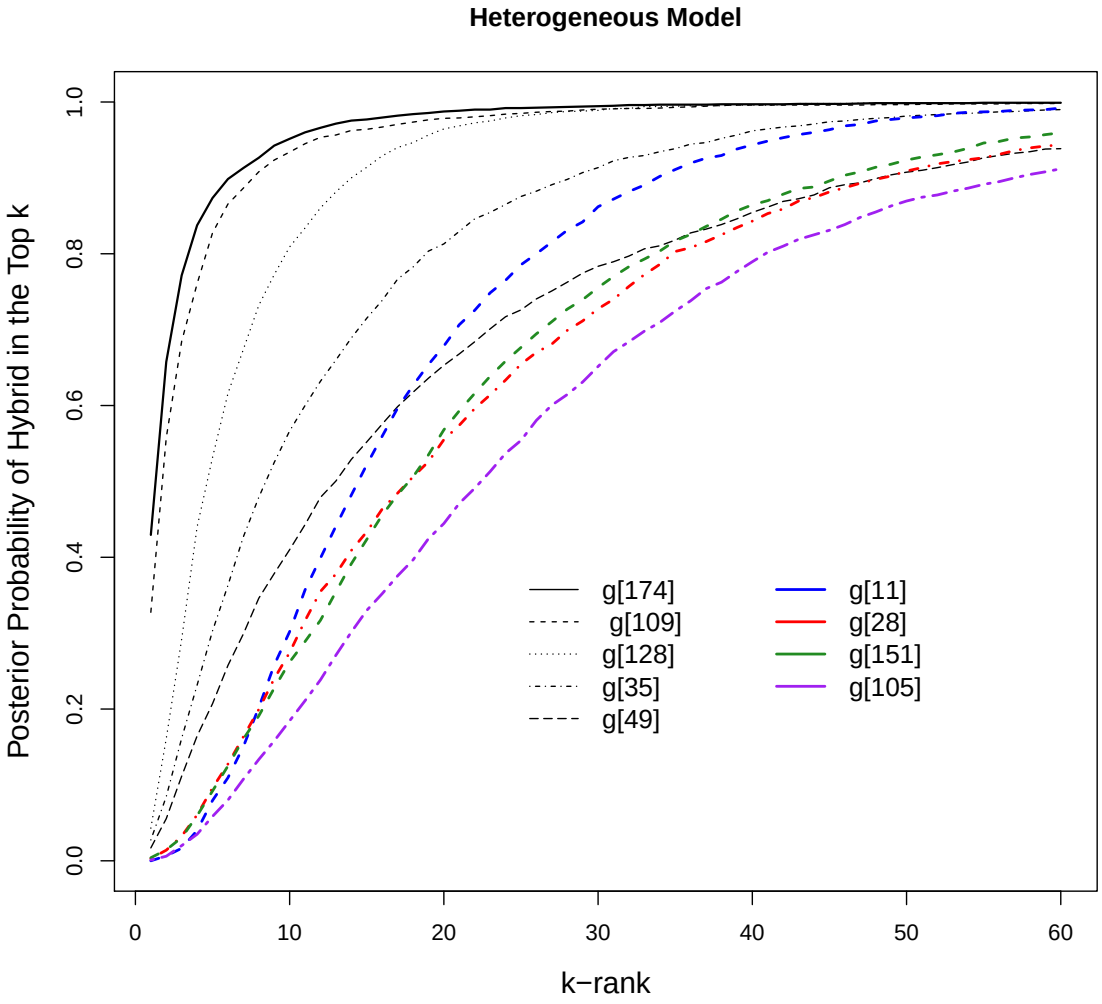

Figure 3.9 Heterogeneous posterior probability ranking plots. Selected genotypes from the Iowa Crop Performance Test, year 2000. Genotypes 11, 28, 151, 105 are genotypes that did not rank among top 5, but are good candidates because they are stable.

