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Bayesian inference to the genetic control of drought tolerance in spring wheat

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Abstract

Drought is the main abiotic stress seriously influencing wheat production and quality in the world. Information about the inheritance of drought tolerance is necessary to determine the type of breeding program and to develop tolerant cultivars. In this study, Bayesian inference was used to explore the nature and amount of gene effects controlling yield and its components under water deficit and normal conditions by assessment of contrasting bread wheat parents (Bam and Arta) and derived generations from them. Bayesian inference using the Gibbs Variable Selection (GVS) approach and the Deviance Information Criterion (DIC) were applied to identify the most important gene effects and to compare models including different gene effects. The GVS and DIC provided an efficient way to perform the analysis and to introduce the more appropriate models. It can be inferred from the results that the Bayesian analysis provides a robust inference of genetic architecture of yield and yield components in wheat. Since the additive, dominance and epistatic gene actions involved in the inheritance of agronomic characters under both water stress and normal conditions, methods which utilize all types of gene effects, such as hybrid seed production, may be useful in improving yield and its stability in wheat.

Keywords: Bayesian inference; DIC; GVS; MCMC; Water deficit; Wheat

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Introduction

Bread wheat (*Triticum aestivum* L.) is the most important cereal crop in Iran, where drought is the main abiotic stress which influences wheat production adversely during the grain filling period and dramatically reduces grain yield and quality (Nezhadahmadi *et al*. 2013). The requirement for the improvement of tolerant cultivars to the water deficit stress is clear. The type of breeding program depends on genetic information about the desired traits. An effective instrument to concentrate on the inheritance of traits under study is the utilization of phenotypic information from segregating populations derived from differentiating parental lines, empowering breeders to devise the most proper breeding methodology (Balestre *et al*. 2012). Joint-scaling test has been used to estimate genetic parameters from the generation means and to test the fitting of genetic models consisting of main and epistatic effects (Mather and Jinks 1971). This methodology can be considered as a model selection issue. Whether a model with both main and epistatic effects is superior to a simpler model can be evaluated by the model selection. Restrictions of degrees of freedom to the number of parameters of the model and the biased estimations of main and epistatic effects are limitations of this method (Balestre *et al*. 2012). An alternative approach to resolving these limitations is to perform Bayesian inference and model selection. In the Bayesian approach, the information about the parameter (as a prior distribution) is combined to the information taken from the data to obtain the posterior distribution. Posterior distribution covers all of the accessible information for inference of the genetic structure of the desired traits and represents the uncertainty about the parameter after the data was considered (Mathew *et al*. 2012). Utilization of Markov chain Monte Carlo (MCMC) technique is the suitable computational method to take samples from the posterior distributions. Common MCMC methods used for sampling are the Metropolis–Hastings (M-H) (Metropolis *et al*. 1953; Hasting 1970) and the Gibbs sampler (Geman and Geman 1984) algorithms. The Gibbs sampler is a special case of M-H sampling that draws sample from the completely conditional posteriors (Lynch 2007).

The main issue in the model selection is the choice of selection criteria. Several distinct techniques have been provided and examined for the model selection. Generally, adjusted R^2 (Neter *et al*. 1996) and Akaike information criterion (AIC) (Akaike 1973) are used in conventional statistics. In contrast to the conventional approaches, the deviance information criterion (DIC) (Spiegelhalter *et al*. 2002) is presented in the Bayesian statistics. DIC was proposed by Spiegelhalter *et al*. (2002) as a generalization of the AIC. This criterion can be used for the model comparison and selection of appropriate models (Spiegelhalter *et al*. 2002). DIC, as a suitable criterion, has been applied for assessing hierarchical models in the studies related to genotype by environment interaction (Fikse *et al*. 2003; Rekaya *et al*. 2003) and multiple quantitative trait loci (QTL) mapping (Shriner and Yi 2009). Calculation of DIC is based on the samples taken from the posterior distribution by the MCMC algorithm. DIC calculates the posterior predictive error by controlling the deviance related to model fitting (Shriner and Yi 2009). Shriner and Yi (2009) presented application of DIC in multiple QTL mapping and concluded that DIC is a proficient approach to model selection.

The Gibbs sampling based techniques are the algorithms that efficiently search the model space and provide estimating of posterior variable inclusion probabilities. Stochastic search variable selection (SSVS) (George and McCulloch 1993) and Gibbs variable selection (GVS) (Dellaportas *et al*. 2002) are some of the Gibbs based approaches for variable and model selection. When we use GVS, the primary goal is to find some effects that are more important than the others, allowing breeders to focus on the most significant effects. The great ability of the GVS to identify the important effects in the model is due to the use of binary vector and efficient MCMC algorithm (Ntzoufras 2011). MCMC techniques, encouraged by the development of the Gibbs sampling algorithm, has been used for the Bayesian inference in quantitative genetics (Wang *et al*. 1993; Jensen *et al*. 1994; Sorensen *et al*. 1995). Waldmann *et al*. (2008) introduced a fast hybrid Gibbs sampler to estimate additive and dominance variances in the mixed model for Scots pine. Another MCMC sampling algorithm in the mixed model was proposed by Mathew *et al*. (2012) to estimate genetic parameters for the data from spring barley lines. Xu (2003) proposed a Bayesian approach to estimate genetic effects related to markers in a barley double haploid population and demonstrated that the Bayesian strategy can be considered as an alternative or even better QTL mapping method. Balestre *et al.* (2012) used the proposed Bayesian method of Xu (2003) to study the genetic control of resistance to gray leaf spot in maize. They showed that genetic control of this trait was mostly additive and concluded that Bayesian shrinkage analysis is a brilliant way to deal with the complex models. Yi *et al*. (2005) used Bayesian model selection approach to identify epistatic QTLs for obesity trait in the experimental crosses from two inbred lines of mice. They proposed an effective MCMC algorithm using the Gibbs and Metropolis-Hasting samplers to obtain the posterior distribution and showed that Bayesian model selection approach is a comprehensive way to QTL mapping. Yi *et al*. (2007) generalized the Bayesian model selection method for epistatic QTL mapping to models consisting environmental effects and gene by environment interaction and proposed a new MCMC algorithm to study the posterior distribution of unknown parameters.

In this study, Bayesian inference using the GVS approach and DIC was applied to explore the nature and amount of gene effects and to identify the most important gene effects related to justification of models for yield and yield components of bread wheat under water deficit and normal conditions.

