

1           **Multi-trait and multi-environment Bayesian analysis to predict the G x E**  
2   **interaction in flood-irrigated rice**

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19  
20 **Abstract**

21 The biggest challenge for the reproduction of flood-irrigated rice is to identify superior  
22 genotypes that present development of high-yielding varieties with specific grain  
23 qualities, resistance to abiotic and biotic stresses in addition to superior adaptation to the  
24 target environment. Thus, the objectives of this study were to propose a multi-trait and  
25 multi-environment Bayesian model to estimate genetic parameters for the flood-irrigated  
26 rice crop. To this end, twenty-five rice genotypes belonging to the flood-irrigated rice  
27 breeding program were evaluated. Grain yield and flowering were evaluated in the  
28 agricultural year 2017/2018. The experimental design used in all experiments was a  
29 randomized block design with three replications. The Markov Chain Monte Carlo  
30 algorithm was used to estimate genetic parameters and genetic values. The flowering is  
31 highly heritable by the Bayesian credibility interval:  $h^2 = 0.039- 0.80$ , and  $0.02- 0.91$ ,  
32 environment 1 and 2, respectively. The genetic correlation between traits was

33 significantly different from zero in the two environments (environment 1: -0.80 to 0.74;  
34 environment 2: -0.82 to 0.86. The relationship of  $CV_e$  and  $CV_g$  higher for flowering in the  
35 reduced model ( $CV_g/CV_e = 5.83$  and  $13.98$ , environments 1 and 2, respectively). For the  
36 complete model, this trait presented an estimate of the relative variation index of:  $CV_e =$   
37  $4.28$  and  $4.21$ , environments 1 and 2, respectively. In summary, the multi-trait and multi-  
38 environment Bayesian model allowed a reliable estimate of the genetic parameter of  
39 flood-irrigated rice. Bayesian analyzes provide robust inference of genetic parameters.  
40 Therefore, we recommend this model for genetic evaluation of flood-irrigated rice  
41 genotypes, and their generalization, in other crops. Precise estimates of genetic  
42 parameters bring new perspectives on the application of Bayesian methods to solve  
43 modeling problems in the genetic improvement of flood-irrigated rice.

44 **Keywords:** *Oryza sativa* L.; genetic parameters; multi-trait and multi-environment;  
45 Bayesian model; biometric methods

46

## 47 **Introduction**

48 Rice (*Oryza sativa* L.) is one of the most important crops in the world and is  
49 considered one of the main annual crops in Brazil [1]. Rice breeding is primarily aimed  
50 at the development of high-yielding varieties with specific grain qualities, resistance to  
51 abiotic and biotic stresses in addition to superior adaptation to the target environment [2,  
52 3]. In this case, the breeder needs to realize mutual relationships, and knowledge of the  
53 interdependence between agronomically important traits that can improve the accuracy  
54 of selection [3].

55 Specifically, in the rice crop, the evaluation of multiple traits rather than a single  
56 trait aims to maximize grain yield and quality. This is possible through the exploration of  
57 genetic correlations between traits. In multi-trait analysis, the prediction of secondary  
58 traits can be used to improve the prediction of primary traits, especially when they have  
59 low heritability. Although consideration of the genetic correlation between traits is  
60 essential, modeling interactions between phenotypes provides important information for  
61 the development of breeding strategies that cannot be carried out with conventional  
62 multivariate approaches alone [2, 4, 5].

63 Biometric methods available are useful for analyzing a single trait measured in a  
64 single environment or across multiple environments with the genotype x environment (G  
65 x E) interaction [6, 7, 8, 9]. This interaction can be defined as the differential response of

66 genotypes to environmental variation [10], and offers an even greater challenge for the  
67 breeder [11]. The information from a network of experiments obtains a multi-trait and  
68 multi-environment (MTME) structure, but present limited statistical methodology that no  
69 correctly represents genetic and phenotypic variation in the data [12]. Therefore, genetic  
70 correlations and G x E interaction, it requires more complex models that are difficult to  
71 converge in the context of mixed linear models [11]. Therefore, Bayesian inference has  
72 become a useful statistical tool for dealing with complex models [13].