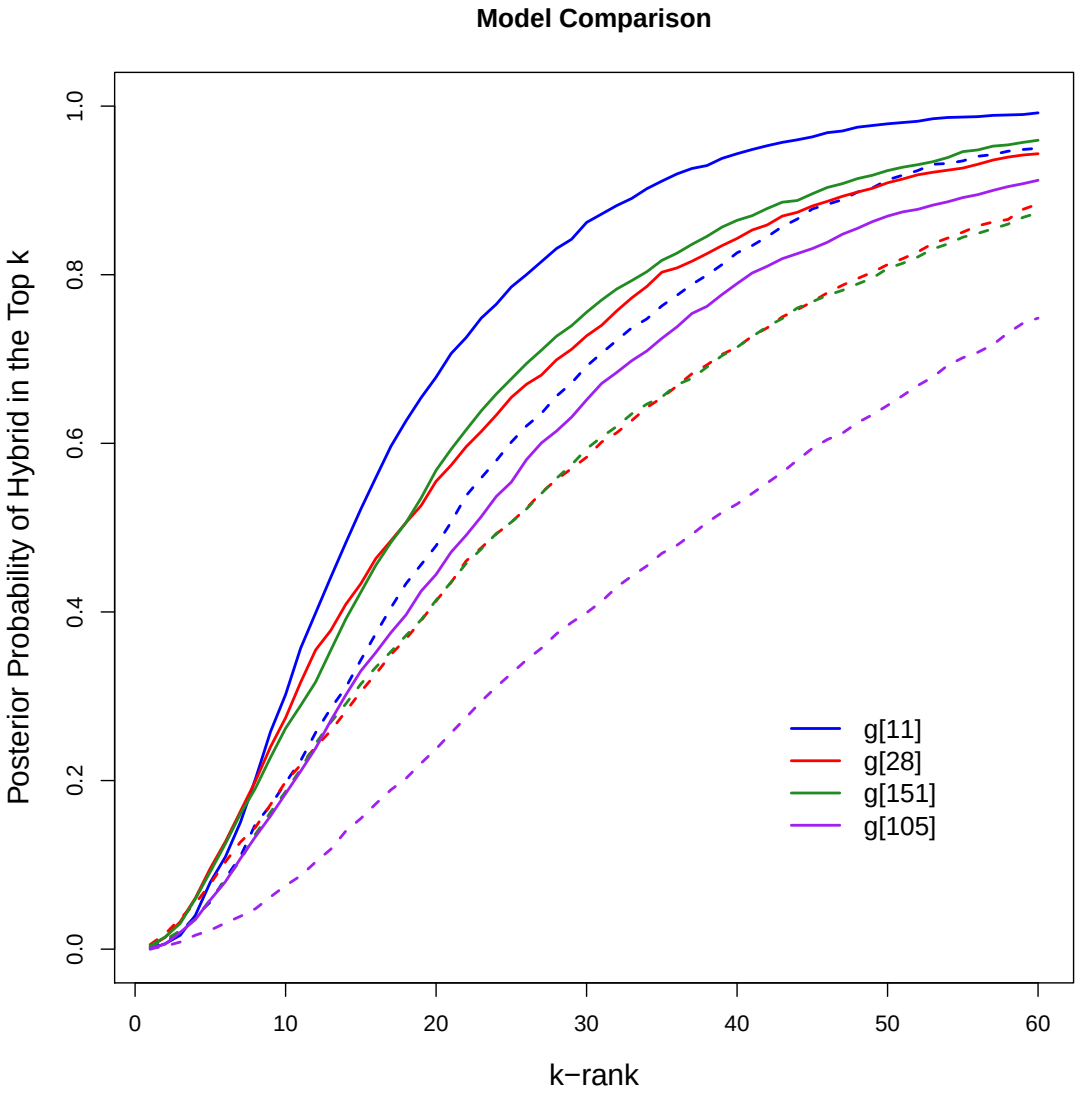

Figure 3.10 Posterior probability ranking plots for data from the Iowa Crop Performance Test (year 2000): Model comparison for 4 cultivars. Solid lines represent the heterogeneous model. Dashed lines, represent the homogeneous model.

3.5 Conclusions

We simulated data under 33 different conditions of repeatability (5%, 13% and 21%), sample size (Nenv = 5, 10, 30) and level of heterogeneity ($\sigma_{b1} = 0.4, 0.8, 1.2$) including 6 data sets simulated from a model that had no heterogeneity (homogeneous model); we considered these sets our control.

The heterogeneous model was able to pick up the lack of variability of the data from the control sets, showing similar results to the homogeneous model in both component of variance estimates and genotypic effects estimates. Both models led to select the same genotypes in most of the cases, suggesting that for cases where the parameter of heterogeneity tends to zero this model will still produce valid results.