Materials and Methods

Plant materials and experiments

The plant materials consisted of the generations derived from a cross between two Iranian spring wheat cultivars, Bam (P_1, as a drought tolerant parent) and Arta (P_2, as a drought sensitive parent). Two field experiments were carried out across two years (2013 and 2014) at the research station of Faculty of Agriculture, University of Tabriz, Iran (38˚0′ N, 46˚4′ E, 1361 asl). Seven generations during 2013 (P_1, P_2, F_2, F_3, F_4, BC_1S_1, BC_2S_1) and 10 generations during 2014 (P_1, P_2, F_2, F_3, F_4, F_5, BC_1S_1, BC_2S_1, BC_1S_2, BC_2S_2) were evaluated. Split plot designs based on randomized complete blocks with two and three replications in 2013 and 2014 growing seasons, respectively, were carried out in which main plots assigned to irrigation treatments (well watered and cessation of irrigation at the pollination stage) and sub-plots given to the generations. Experimental units had a different number of plants, depending on the genetic uniformity of each generation. For the non-segregating generations (P_1 and P_2) the experimental units contained of 30 plants, while for the segregating generations 90 and 60 were used during 2013 and 2014 growing seasons, respectively. The number of families used for different generations are presented in Table 1. The length of each row was 90 cm and the seeds were planted 5 cm apart with 15 cm row to row spacing. At the beginning and end of the planting rows, marginal rows were considered. All field preparations and agronomical operations from sowing until harvest were carried out in accordance with conventional practices. During harvest, marginal effects were considered and 2/3 of the plants in the sub-plots were randomly chosen to measure grain yield (g/plant) and its components. Before performing analysis of variance, normality test of residuals was conducted. Before conducting the combined analysis, Bartlett test was used to assess the homogeneity of experimental errors. Analysis of variance was first performed as combined across years and then, based on the significance of the genotype by year interaction, individually for each year. The statistical analyses were performed by the SAS software (SAS 2002).

Bayesian modeling

It is assumed that the generation means follow the linear model bellow:

$$Y_i = \beta_0 + \sum_{j=1}^{p=5} \beta_j x_{ij} + e_i$$

$$Y_i = \beta_0 + \beta_1 x_{i1} + \ldots + \beta_5 x_{i5} + e_i$$

$$i = 1, \ldots, n$$

Table 1. Number of families for different generations obtained from the cross between Bam and Arta wheat cultivars.

Generation	Year	
	2013	2014
F_3	45	126
F_4	37	53
F_5	-	52
BC_1S_1	17	13
BC_2S_1	19	12
BC_1S_2	-	20
BC_2S_2	-	20

where Y_i is the observed phenotypic value of generation *i*, β_0 is the grand mean, x_{i1} to x_{i5} are the coefficients related to additive ([a]), dominance ([d]), additive × additive ([aa]), additive × dominance ([ad]) and dominance × dominance ([dd]) effects, respectively, $\boldsymbol{\beta} = (\beta 1, \beta 2, \ldots \beta 5)^t$ are the coefficients of the model and are the expectation of the effects ([a], [d], [aa], [ad], [dd]), and e_i is the residual error assuming $N\left(0, \sigma^2\right)$.

In the Bayesian approach, the distribution of dependent variable vector **Y** is specified conditional on the parameters $\boldsymbol{\beta}$ and σ^2:

$$\mathbf{Y} \mid \boldsymbol{\beta}, \sigma^2 \sim N\left(\mathbf{X}\boldsymbol{\beta}, \sigma^2 \mathbf{I}_n\right)$$

where, $\mathbf{X} = \left(X_1, \ldots, X_p\right)^t$ and $\mathbf{I}_n$ is an identity matrix.

In the Bayesian inference the supposition with regards to the model characterize a likelihood function and prior distributions are allotted to the unknown model parameters. There is prior uncertainty about each genetic effects ought to be incorporated into the model. It is assumed that all parameters have an independent prior structure (Ntzoufras 2011):

$$f(\beta, \tau) = \prod_{j=1}^{p} f(\beta_j) f(\tau)$$

$$\beta_j \sim N\left(\mu_{\beta_j}, c_j^2\right) \text{for} j = 1, \ldots, p$$

and

$$\tau \sim gamma(a, b)$$

In this study, normal distribution with mean zero ($\mu_{\beta_j} = 0$) and unique variance was assigned to each gene effect as a prior distribution. The distribution devoted to each effect was further assigned a vague prior ($c_j^2 = 10^4$) so that the variance can be estimated from the data. In order to be compatible with WinBUGS notation, σ^2 was substituted by the corresponding precision parameter τ (Ntzoufras 2002). The prior mean and variance related to the gamma prior distribution of the precision parameter were determined by the following formula:

$$E(\tau) = \frac{a}{b} \text{ and}$$

$$Var(\tau) = \frac{a}{b^2}$$

Similarly, for τ the low prior parameter values (a= b = 0.001) were used making its prior mean equal to one and its prior variance large.

The purpose of Bayesian analysis is to infer the posterior distribution and the conditional distribution of the parameters, considering the observed data. In this study, the sampling was performed by the Gibbs sampler algorithm (Geman and Geman 1984). Gibbs sampling includes an iterative process to draw samples from the posterior distribution for each parameter and repeats this updating process (Lynch 2007). The length of the Markov chain contained 8000 iterations. The sampled parameter values from the first 1000 iterations of the chain (burn-in period) were discarded from the analysis. From that point on, the observations were saved for every 50 iterations to diminish serial correlation. In order to follow the sampled parameters from the posterior distribution, it is imperative that the chain is converged with the stationary distribution (Ntzoufras 2011). In this study the trace plots were used to assess the convergence of the algorithm.

Calculation of DIC

DIC was introduced by Spiegelhalter *et al.* (2002) as a measure of model comparison and adequacy (Ntzoufras 2011):

$$DIC(m) = 2\overline{D(\theta_m, m)} - D(\bar{\theta}_m, m) = D(\bar{\theta}_m, m) + 2p_m$$

where, $D(\theta_m, m) = -2\log f(y \mid \theta_m, m)$ is the posterior mean and p_m is the number of effective parameters for the model m: $p_m = \overline{D(\theta_m, m)} - D(\bar{\theta}_m, m)$; $\bar{\theta}_m$ is the posterior mean of the parameters involved in the model *m*.