73 Bayesian inference has been used successfully in studies with complex models.  
74 [11] evaluated the multi-trait and multi-environment Bayesian model considering the G  
75 x E interaction for nitrogen use efficiency components in tropical corn. [13], applied such  
76 models through Bayesian inference applied to the breeding of *Jatropha curcas* for  
77 bioenergy. [14], used these models in the genetic selection of soybean progenies. [15],  
78 demonstrate such models in phenotypic and genotypic data in corn and wheat. However,  
79 few studies combine models of multiple traits in a multi-environment under a Bayesian  
80 point of view, mainly for rice cultivation.

81 Therefore, the objectives of this study were to propose a multi-trait and multi-  
82 environment Bayesian model to estimate genetic parameters for the flood-irrigated rice  
83 crop. In addition to comparing: (i) the complete model (considering the interaction  
84 between genotypes and environment) with the restricted model (not considering the  
85 interaction); (ii) estimates of genetic parameters of models with single and multiple traits,  
86 for grain yield and flowering.

87

## 88 **Material and Methods**

### 89 **Description of the experiment**

90 The experiments were carried out in the State of Minas Gerais - Brazil, in the  
91 experimental fields of Agricultural Research Corporation of Minas Gerais State  
92 (EPAMIG), in the cities of Lambari (21° 58' 11.24" S, 45° 20' 59.6" W) and Janaúba (15°  
93 48' 77" S, 43° 17' 59.09" W). Twenty-five genotypes belonging to the flood-irrigated rice  
94 breeding program of the Southeast region of the state of Minas Gerais were evaluated,  
95 and five of these genotypes were used as experimental controls (Rubelita, Seleta,  
96 Ourominas, Predileta, and Rio Grande). These genotypes were evaluated in comparative  
97 trials after multiple generations of selection, and in addition, they are known for their high  
98 yield, uniform growth rate and plant growth, resistance to major diseases, and for their  
99 excellent grain quality. Grain yield (GY, Kg ha<sup>-1</sup>) and flowering period in days (FL) were

100 evaluated in the agricultural year 2017/2018. The experimental design was a randomized  
101 complete block design with three replications. The experiments were conducted in  
102 floodplain soils with continuous flood irrigation. Grain production data in grams per  
103 useful plot were used, later converted into kilograms per hectare. Management practices  
104 were carried out according to recommendations for flood-irrigated rice in the region.

105 The useful area consisted of 4 m central of three internal rows (4 m x 0.9 m,  
106 totaling 3.60 m<sup>2</sup>). The soil preparation was carried out by plowing and harrowing around  
107 30 days before sowing. For planting fertilization, a mixture of 100 kg ha<sup>-1</sup> of ammonium  
108 sulfate, 300 kg ha<sup>-1</sup> of simple superphosphate, and 100 kg ha<sup>-1</sup> of potassium chloride was  
109 used, applied in the plot, and incorporated into the soil before planting. The fertilization  
110 in the top dressing was carried out approximately 60 days after the installation of the  
111 experiments, with 200 kg ha<sup>-1</sup> of ammonium sulfate. The weeds were controlled with the  
112 use of herbicides and manual weeding. Sowing was carried out in the planting line with  
113 a density of 300 seeds m<sup>-2</sup>. The irrigation started around 10-15 days after the implantation  
114 of the experiments, and the water was only removed close to the maturation of the  
115 materials. The harvest was carried out when the grains reached a humidity of 20-22%.  
116 Grain production data were obtained by weighing all grains harvested in the useful plot,  
117 after cleaning and uniform drying in the sun, until they reached a humidity of 13%. Days  
118 for flowering, correspond the number of days from sowing to flowering, when the plot  
119 presented approximately 50% of plants with panicles.