In the case of data simulated from the heterogeneous model, the estimates of the component of variance where more accurate when using the heterogeneous model, we observed a very large improvement on the estimates of GEI variances, which in our study was the only term truly heterogeneous.

The Bayesian framework provides mean and variance estimators of cultivar performance that are weighted averages and represent a compromise between the prior and posterior distributions. As the heterogeneity or sample size of the data increases, more weight will be assigned to the individual cultivar variance estimates. Similarly, individual cultivar posterior means will increase their contribution to the final estimate when the repeatability increases; if the repeatability is low, most of the weight will rely on the prior (given by the overall mean).

The genetic gain differential after selection using the heterogeneous model was slightly in favor of the heterogeneous model. We believe that this is a promising indication that confirms our hypothesis that selections made under the heterogeneous model lead to bigger increments in yield compared to the homogeneous model. We plan to continue our work incrementing the number of replicates to prove that our findings are consistent.

Some cultivars with high genotype-by-environment interaction variance may still have a high estimated performance and therefore they may be advanced to the next stage. In this work we not only showed that taking into account the heterogeneity of GEI variances leads to selection of more stable

genotypes but also provide a tool that helps to visualize and identify promising genotypes.

By modeling the heterogeneity of genotype-by-environment interaction variances we account for differences in both environments and genotypes in the variability of responses to environments. Therefore the estimates provide information not only on the cultivars genotypic effect, but also on their stability and by advancing candidates on these criteria breeders will be making better decisions when the objective is to select high performing cultivars across multiple environments.

3.6 References

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CHAPTER 4. GENERAL CONCLUSIONS

In the previous chapters we presented and dicussed our results from two studies that we designed in order to answer two main questions:

do corn yield trials exhibit enough heterogeneity to justify using a different model?

can we improve advancement decisions by modeling heterogeneity?

In the work presented Chapter 2, we used Bayesian inference to study the presence of heterogeneity in GEI and error variances. We found very convincing evidence of variance heterogeneity at both levels. Our results suggested that using a model that takes into account the heterogeneity at both genotype-by-environment interactions and error variances levels may lead to differential genotypic effects estimates. The amount of heterogeneity of variances revealed by our results even in cases where we expected very little variation, demonstrates that by using the homogeneous model the practitioner is violating a very strong assumption.

We used the parameter estimates provided by the heterogeneous model in the first study to design our simulation study. We decided to use the three factors that control the weights used by the Bayesian estimator in both the individual cultivar variance and means estimates: number of environments, repeatability and level of heterogeneity.

Our results from the simulation study, shown in Chapter 3, support what we expected from the description of the posterior estimates provided by Leonard (1975). The posterior mean of the GEI variance was adjusted depending on the variability of the data. When data was simulated from the homogeneous model, the estimates obtained from the heterogeneous model were very similar to the estimates obtained from the homogeneous model. However, when data was simulated from the heterogeneous model, this model largely outperformed the homogeneous model (Figure 3.1).

The performance estimate, given by the posterior mean of the genotypic effect also presented a behavior that was in concordance to our expectations; cultivars with high variance of genotype-by-environment interaction are deemed as unstable. We showed that the precision on the estimation of performance for more unstable cultivars decreased as the repeatability decreased (Figure 3.5), and thus, their estimates were shrunk towards the mean of all cultivars more than stable cultivar (Figure 3.7). This represents an advantage for breeders because even if an unstable cultivar presented high average performance, breeders may want to discard it in favor of a more stable cultivar.

Besides presenting a very clear example of the impact of modeling the heterogeneity of genotype by environment interaction variance on the advancement decision for the simulated data and also real data, our results show that by using the heterogeneous model we are selecting more stable genotypes. We provide a promising visualization tool that allows the comparison of all genotypes taking into account the not only the estimation of performance but also the stability of the cultivars.

4.1 Future Work

This is an outline of what I would like to explore next:

- Increase number of replicates to confirm the observed trend that suggests that modeling heterogeneity lead to improved genetic gain.
- Expanding the scope of the study to evaluate these models in other type of genetic material (e.g. include earlier stages of the breeding process)
- include other type of data such as pedigree information, or spatial.
- evaluate these models on data from more challenged regions outside the U.S.
- study of prior distributions. A sensitivity analysis would help understand how the choice of prior distributions may be affecting the analysis.