GVS

In order to setup GVS, we used structural properties of the model described by Ntzoufras (2011). Vector of binary indicators γ in the issues relating to Bayesian variable and model selection is applied to determine the most effective combination of the variables in the model (Ntzoufras 2011). Therefore, the linear model can be considered as:

$$y = \sum_{j=1}^{p} \gamma_j X_j \beta_j$$

Considering the partitioning of β into β_γ (included variables) and $\beta_{\backslash\gamma}$ (excluded variables), then the prior distribution of $f\left(\beta \mid \gamma\right)$ was also divided into $f\left(\beta_\gamma \mid \gamma\right)$ (model parameter prior) and $f\left(\beta_{\backslash\gamma} \mid \beta_\gamma, \gamma\right)$ (pseudo-prior). Therefore, the posterior distribution for the model parameters by assuming independence of β_γ and $\beta_{\backslash\gamma}$ were calculated as follows:

$$f\left(\beta_j \mid \gamma_j, \beta_{\backslash j}, y\right) \propto \begin{cases} f\left(y \mid \gamma, \beta\right) N\left(0, \sum_j\right) & \gamma_j = 1 \\ N\left(\overline{\mu_j}, \overline{S_j}\right) & \gamma_j = 0 \end{cases}$$

The hyper-parameters $\overline{\mu_j}$ and $\overline{S_j}$ are parameters of the pseudo-prior distribution. Here, the proposed parameters were estimated by a pilot MCMC run of the full model. The posterior distribution for γ_j is Bernoulli distribution with success probability of ($\frac{O_j}{1+O_j}$):

$$\gamma_j \mid \beta, \gamma_{\backslash j}, y \sim \text{Bernoulli}\left(\frac{O_j}{1+O_j}\right)$$

$$\text{with } O_j = \frac{f\left(\gamma_j = 1 \mid \gamma_{\backslash j}, \beta, y\right)}{f\left(\gamma_j = 0 \mid \gamma_{\backslash j}, \beta, y\right)} = \frac{f\left(y \mid \beta, \gamma_j = 1, \gamma_{\backslash j}\right)}{f\left(y \mid \beta, \gamma_j = 0, \gamma_{\backslash j}\right)} \frac{f\left(\beta \mid \gamma_j = 1, \gamma_{\backslash j}\right)}{f\left(\beta \mid \gamma_j = 0, \gamma_{\backslash j}\right)} \frac{f\left(\gamma_j = 1, \gamma_{\backslash j}\right)}{f\left(\gamma_j = 0, \gamma_{\backslash j}\right)}$$

where $\gamma_{\backslash j}$ means all terms of γ except γ_j. From the MCMC output, we estimated the posterior inclusion probabilities of each variable as follows:

$$f\left(\gamma_j = 1 \mid y\right) = \sum_{\gamma_{\backslash j} \in \{0,1\}^{p-1}} f\left(\gamma_j = 1, \gamma_{\backslash j} \mid y\right)$$

using the simple estimator of

$$f\left(\gamma_j = 1 \mid y\right) = \frac{1}{T - B} \sum_{t=B+1}^{T} I\left(\gamma_j^{(t)} = 1\right)$$

where, T and B are the total and burn-in iterations of the algorithm.

We implemented the WinBUGS software (Speigelhalter *et al.* 2003) to perform GVS and calculate DIC of the models. WinBUGS is a freely distributed package that provides several methods for summarizing and interpreting the posterior samples numerically and graphically and monitoring the convergence of the Markov chain.

Results

Results of the combined analysis with considering the constant and random effects for generations and years, respectively, were presented in Table 2. The effects of year, water regime (except for grain number) and generation were significant suggesting the existence of differences within these factors in terms of grain yield and its components. The year × generation interaction was significant for all of the traits under study suggesting that generations had no stable reaction to the climatic conditions of different years. The three order interaction of year × water regime × generation was also significant for grain yield and spike weight, indicating that generations showed no similar reaction to the different water regimes and weather conditions in terms of these two characters.

Table 2. Combined analysis of variance for the studied traits of different generations obtained from the cross between Bam and Arta bread wheat cultivars under two water regimes in two growing seasons.

Sources of variation	Degrees of freedom	Mean squares				
		Grain yield	1000 grain weight	Grain number	Spike length	Spike weight
Year (Y)	1	4.66^{**}	801.79^{**}	1443.25^{**}	55.90^{**}	61.22^{**}
Replication/Y	3	0.22^{**}	201.87^{**}	2246.85^{**}	0.61^{**}	4.03^{**}
Water regime (W)	1	2.79^{**}	479.38^{**}	760.98^{ns}	0.59^{*}	4.79^{**}
Y × W	1	0.01^{ns}	0.08^{ns}	1314.97^{*}	3.78^{**}	0.64^{ns}
W × Rep/Y	3	0.33^{**}	46.94^{**}	827.74^{*}	0.68^{**}	1.31^{**}
Generation (G)	9	3.33^{*}	88.08^{*}	3071.23^{**}	4.41^{**}	18.06^{**}
W × G	9	0.32^{**}	10.95^{ns}	380.71^{ns}	0.03^{ns}	0.51^{**}
Y × G	6	0.46^{**}	52.79^{**}	1261.86^{**}	1.27^{**}	4.89^{**}
Y × W × G	6	0.38^{**}	6.84^{ns}	416.87^{ns}	0.14^{ns}	0.63^{**}
Error	48	0.05	7.17	203.29	0.10	0.17
CV(%)		10.22	10.48	7.09	3.35	8.42

^{ns}, *, **: not significant and significant at 0.05 and 0.01 probability levels, respectively.

Further analyses were performed for each year separately because there were three more generations in the second year (Tables 3 and 4). Analysis of variance showed that the effect of water regime was significant for the grain yield and 1000 grain weight in the first year but not in the second year. However, significant genotypic effects were observed for all traits in both years. The interaction of water regime × generation was only significant for grain yield in the first year and for grain yield, 1000 grain weight and spike weight in the second year indicating different reaction of generations to non-stress and terminal water stress conditions for the above mentioned traits.

Table 3. Analysis of variance for grain yield and its components using different generations obtained from the cross between Bam and Arta bread wheat cultivars under two water regimes in 2013.

Sources of variation	Degrees of freedom	Mean squares				
		Grain yield	1000 grain weight	Grain number	Spike length	Spike weight
Replication	1	0.43^{ns}	574.67^{ns}	6431.47^{ns}	1.10^{ns}	3.70^{ns}
Water regime (W)	1	0.77^{ns}	178.26^{ns}	76.95^{ns}	0.72^{ns}	0.02^{ns}
Main plot error	1	0.18	22.95	1422.00	0.05	1.09
Generation (G)	6	0.79^{**}	54.79^{**}	1560.42^{*}	1.38^{**}	4.56^{**}
W × G	6	0.67^{**}	12.08^{ns}	668.17^{ns}	0.05^{ns}	0.31^{ns}
Sup-plot error	12	0.11	16.24	350.55	0.18	0.45
CV(%)		14.08	9.71	15.73	5.13	10.01

^{ns}, *, **: not significant and significant at 0.05 and 0.01 probability levels, respectively; $^{+}$since main plot error was not significant in the first year, it was pooled with the sub-plot error to test the water treatment and replication.

Trace plot for parameter [a] of the grain yield model in 2013 under non-stress condition was depicted in Figure 1 as an example. Based on the trace plots, it can be inferred that all generated values were within a parallel zone and there were not obvious tendencies or periodicities, so the parameters of interest were calculated with the increased precision. The posterior summary estimates of parameters (mean, standard deviation, Monte Carlo error, selected percentiles) were provided in Table 5. Monte Carlo error was estimated using the batch mean method (Ntzoufras 2011). Results of the model comparisons and best-fitted models using the DIC were provided in Tables 6 and 7, respectively. The lower the DIC, the higher is the evidence that the model is the best model. Nevertheless, Spiegelhalter *et al.* (2002) recommended that models with DIC difference within the minimum value lower than two should be considered as similarly well. Thus, the results of model comparisons using the DIC were presented in Table *7*.