120

## 121 **Biometric analysis**

122 Grain yield (GY) and flowering period in days (FL) were analyzed using single-  
123 and multi-trait models using the Bayesian Markov Chain Monte Carlo (MCMC)  
124 approach. The objective was to compare: (i) the complete model (considering the  
125 interaction between genotypes and environments) with the restricted model (not  
126 considering the interaction); (ii) estimates of genetic parameters of models with single  
127 and multiple traits, for grain yield and flowering period.

128 The multi-trait and multi-environment (MTME) model was given by:

$$129 \quad y = X\beta + W_1r + W_2u + \varepsilon$$

130 which can be rewritten as:

$$131 \quad \begin{pmatrix} Y_1 \\ \dots \\ Y_2 \end{pmatrix} = X \begin{pmatrix} \beta(E1,1) \\ \beta(E2,1) \\ \dots \\ \beta(E1,2) \\ \beta(E2,2) \end{pmatrix} + W_1 \begin{pmatrix} r_1(E1,1) \\ r_2(E2,1) \\ \dots \\ r_1(E1,2) \\ r_2(E2,2) \end{pmatrix} + W_2 \begin{pmatrix} u(E1,1) \\ u(E2,1) \\ \dots \\ u(E1,2) \\ u(E2,2) \end{pmatrix} + \begin{pmatrix} \varepsilon(E1,1) \\ \varepsilon(E2,1) \\ \dots \\ \varepsilon(E1,2) \\ \varepsilon(E2,2) \end{pmatrix},$$

132 where:  $y$  is the vector of the phenotypic values of the two evaluated traits (grain yield,  
 133  $Y_1$ ; and flowering period,  $Y_2$ );  $X$  is the incidence matrix of the systematic effects  
 134 represented by  $\beta$ , assuming  $\beta \sim N(\mu_\beta, I_{\otimes} \Sigma_\beta)$  so that  $E1$  and  $E2$  represent the two  
 135 environments studied;  $W_1$  it is the incidence matrix of the random effect of the  
 136 environment;  $r$  is the ambient effect vector,  $r \sim N(0, I_{\otimes} \Sigma_r)$ ;  $W_2$  is the incidence matrix  
 137 of the effects of the genotype x environment interaction;  $u$  is the random effects vector of  
 138 the genotype x environment interaction,  $u \sim N(0, I_{\otimes} \Sigma_u)$ ; and  $\varepsilon$  is the residual effects  
 139 vector,  $\varepsilon \sim N(0, I_{\otimes} \Sigma_\varepsilon)$ .

140 The (co)variance matrices are given by:

$$141 \quad \Sigma_r = \begin{pmatrix} \sigma_{ry(1)}^2 & \sigma_{ry(1,2)} & \sigma_{ry,E(1)} & \sigma_{ry,E(1,2)} \\ \sigma_{ry(1,2)} & \sigma_{ry(2)}^2 & \sigma_{ry,E(2,1)} & \sigma_{ry,E(2)} \\ \sigma_{ry,E(1)} & \vdots & \sigma_{rE(1)}^2 & \dots \\ \sigma_{ry,E(1,2)} & \dots & \dots & \sigma_{rE(2)}^2 \end{pmatrix}$$

$$142 \quad \Sigma_u = \begin{pmatrix} \sigma_{uy(1)}^2 & \sigma_{uy(1,2)} & \sigma_{uy,E(1)} & \sigma_{uy,E(1,2)} \\ \sigma_{uy(1,2)} & \sigma_{uy(2)}^2 & \sigma_{uy,E(2,1)} & \sigma_{uy,E(2)} \\ \sigma_{uy,E(1)} & \vdots & \sigma_{uE(1)}^2 & \dots \\ \sigma_{uy,E(1,2)} & \dots & \dots & \sigma_{uE(2)}^2 \end{pmatrix}$$

$$143 \quad \Sigma_\varepsilon = \begin{pmatrix} \sigma_{\varepsilon y(1)}^2 & \sigma_{\varepsilon y(1,2)} & \sigma_{\varepsilon y,E(1)} & \sigma_{\varepsilon y,E(1,2)} \\ \sigma_{\varepsilon y(1,2)} & \sigma_{\varepsilon y(2)}^2 & \sigma_{\varepsilon y,E(2,1)} & \sigma_{\varepsilon y,E(2)} \\ \sigma_{\varepsilon y,E(1)} & \vdots & \sigma_{\varepsilon E(1)}^2 & \dots \\ \sigma_{\varepsilon y,E(1,2)} & \dots & \dots & \sigma_{\varepsilon E(2)}^2 \end{pmatrix},$$