Table 4. Analysis of variance for grain yield and its components using different generations obtained from the cross between Bam and Arta bread wheat cultivars under two water regimes in 2014.

		Mean squares				
Sources of variation	Degrees of freedom	Grain yield	1000 grain weight	Grain number	Spike length	Spike weight
Replication	2	0.07^{ns}	12.37^{ns}	154.53^{ns}	0.31^{ns}	0.13^{ns}
Water regime (W)	1	2.32^{ns}	343.57^{ns}	3135.35^{ns}	5.76^{ns}	5.71^{ns}
Main plot error	2	0.33	52.75	530.61	1.00	0.72
Generation (G)	9	3.42**	97.51**	3225.20**	5.34**	22.79**
W × G	9	0.06*	8.64*	66.84^{ns}	0.10^{ns}	0.28**
Sub-plot error	36	0.02	3.52	41.35	0.08	0.07
CV(%)		6.31	6.72	7.57	2.82	4.74

^{ns}, *, **: not significant and significant at 0.05 and 0.01 probability levels, respectively; $^{+}$since main plot error was not significant in the second year, it was pooled with the sub-plot error to test the water treatment and replication.

Trace plot for parameter [a] of the grain yield model in 2013 under non-stress condition was depicted in Figure 1 as an example. Based on the trace plots, it can be inferred that all generated values were within a parallel zone and there were not obvious tendencies or periodicities, so the parameters of interest were calculated with the increased precision. The posterior summary estimates of parameters (mean, standard deviation, Monte Carlo error, selected percentiles) were provided in Table 5. Monte Carlo error was estimated using the batch mean method (Ntzoufras 2011). Results of the model comparisons and best-fitted models using the DIC were provided in Tables 6 and 7, respectively. The lower the DIC, the higher is the evidence that the model is the best

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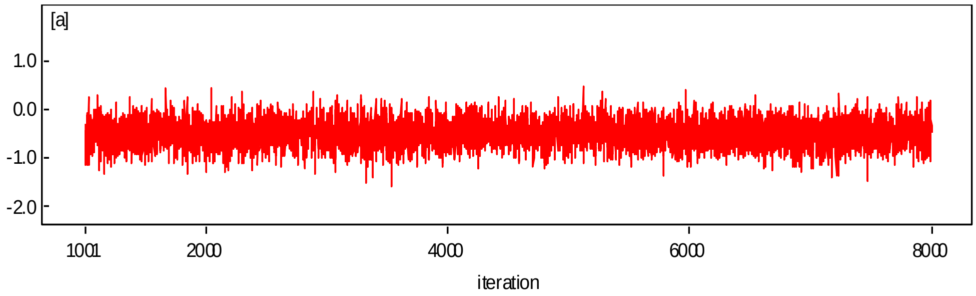

Figure 1. Trace plot for the [a] effect of the grain yield model estimated from different generations of the cross between Bam and Arta bread wheat cultivars at the normal condition in the 2013 growing season.

Table 5. Posterior summaries for parameters of the model estimated from different generations of the cross between Bam and Arta wheat cultivars at two water regimes in two growing seasons.

Trait	Parameter	Mean	SD	Monte Carlo error	2.5%	Median	97.5%
Grain yield (2013; Normal)	[m]	2.67	0.24	0.002	2.20	2.67	3.13
	[a]	1.14	0.39	0.005	0.37	1.14	1.92
	[d]	-4.76	1.78	0.019	-8.23	-4.78	-1.28
	[aa]	-0.03	0.31	0.003	-0.63	-0.03	0.58
	[ad]	-1.31	1.74	0.024	-4.77	-1.30	2.07
	[dd]	6.29	3.20	0.033	-0.005	6.28	12.56
Grain yield (2013; Stress)	[m]	2.00	0.22	0.002	1.58	2.00	2.43
	[a]	0.12	0.35	0.004	0.81	0.12	-0.57
	[d]	-1.91	1.60	0.017	-5.03	-1.96	1.23
	[aa]	-0.26	0.28	0.003	-0.80	-0.26	0.29
	[ad]	2.56	1.56	0.021	-0.56	2.56	5.62
	[dd]	3.85	2.89	0.030	-1.85	3.85	9.48
Grain yield (2014; Normal)	[m]	2.57	0.05	5.14E-4	2.48	2.57	2.65
	[a]	1.10	0.12	0.001	0.86	1.10	1.34
	[d]	1.25	0.11	0.001	1.04	1.25	1.46
	[aa]	0.28	0.13	0.001	0.04	0.28	0.53
	[ad]	3.33	0.74	0.010	1.87	3.33	4.78
	[dd]	-8.08	0.49	0.005	-9.04	-8.08	-7.15
Grain yield (2014; Stress)	[m]	1.92	0.04	5.02E-4	1.84	1.92	2.01
	[a]	1.08	0.11	0.001	0.84	1.08	1.31
	[d]	1.34	0.10	0.001	1.13	1.34	1.54
	[aa]	0.62	0.12	0.001	0.38	0.62	0.86
	[ad]	3.22	0.73	0.010	1.79	3.22	4.64
	[dd]	-3.99	0.47	0.005	-4.93	-3.99	-3.07
Grain number (2013)	[m]	67.390	6.55	0.085	54.45	67.47	80.21
	[a]	22.94	12.70	0.159	-1.37	23.98	48.74
	[d]	136.10	41.84	0.511	54.93	135.40	217.80
	[aa]	45.91	11.68	0.138	23.19	45.95	68.96
	[ad]	-9.15	54.48	0.756	-116.20	-9.19	97.55
	[dd]	-160.0	71.65	0.785	-304.00	-160.10	-21.48
Grain number (2014)	[m]	88.53	1.24	0.014	86.12	88.54	90.95
	[a]	30.29	3.32	0.045	23.66	30.28	36.86
	[d]	4.07	2.97	0.038	-1.83	4.09	9.94
	[aa]	-4.23	3.45	0.042	-10.97	-4.21	2.56
	[ad]	59.54	20.13	0.289	19.68	59.67	98.95
	[dd]	-178.0	13.47	0.160	-204.50	-177.80	-152.30
Spike length (2013)	[m]	8.84	0.18	0.002	8.47	8.84	9.20
	[a]	0.55	0.30	0.003	-0.04	0.56	1.15
	[d]	-3.30	1.38	0.015	-5.96	-3.31	-0.59
	[aa]	0.23	0.24	0.002	-0.24	0.23	0.71
	[ad]	0.09	1.35	0.018	-2.57	0.09	2.74
	[dd]	4.06	2.48	0.026	-0.85	4.06	8.89
Spike length (2014)	[m]	9.80	0.05	5.77E-4	9.70	9.80	9.90
	[a]	1.10	0.13	0.001	0.83	1.10	1.38
	[d]	2.29	0.12	0.001	2.05	2.29	2.53
	[aa]	-0.68	0.14	0.001	-0.96	-0.68	-0.40
	[ad]	3.22	0.84	0.012	1.55	3.23	4.87
	[dd]	-4.15	0.55	0.006	-5.25	-4.15	-3.09
1000 grain weight (2013)	[m]	35.05	1.37	0.017	32.38	35.06	37.74
	[a]	0.58	2.26	0.029	-3.91	0.58	5.04
	[d]	-88.24	10.10	0.115	-107.80	-88.34	-68.25
	[aa]	-12.45	1.82	0.021	-16.01	-12.45	-8.83
	[ad]	7.03	10.10	0.140	-12.93	7.031	26.76
	[dd]	130.40	18.22	0.194	94.30	130.40	165.7

Table 5 Continued

Trait	Parameter	Mean	SD	Monte Carlo error	2.5%	Median	97.5%
1000 grain weight (2014; Normal)	[m]	35.24	0.52	0.005	34.24	35.25	36.26
	[a]	4.30	1.40	0.018	1.49	4.31	7.04
	[d]	-8.00	1.24	0.016	-10.47	-7.99	-5.55
	[aa]	-6.02	1.44	0.017	-8.84	-6.01	-3.17
	[ad]	-0.44	8.54	0.124	-17.28	-0.44	16.31
	[dd]	56.06	5.63	0.061	-67.17	-56.04	-45.26
1000 grain weight (2014; Stress)	[m]	26.65	0.52	0.005	25.65	26.65	27.67
	[a]	5.33	1.40	0.018	2.52	5.34	8.07
	[d]	-2.75	1.24	0.016	-5.21	-2.74	-0.30
	[aa]	-1.08	1.44	0.017	-3.90	-1.07	1.76
	[ad]	4.44	8.53	0.124	-12.38	4.44	12.19
	[dd]	-13.40	5.63	0.061	-24.51	-13.38	-2.60
Spike weight (2013)	[m]	4.50	0.26	0.003	3.99	4.50	5.02
	[a]	1.18	0.42	0.005	0.33	1.18	2.01
	[d]	-6.36	1.93	0.022	-10.09	-6.38	-2.57
	[aa]	0.08	0.34	0.004	0.74	0.08	-0.58
	[ad]	0.54	1.89	0.026	4.28	0.54	-3.14
	[dd]	10.22	3.46	0.037	3.34	10.22	16.98
Spike weight (2014; Normal)	[m]	6.00	0.10	0.001	5.80	6.00	6.20
	[a]	2.47	0.27	0.003	1.92	2.47	3.01
	[d]	3.15	0.24	0.003	2.67	3.16	3.63
	[aa]	-0.91	0.28	0.003	-1.46	-0.91	-0.35
	[ad]	5.42	1.67	0.024	2.12	5.42	8.70
	[dd]	-21.85	1.10	0.011	24.02	-21.85	-19.74
Spike weight (2014; Stress)	[m]	4.94	0.09	0.001	4.76	4.94	5.12
	[a]	2.41	0.24	0.003	1.91	2.41	2.90
	[d]	3.24	0.21	0.002	2.82	3.26	3.69
	[aa]	-0.34	0.25	0.003	-0.83	-0.33	0.16
	[ad]	5.27	1.51	0.021	2.28	5.27	8.23
	[dd]	-15.12	0.99	0.010	-17.09	-15.12	-13.21

Posterior densities for parameters of the grain yield model at both water regimes in the 2013 growing season were depicted as examples in Figures 2 and 3. The posterior distributions related to non-important effects displayed high spike at zero, whereas the posterior distributions of the most important ones were well placed away from zero (Ntzoufras 2011). The posterior distributions related to some effects were bimodal. However, the corresponding posterior inclusion probabilities indicate that these effects should be included or excluded from the model (Table 8). Posterior variable inclusion probabilities were presented in Table 8. Following the Fouskakis *et al*. (2009), we eliminated variables with posterior variable inclusion probabilities lower than 0.20.

Grain yield

It can be seen that in the first year (2013) and under non-stress water regime, models including additive effects compared to the models without this effect had smaller DICs (Table 7). Therefore, it seems that additive effect improves model fitting and provides better fit to the data of grain yield. Of the fitted models, the three-parameter model [m] [a] [d] with the lowest estimated DIC (5.28) was identified as the best model (Table 6). Under the stress condition, epistatic effects were also added to the model, thus the six-parameter model was selected as the best model and had the best fit and the lowest DIC. The importance of the epistatic gene effects for grain yield was previously reported by Novoselovic *et al*. (2004), Khattab *et al*. (2010) and Ijaz and Kashif (2013). In 2014, under both conditions, DIC differences in the models including dominance × dominance epistasis with those without this effect were high and the six-parameter model was the best model (Tables 6 and 7). The sign of dominance [d] and dominance × dominance [dd] gene effects were opposite, suggesting duplicate type of interaction for the grain yield. This kind of epistasis generally prevents the improvement through selection. Based on the GVS results, under non-stress condition in 2013, the additive effect was the most important effect in the model and [d], [ad] and [dd] were also included in the model having posterior probabilities of 0.59, 0.23 and 0.44, respectively (Figure 2 and Table 8). Under water stress condition in 2013 and normal condition in 2014, [aa] had very low posterior probabilities and was eliminated from the model (Table 8). Under water stress condition in 2014, all effects had very high probabilities and were included in the model (Table 8).

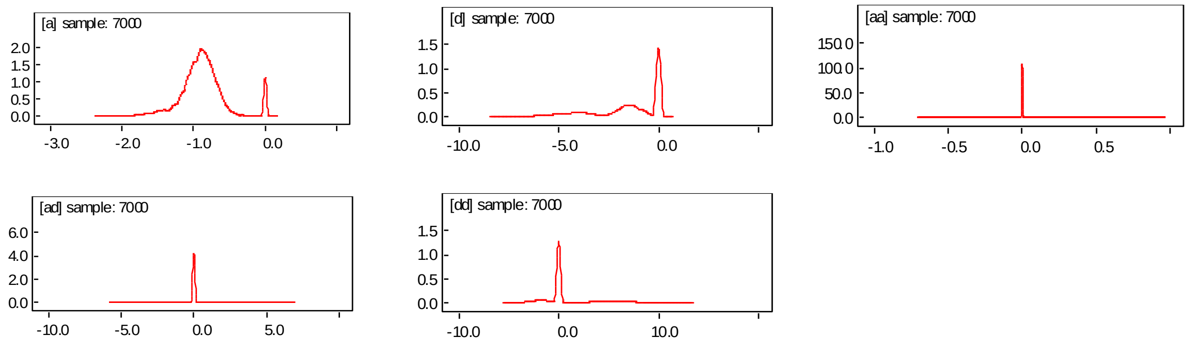

Figure 2. Posterior densities of the model parameters for grain yield estimated from different generations of the cross between Bam and Arta bread wheat cultivars at the normal condition in the 2013 growing season.