144 where:  $y$  represents grain yield and  $h$  represents flowering period in days; 1 and 2  
 145 represent the two environments studied. The variance-covariance matrices follow an  
 146 inverted Wishart distribution, which was used as a priori to model the variance-covariance  
 147 matrix [16].

148 The package “MCMCglmm” [17] was used. A total of 10,000,000 samples were  
 149 generated and assuming a burn period and sampling interval of 500,000 and 10 iterations,  
 150 respectively, this resulted in a final total of 50,000 samples. The convergence of the

151 MCMC was verified by the criterion of [18], performed in two packages R "boa" [19]  
152 and "CODA" (convergence diagnosis) [20]. Even though Bayesian and frequentist  
153 structures were not directly compared, especially in the field of genetics [21], the same  
154 models were also adjusted based on the REML estimation method (Restricted Maximum  
155 Likelihood).

156 The complete models (considering the interaction between genotypes and  
157 environments) were compared with the null models (not considering the interaction) by  
158 the deviation information criterion (DIC) proposed by [22]:

$$159 \quad DIC = D(\bar{\theta}) + 2p_D$$

160 where  $\bar{\theta}$  is a point estimate of the deviation obtained by replacing the parameters with their  
161 later means estimates in the probability function and  $p_D$  is the effective number of model  
162 parameters. Models with a lower DIC should be preferred over models with a higher DIC.

163

164 The components of variance, broad-sense heritability, coefficient of variation  
165 residual and genetic, variation index, and genotypic correlation coefficients between  
166 genetic traits and values were calculated from the posterior distribution. The package  
167 "boa" [19] was used to calculate the intervals of greater posterior density (HPD) for all  
168 parameters. The later estimates for the broad-sense heritability of grain yield and  
169 flowering period in days for each interaction were calculated from the later samples of  
170 the variance components obtained by the model, using the expression:

$$171 \quad h^{2(i)} = \frac{\sigma_g^{2(i)}}{(\sigma_g^{2(i)} + \sigma_r^{2(i)} + \sigma_\varepsilon^{2(i)})}$$

172 where:  $\sigma_g^{2(i)}$ ,  $\sigma_r^{2(i)}$ , and  $\sigma_\varepsilon^{2(i)}$  are the genetic, replication, and residual variations for each  
173 iteration, respectively.

174 The genetic correlation coefficients between the pairs of traits in each  
175 environment were obtained, as suggested by [23], using the expression below for all  
176 models:

$$177 \quad \rho_{l(1,2)} = \frac{\sigma_{gl(1,2)}}{\sqrt{\sigma_{gl(1)}^2 \sigma_{gl(2)}^2}} : \text{genetic correlation between environment and grain yield and } \rho_{h(1,2)}$$
$$178 \quad = \frac{\sigma_{gh(1,2)}}{\sqrt{\sigma_{gh(1)}^2 \sigma_{gh(2)}^2}} : \text{genetic correlation between environment and flowering period in days.}$$