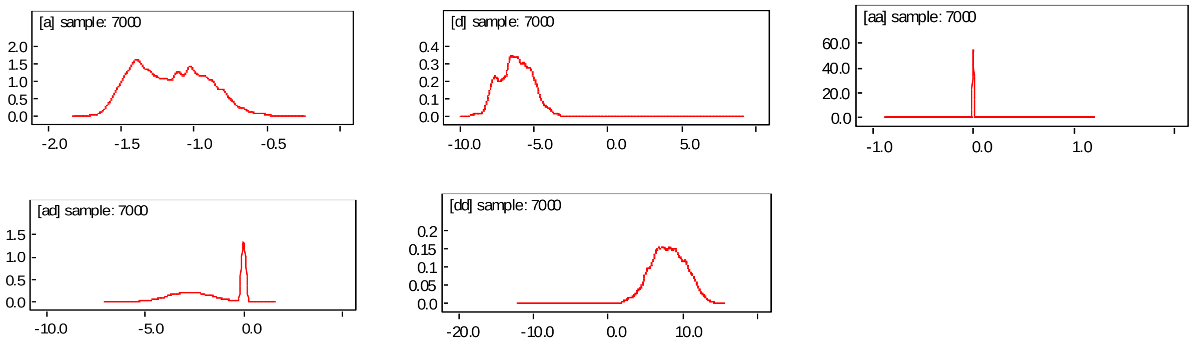

Figure 3. Posterior densities of model parameters for grain yield estimated from different generations of the cross between Bam and Arta bread wheat cultivars at the water stress condition in the 2013 growing season.

Table 6. The best models fitted for different generations of the cross between Bam and Arta bread wheat cultivars at two water regimes in two growing seasons.

Traits	The best model	Dbar	Dhat	pD	DIC
Yield (2013; Normal)	[m][a][d]	5.073	4.864	0.210	5.283
Yield (2013; Stress)	[m][a][d][aa][ad][dd]	0.099	-0.207	0.307	0.406
Yield (2014; Normal)	[m][a][d][aa][ad][dd]	13.861	41.747	-27.886	-14.025
Yield (2014; Stress)	[m][a][d][aa][ad][dd]	12.267	43.765	-31.499	-19.232
Grain number (2013)	[m][a][aa][dd]	49.114	48.854	0.260	49.375
Grain number (2014)	[m][a][d][dd]	82.549	82.362	0.187	82.736
Spike length (2013)	[m][a]	-2.034	-2.043	0.008	-2.026
Spike length (2014)	[m][a][d][aa][ad][dd]	24.742	38.424	-13.682	11.060
1000 grain weight (2013)	[m][d][aa][dd]	33.569	33.291	0.278	33.846
1000 grain weight (2014; Normal)	[m][a][d][aa][dd]	48.209	49.137	-0.928	47.280
1000 grain weight (2014; Stress)	[m][a][d][aa][dd]	44.666	45.562	-0.896	43.770
Spike weight (2013)	[m][a][d][aa][dd]	6.361	6.110	0.251	6.612
Spike weight (2014; Normal)	[m][a][d][aa][ad][dd]	36.109	39.894	-3.785	32.323
Spike weight (2014; Stress)	[m][a][d][aa][ad][dd]	36.235	39.861	-3.626	32.608

1000 grain weight

For 1000 grain weight in 2013, the differences among the DIC of the models were relatively low. However, the models including [aa] effect had lower DIC. Among the fitted models, the four-parameter model [m] [d] [aa] [dd] had the lowest DIC (Table 7). Under normal condition in 2014, the model consisting additive and dominance effects had lower DIC. The models including [a] was better than those without this effect under water stress condition (Table 7). Based on the results of GVS for 1000 grain weight in 2013, the posterior distribution for [d], [aa] and [dd] were very far from zero and their posterior inclusion probabilities were 100%. The [a] and [ad] effects with posterior inclusion probabilities of 0.26 and 0.63 were also included in the model (Table 8). In 2014, under normal condition, the most important effects in the model were [a] and [d] with the posterior inclusion probabilities of 100%, that were included in the model along with [aa] and [ad] (Table 8). Under water stress condition, [a] was the most important effect and [d], [ad] and [dd] also remained in the model with the posterior inclusion probabilities of 0.29, 0.49 and 0.71, respectively (Table 8).

Grain number

For grain number in 2013, the models consisting additive effect had better fit. The [d] effect did not contribute to the best fitted model and finally the four-parameter model [m] [a] [aa] [dd] with the lowest DIC was identified as the best model (Table 7). Similarly, the models including [a] were better than the others in 2014. Among the models with [a], the models consisting [a] and [dd] simultaneously showed the lowest DIC and the four-parameter model of [m] [a] [d] [dd] was selected as the best model (Table 7). The results of GVS for grain number in 2013 showed that all effects had posterior inclusion probabilities above 50% and [a], [d] and [aa] were the most important parameters (Table 8). In 2014, all effects were included in the model and [a], [d] and [dd] were identified as the most important effects in the model (Table 8).

Spike length

For spike length in 2013, the models containing [a] effect had the lowest DIC and the simple model [m] [a] was identified as the best model (Tables 6 and 7). In 2014, the models including [dd] and [aa] showed better fit and the six-parameter model had the lowest DIC and was selected as the best model (Table 7). Based on the GVS results in 2013, all effects except [aa] remained in the model and [a] was the most important effect in the model (Table 8). In 2014, all effects had posterior inclusion probabilities of above 0.99 and were included in the model (Table 8).

Spike weight

In 2013, the models with the [a] effect were better than those without this effect and finally the five-parameter model of [m] [a] [d] [aa] [dd] with the lowest DIC was considered as the best model (Table 7). In 2014, under both conditions, the six-parameter model was regarded as the best model (Table 7). Based on the GVS results in 2013, [aa] was excluded from the model and [a] was recognized as the most important effect (Table 8). Under normal condition in 2014, all effects with posterior inclusion probabilities of above 0.78 were included in the model (Table 8). Under stress condition, additive effect was the most important effect and along with [d], [ad] and [dd] remained in the model with posterior inclusion probabilities of 0.29, 0.49 and 0.71, respectively (Table 8)

Discussion

The joint- scaling test proposed by Mather and Jinks (1971) is ordinarily used for parameter estimation in the investigation of the hereditary model. However, this approach exhibits several disadvantages that may limit its application. Specifically, this approach cannot deal with the models where the number of the parameters is larger than or equal the number of observations (Balestre *et al*. 2012). Moreover, the epistatic effects are considered as factors for non-adjustment of the additive-dominance model. Since the main and epistatic effects are estimated without error in the least square model, it is likely that these effects are over- or under-estimated (Balestre *et al*. 2012). An alternative way to overcome these limitations is to use Bayesian inference and perform shrinkage analysis or model selection (Balestre *et al*. 2012). In the shrinkage analysis, instead of removing non-significant variables, all of the model variables are considered but non-significant variable estimates shrink toward zero (Xu 2007). Bayesian model selection methods are powerful and effective way to determine the most important effects in the model (Ntzoufras 2011). Among the definitely known favorable characteristics of Bayesian inference over conventional analysis, the potential utilization of prior distributions, adaptability in complex models, accurate credibility intervals and smaller squared error estimators can be remarkable (Balestre *et al*. 2012). Bayesian inference considers prior information so that to inform the current model, prior knowledge or results of a previous model can be used; it makes this approach extremely appealing in terms of inference on genetic parameters (Xu, 200). The utilization of Bayesian inference to study trait inheritance has been valuable in plant breeding (Mathew *et al*. 2012; Omer *et al*. 2014). In the least square method, the unknown parameters are fixed and the only source of randomness is distribution of the data, whereas Bayesian inference is uncertain about the parameters of interest and tackles them as random variables, so prior distributions are defined for parameters of the model (Mettle *et al*. 2016). In spite of the fact that the least square method is adequate for parameter estimation, estimates obtained from the Bayesian method have very small standard errors, making the Bayesian method more robust (Mettle *et al*. 2016). Also, the use of prior distribution is the main advantage of Bayesian inference. Furthermore, the Bayesian method results in a posterior distribution that incorporates prior distribution with the information from the data and provides comprehensive information about the parameters after analyzing the data. The least square method is less flexible in that specific assumption about the data (Elster and Wubbeler 2016). The objective of the DIC is to determine the model that best clarifies the observed data as well as minimizes uncertainty about future observations (Shriner and Yi 2009). The minimum DIC shows the model with the most effective combinations of variables. The DIC approach provides a comprehensive solution to model comparison using the posterior distribution. In

Table 7. Fitted models and their DIC values for grain yield and its components using different generations of the cross between Bam and Arta wheat cultivars at two water regimes in two growing seasons.

Model	Yield (2013; Normal)	Yield (2013; Stress)	Yield (2014; Normal)	Yield (2014; Stress)	1000 grain weight (2013)	1000 grain weight (2014; Normal)	1000 grain weight (2014; Stress)
[m][a]	5.295	9.463	20.462	18.885	37.542	50.116	46.998
[m][d]	16.057	6.344	22.850	22.374	37.127	56.440	57.419
[m][aa]	15.983	4.916	23.440	22.432	34.973	57.405	57.442
[m][ad]	15.878	8.875	23.743	22.619	37.480	57.311	57.194
[m][dd]	16.084	6.965	-3.986	-11.255	36.927	56.756	54.410
[m][a][d]	5.283	5.071	19.833	18.962	37.029	49.101	47.074
[m][a][aa]	5.357	6.499	20.472	19.020	34.874	50.061	47.096
[m][a][dd]	5.385	7.121	-6.953	-14.667	36.829	49.412	44.065
[m][a][ad]	5.603	8.744	20.270	18.698	37.516	50.439	47.337
[m][d][aa]	16.066	1.181	23.078	22.608	34.223	56.541	57.545
[m][d][dd]	16.108	6.503	-8.951	-14.009	37.102	54.815	54.286
[m][d][ad]	15.940	5.911	23.164	22.969	36.967	56.297	57.271
[m][ad][dd]	15.968	6.533	-3.672	-10.933	36.767	56.608	54.261
[m][aa][dd]	16.086	2.203	-6.119	-12.977	34.069	56.413	54.212
[m][aa][ad]	15.866	4.483	23.754	22.754	34.813	57.257	57.293
[m][a][d][aa]	5.366	1.336	20.111	19.196	34.124	49.198	47.200
[m][a][d][dd]	5.408	6.658	-11.917	-17.421	37.003	47.471	43.941
[m][a][d][ad]	5.666	5.780	19.692	18.775	37.003	49.424	47.413
[m][a][ad][dd]	5.693	6.401	-7.145	-14.854	36.803	49.736	44.404
[m][a][aa][dd]	5.386	2.358	-9.085	-16.389	33.970	49.070	43.867
[m][a][aa][ad]	5.591	4.352	20.282	18.833	34.848	50.385	47.435
[m][aa][ad][dd]	15.969	1.770	-5.805	-12.655	33.909	56.266	54.063
[m][d][ad][dd]	15.991	6.070	-8.636	-13.687	36.942	54.667	54.137
[m][d][aa][dd]	16.130	0.970	-10.867	-15.633	34.006	54.624	54.115
[m][d][aa][ad]	15.949	0.748	23.392	22.930	34.063	56.394	57.396
[m][d][aa][ad][dd]	16.013	0.537	-10.553	-15.311	33.845	54.476	53.966
[m][a][aa][ad][dd]	5.695	1.639	-9.277	-16.577	33.945	49.393	44.206
[m][a][d][ad][dd]	5.716	5.939	-12.109	-17.608	36.978	47.795	44.280
[m][a][d][aa][dd]	5.430	1.125	-13.833	-19.045	33.908	47.280	43.770
[m][a][d][aa][ad]	5.674	0.617	19.919	19.009	34.098	49.521	47.539
[m][a][d][aa][ad][dd]	5.739	0.406	-14.025	-19.232	33.882	47.604	44.109