179 All data analysis was conducted using the statistical software package R version 4.1.0.

180

181 **Results**

182 Geweke's convergence criterion indicated convergence for all dispersion  
183 parameters by generating 10,000,000 MCMC strings, 500,000 samples for burn-in, and a  
184 sampling interval of 10, totaling 50,000 effective samples used for estimating variance  
185 components. Similar posterior mean, median and modal estimates were obtained for  
186 variance components, suggesting normal-appearing density. However, all chains reached  
187 convergence by this criterion. According to the deviation information criteria (DIC), there  
188 was positive evidence of interactions between genotypes and environments for all  
189 analyzed models (Table 1). However, the DIC values were lower when using the complete  
190 model (considering the effects of genotype x environment interaction), in which the  
191 difference in relation to the complete model was greater than 2 (Table 1), which according  
192 to [22] the use of full model can lead to greater precision in estimating parameters (Table  
193 1). Therefore, since the obtained DIC values were greater than two, it is possible to  
194 indicate the superiority of the complete model over the restricted models. On the other  
195 hand, as this component of the model is important, the “best” genotypes measured in  
196 different environments cannot be the same. However, convergence was not achieved by  
197 the AI (Average Information) and EM (Expectation-Maximization) algorithms.

198

199 **Table 1.** Deviation information criteria for the full (considering the G x E interaction)  
 200 and null (not considering the interaction) models.

Model	Trait	Deviance information criteria (DIC)	
		Full Model	Null Model
202 Mult-trait	GY, FL	-308.83	1967.79
203 Single-trait	GY	1867.49	1868.28
204 Single-trait	FL	162.19	697.67

205 GY: Grain Yield; FL: Flowering Period.

206

207 The posterior inferences for mean and higher posterior density range (HPD)  
 208 considering the multi-trait and multi-environment (MTME) model are described in Table  
 209 2. The average values for the grain yield trait varied from 4210.91 – 3901.56 kg ha<sup>-1</sup> and  
 210 flowering in days of 99.40 – 76.43, in environments 1 and 2, respectively (Table 2). The  
 211 Bayesian credibility interval (95% probability) for average grain yield corresponds to  
 212 4191.70 – 4227.86 kg ha<sup>-1</sup>, and 3852.60 – 3946.07 kg ha<sup>-1</sup> (p<1e-05), in environments 1  
 213 and 2, respectively. In relation to the flowering period in days, this interval corresponds  
 214 to 98.09 – 100.69 e 74.56 – 78.22 (p<1e-05), environments 1 and 2, respectively.

215

216 **Table 2.** Posterior inferences for mean and highest posterior density range (HPD)  
 217 considering the proposed complete multi-trait multi-environment model.

Trait	EN	post.mean	HPD 95%	
			LOWER	UPPER
GY	1	4210.91***	4191.7	4227.86
FL	1	99.4***	98.09	100.69
GY	2	3901.56***	3852.6	3946.07
FL	2	76.43***	74.56	78.22

218 \*\*\* Significância estatística:  $p \leq 0.001$ . GY: Grain Yield; FL: Flowering Period; EN:  
 219 environment.

220 Table 3 presents the subsequent inferences for mean and genetic variance; mode,  
 221 mean, median, and highest posterior density range (HPD) of heritability in the broad  
 222 sense; and the mode, mean, median, and greater posterior density interval (HPD) of the  
 223 genetic correlation, considering MTME. The grain yield trait in environment 2 was  
 224 considered weakly heritable with Bayesian credibility interval (95% probability):  $h^2 =$   
 225 4.36E-07 - 9.21E-06, and in environment 1, it was moderately heritable  $h^2 = 0.39 - 0.757$ .  
 226 The low estimate of heritability observed does not depend on the number of samples



227 evaluated, since the Bayesian structure used is essentially recommended for situations  
 228 involving small sample sizes. In addition, the grain yield trait is largely influenced by the  
 229 environment as it is a quantitative character [24], which reflects this low estimate of  
 230 heritability. In relation to flowering period, it is highly heritable by the Bayesian  
 231 credibility interval (95% probability):  $h^2 = 0.039 - 0.80$ , and  $0.02 - 0.91$ , environment 1  
 232 and 2, respectively. And the posterior mean of the genetic correlation between traits was  
 233 significantly different from zero (95% credibility intervals) in the two environments  
 234 (environment 1: -0.80 to 0.74; environment 2: -0.82 to 0.86) (Table 3).

235

236 **Table 3.** Resume of inferences for mean and genetic variance; mode, mean, median, and  
 237 highest posterior density range (HPD) of heritability in the broad sense; and the mode,  
 238 mean, median, and highest posterior density range (HPD) of the genetic correlation,  
 239 considering the complete model multi-trait and multi-environment.