Table 7 Continued

Model	Spike weight (2013)	Spike weight (2014; Normal)	Spike weight (2014; Stress)	Grain number (2013)	Grain number (2014)	Spike length (2013)	Spike length (2014)
[m][a]	7.271	38.091	37.355	50.804	84.857	-2.026	25.668
[m][d]	17.830	40.899	40.946	58.642	90.778	7.753	26.479
[m][aa]	18.064	41.659	41.052	59.565	91.168	7.808	26.279
[m][ad]	17.160	41.929	41.273	58.888	91.238	5.907	26.631
[m][dd]	17.857	38.357	37.190	58.424	89.884	7.750	13.584
[m][a][d]	6.889	38.119	37.423	49.770	84.913	-1.958	25.726
[m][a][aa]	7.124	37.360	37.317	50.693	84.523	-1.903	25.526
[m][a][dd]	6.917	34.817	33.561	49.552	83.629	-1.961	12.832
[m][a][ad]	7.868	37.956	37.241	51.299	84.949	-1.560	25.477
[m][d][aa]	17.626	41.026	41.056	58.445	90.823	7.886	26.367
[m][d][dd]	17.793	36.238	36.545	58.545	88.992	7.847	13.424
[m][d][ad]	16.777	41.198	41.235	57.854	90.905	5.974	26.689
[m][ad][dd]	16.805	38.655	37.479	57.635	90.011	5.972	13.795
[m][aa][dd]	17.673	38.017	36.953	58.247	90.004	7.878	12.134
[m][aa][ad]	17.012	41.957	41.341	58.777	91.294	6.030	26.489
[m][a][d][aa]	6.682	37.487	37.427	49.573	84.568	-1.825	25.614
[m][a][d][dd]	6.852	32.699	32.917	49.673	82.736	-1.863	12.672
[m][a][d][ad]	7.486	37.225	37.203	50.265	84.615	-1.493	25.535
[m][a][ad][dd]	7.513	34.682	33.446	50.047	83.721	-1.495	12.641
[m][a][aa][dd]	6.732	34.478	33.325	49.375	83.749	-1.833	11.381
[m][a][aa][ad]	7.721	37.984	37.308	51.188	85.005	-1.437	25.335
[m][aa][ad][dd]	16.620	38.315	37.242	57.458	90.130	6.099	12.344
[m][d][ad][dd]	16.740	36.537	36.834	57.757	89.118	6.069	13.634
[m][d][aa][dd]	17.552	35.998	36.351	58.281	89.100	7.985	12.003
[m][d][aa][ad]	16.574	41.325	41.345	57.656	90.949	6.107	26.577
[m][d][aa][ad][dd]	16.500	36.296	36.640	57.493	89.226	6.207	12.213
[m][a][aa][ad][dd]	7.329	34.343	33.210	49.870	83.841	-1.368	11.190
[m][a][d][ad][dd]	7.449	32.564	32.802	50.168	82.828	-1.398	12.481
[m][a][d][aa][dd]	6.612	32.458	32.723	49.409	82.844	-1.726	11.250
[m][a][d][aa][ad]	7.282	37.352	34.313	50.068	84.660	-1.360	25.423
[m][a][d][aa][ad][dd]	7.209	32.323	32.608	49.904	82.936	-1.260	11.060

Table 8. Posterior inclusion probabilities for the estimated parameters of grain yield and its components using different generations of the cross between Bam and Arta bread wheat cultivars at two water regimes in two growing seasons.

Traits	[a]	[d]	[aa]	[ad]	[dd]
Yield (2013; Normal)	0.943	0.598	0.032	0.235	0.440
Yield (2013; Stress)	1.0	1.0	0.058	0.633	1.0
Yield (2014; Normal)	1.0	1.0	0.173	1.0	1.0
Yield (2014; Stress)	1.0	1.0	0.999	0.998	1.0
Grain number (2013)	0.995	1.0	0.962	0.506	0.552
Grain number (2014)	1.0	0.981	0.302	0.694	1.0
Spike length (2013)	0.718	0.664	0.049	0.362	0.448
Spike length (2014)	1.0	1.0	0.999	1.0	1.0
1000 grain weight (2013)	0.267	1.0	1.0	0.632	1.0
1000 grain weight (2014; Normal)	1.0	1.0	0.456	0.411	0.000
1000 grain weight (2014; Stress)	1.0	0.392	0.123	0.419	0.711
Spike weight (2013)	0.906	0.718	0.030	0.248	0.637
Spike weight (2014; Normal)	1.0	1.0	0.787	0.991	1.0
Spike weight (2014; Stress)	1.0	1.0	0.050	0.991	1.0

cases where DIC difference among the models is low (less than 2) and the inferences from the models is very different from each other, reportingof the model with the lowest DIC may be misleading (Ntzoufras 2011). In this study, the DIC for models including all possible combinations of parameters was provided. Accordingly, it can be observed by adding or removing any of the effects, what changes occurs in the model fitting and selection in relation to the most important factors for the improvement of model fitting simply on the basis of a detailed statistical criterion. The Gibbs variable selection algorithm estimates the posterior variable inclusion probabilities efficiently. We followed the strategy of Fouskakis *et al*. (2009) and reduced the model space by removing variables with very low inclusion probabilities and identified effects that have the greatest discriminating power. Based on our results, it can be inferred that the Bayesian analysis provides a robust inference of the genetic architecture. Furthermore, we observed that additive, dominance and epistatic effects control the inheritance of the grain yield and yield components under both water stress and non-stress conditions. Therefore, methods which exploit these effects may be useful for covering all types of gene effects. It is advisable to delay selection to later generations with increased homozygosity as the breeding strategy to obtain tolerant breeding populations in wheat for the purpose of obtaining pure lines. Also, the production of hybrid varieties is recommended if pollination and male sterility problems can be solved in the wheat breeding programs because it has been shown that hybrid varieties in wheat are more productive than pure lines and are more stable in the stress prone environments (Longin *et al.* 2012).

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استنباط بیزی برای کنترل ژنتیکی تحمل به تنش خشکی در گندم بهاره

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چکیده

خشکی تنش غیرزیستی اصلی است که به طور جدی بر تولید و کیفیت گندم در جهان تأثیر می‌گذارد. اطلاعات مربوط به وراثت تحمل به خشکی برای تعیین نوع برنامه اصلاحی و تکوین ارقام متحمل ضروری است. در این مطالعه، استنباط بیزی برای بررسی ماهیت و میزان اثرهای ژنی کنترل کننده عملکرد و اجزای آن در شرایط کمبود آب و شرایط عادی با استفاده از ارزیابی ارقام گندم نان (بم و آرتا) و نسل های مشتق شده از آن‌ها مورد استفاده قرار گرفت. استنباط بیزی با استفاده از روش گزینش متغیر گیبز (GVS) و معیار اطلاعات انحراف (DIC) برای شناسایی مهم ترین اثرهای ژنی و مقایسه مدل‌هایی با اثرهای ژنی مختلف مورد استفاده قرار گرفت. GVS و DIC روشی کارآمد برای انجام تجزیه و تحلیل و معرفی مدل های مناسب ارایه کردند. می‌توان نتیجه گرفت که تجزیه و تحلیل بیزی استنباط قوی از ساختار ژنتیکی عملکرد و اجزای عملکرد در گندم ارایه می دهد. از آن جا که اثرهای افزایشی، غالبیت و اپیستازی در وراثت صفات زراعی درگیر بودند، روش‌هایی که از همه انواع اثرهای ژنی استفاده می‌کنند مانند اصلاح ارقام هیبرید، در صورت رفع موانع تولید این ارقام، می‌تواند در بهبود عملکرد و پایداری آن در گندم سودمند باشد.

واژه‌های کلیدی: استنباط بیزی؛ روش‌های زنجیر-مونت کارلو؛ کمبود آب؛ گزینش متغیر گیبز؛ گندم؛ معیار اطلاعات انحراف