Trait	EN	$h^2$			HPD 95%	
		Mode	Mean	Median	LOWER	UPPER
GY	1	0.11	0.28	0.18	0.39	0.757
GY	2	1.30E-06	3.32E-06	2.24E-06	4.36E-07	9.21E-06
FL	1	0.12	0.31	0.24	0.039	0.80
FL	2	0.06	0.27	0.13	0.02	0.91

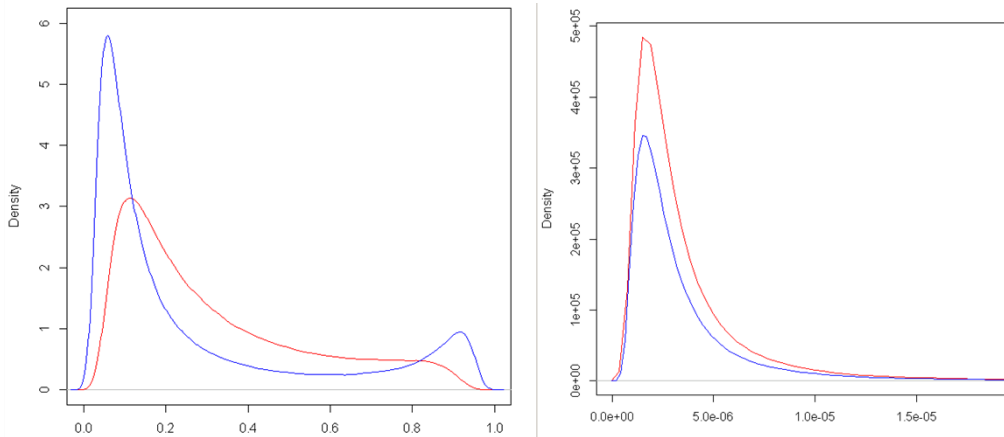
  

		Genotypic Correlation			HPD 95%	
		Mode	Mean	Median	LOWER	UPPER
GY,FL	1	-0.0076	-0.027	-0.028	-0.80	0.74
GY,FL	2	0.037	0.018	0.019	-0.82	0.86

240 EN: environment; GY: Grain Yield; FL: Flowering Period;  $h^2$ : heritability.

241

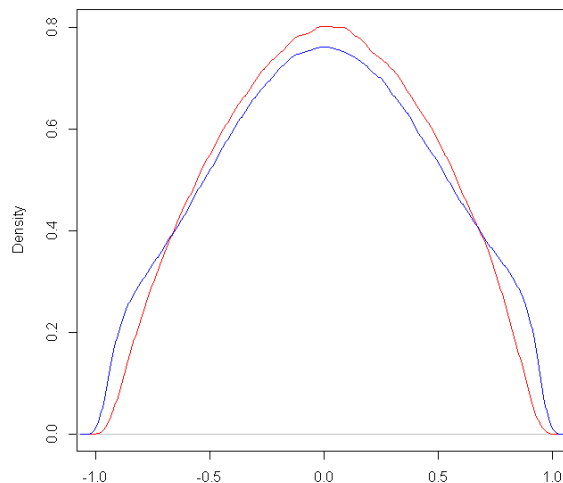
242 Bayesian methods access the posterior density ranges of genetic parameters  
 243 (Figure 1). The genetic parameters of the flood-irrigated rice genotypes for each trait and  
 244 their larger posterior density ranges (HPD) were obtained to assist in the selection of  
 245 genotypes.



246

247 **Figure 1.** Posterior density for the complete model proposed by multi-traits multi-  
248 environment (left: flowering period and right: grain yield). The red line represents the  
249 posterior density for environment 1, while the blue line represents the posterior density  
250 for environment 2.

251 In Figure 2, there is a unimodal distribution in which there is a mixture of two  
252 distinct populations for posterior density in relation to the genotypic correlation between  
253 traits for the complete MTME model. The red line represents the posterior density for  
254 environment 1, while the blue line represents the posterior density for environment 2.



255

256 **Figure 2.** Posterior density for the genotypic correlation between the grain yield trait and  
257 flowering period in days for the model proposed by multi-traits and multi-environment.  
258 The red line represents the posterior density for environment 1, while the blue line  
259 represents the posterior density for environment 2.

260

261 **Variance Estimate**

262 The a posteriori estimates of the genotypic and residual variances for the reduced  
 263 model (MTME) were very discrepant among the environments (Table 4). The grain yield  
 264 trait in the reduced model obtained a greater estimate of genotypic variance in  
 265 environment 1, corresponding to a difference of approximately 60% greater, in relation  
 266 to environment 2. This indicates a greater influence of genetic components on  
 267 environmental components in the expression of traits. On the other hand, this estimate for  
 268 the complete model showed less variation between environments, especially for the  
 269 flowering period in days trait. This result showed the best consistency for the complete  
 270 model (MTME). Estimates of the variance of the greatest interaction were observed for  
 271 the flowering period trait.

272 **Table 4.** Genetic parameters for traits grain yield and flowering period in days, in two  
 273 environments, using multi-trait multi-environment (MTME) models.

Model	Trait	EM	Component		
			$\sigma_g^2$	$\sigma_r^2$	$\sigma_{int}^2$
Null	GY	1	38.93	8.86	-
	GY	2	23.19	6.13	-
	FL	1	14.95	4.45E-5	-
	FL	2	32.63	0.19	-
Multi trait	GY	1	2.63	7.24	4.64
	GY	2	2.70	7.39	4.77
	FL	1	3.35	0.18	7.57
	FL	2	5.69	0.34	15.91

274 EN: environment; GY: Grain Yield; FL: Flowering Period;  $\sigma_g^2$ ,  $\sigma_r^2$ ,  $\sigma_{int}^2$ : are the genetic,  
 275 replication, and interaction variations, respectively.

276

### 277 ***Relative variation index***

278 The ratio of the coefficient of variation genotypic and the coefficient of variation  
 279 residual ( $CV_g/CV_e$ ) corresponded to the relative variation index. When this index is greater  
 280 than one unit, it suggests that genetic variation is more influential than residual variation.  
 281 This was observed in this study for both traits, in the reduced model proposed by MTME  
 282 (Table 5). For the complete model in the grain yield trait, this relationship was less than  
 283 one unit. The relationship of  $CV_e$  and  $CV_g$  higher for flowering period trait in the reduced  
 284 model ( $CV_g/CV_e = 5.83$  and  $13.98$ , environments 1 and 2, respectively). This trait has  
 285 greater variability and is highly promising for selection. This is due to its complex genetic  
 286 inheritance resulting from the involvement of several genes with little effect on the

287 phenotype [24, 25]. For the complete model, this trace presented an estimate of the  
 288 relative variation index of:  $CV_g/CV_e= 4.28$  and  $4.21$ , environments 1 and 2, respectively  
 289 (Table 5). Then, this trait presented a higher posterior density interval (HPD) for 80 and  
 290 91% heritability, environment 1 and 2, respectively, reinforcing the possibility of genetic  
 291 gain (Table 3). This implies that the variability observed in these traits has genetic  
 292 predominance, which is interesting in the process of genetic gain in a flood-irrigated rice  
 293 breeding program. The coefficient of variation genotypic for the grain yield trait was low  
 294 in both environments. This is justified by the fact that these genotypes belong to advanced  
 295 comparative trials in which they have gone through several generations of selection.

296

297 **Table 5.** Coefficient of variation residual ( $CV_e$ , %), coefficient of variation genotypic ( $CV_g$ , %) and relative variation index ( $CV_g/CV_e$ ) for the multi-trait and multi-environment  
 298 model.  
 299

Model	Trait	EN	$CV_g$ (%)	$CV_e$ (%)	$CV_g/CV_e$
Null	GY	1	0.149	0.071	2.11
	GY	2	0.122	0.063	1.92
	FL	1	3.89	0.67	5.83
	FL	2	7.47	0.57	13.98
Full	GY	1	0.039	0.064	0.61
	GY	2	0.042	0.070	0.60
	FL	1	1.84	0.43	4.28
	FL	2	3.20	0.76	4.21

300 EN: environment; GY: Grain Yield; FL: Flowering Period; EN: environment.

301

## 302 Discussion

303 One of the ways to succeed in breeding programs is related to the accurate  
 304 prediction of genotypic values, which is closely related to the adoption of adequate  
 305 models. Thus, in this study, we apply a new statistical approach for estimating variance  
 306 components in floodplain rice breeding schemes. The implementation of multi-trait multi-  
 307 environment models Bayesian is straight forward and currently has been widely used due  
 308 to the possibility of considering a priori knowledge in modeling. In addition to its  
 309 application wide application in animal breeding [26, 27], Bayesian multi-trait analysis  
 310 has been reported in plant breeding [11, 13, 14, 15, 28].

311 Bayesian inference has been used since 1986 [29] and has been further explored  
312 in recent years [2, 11, 13, 14, 15, 30, 31 ] due to major computational advances and new  
313 applications and methodologies [32]. However, Bayesian analysis is based on knowledge  
314 of the posterior distribution of the parameters to be estimated. This allows the  
315 construction of exact credibility intervals for estimates of random variables and variance  
316 components [33]. Values for the 95% distribution credibility interval for the broad-sense  
317 heritability parameter found in this study (Table 3) were also presented in the study by  
318 [11] to estimate genetic parameters for efficiency of uptake and efficiency of use of N  
319 under contrasting soil N levels via MTME models. Another study, based on the estimation  
320 of genetic parameters for genetic selection of segregating soybean progenies using the  
321 MTME model [14]. The difference between mean, mode, and median of the broad-sense  
322 heritability estimates (Table 3) reflects some lack of symmetry in the posterior  
323 distribution estimates. The lack of symmetry between mean, mode, and median  
324 heritability estimates in posterior distribution estimates was reported by [11] and [30].

325 The low broad-sense heritability observed in the traits does not depend on the  
326 number of samples evaluated, since the Bayesian structure used is essentially  
327 recommended for situations involving small samples. On the other hand, quantitative  
328 traits of agronomic interest, determined by several genes, demonstrate low expression and  
329 significantly influenced by the environment [24], reflected in the traits grain yield and  
330 flowering period in days.

331 Based on the results of heritability estimation in the broad sense for the GY and  
332 FL traits varied in:  $h^2 = 0.39 - 0.757$  and  $h^2 = 4.36E-07 - 9.21E-06$ ;  $h^2 = 0.039 - 0.80$ ,  
333 and  $0.02 - 0.91$ , environment 1 and environment 2, respectively (Table 3). [34] found  
334 heritability estimates of 0.48 and 0.94 for GY and FL, respectively, using 198 rice  
335 progenies by the ANOVA technique. [35] evaluated upland rice genotypes, by this same  
336 technique, and obtained an estimate of  $h^2$  for GY and FL traits 0.35 and 0.77, respectively.  
337 [36] obtained results of  $h^2$  ranging from 0.44 - 0.87 for GY, 0.46 - 0.94 for FL. [37]  
338 applied a mixed model in studies using FL and GY traits, found an estimate of  $h^2$  de  
339 0,88, and 0,71, respectively. [38], using the ANOVA method, found  $h^2$  of 0.76 for FL and  
340 [39] estimate of 0.30 for GY. Regarding the estimate of CVs using the ANOVA method  
341 for the FL and GY traits, representing 2.98% and 15.28%, respectively [34].

342 The amounts of data that breeding programs around the world are generating  
343 continue to increase; consequently, there is a growing need to extract more knowledge  
344 from the data being produced. For this, MTME models are commonly used to take

345 advantage of correlated traces to improve parameter estimation and prediction accuracy.  
346 However, when there are a large number of features, implementing these types of models  
347 is a challenge. Therefore, it is necessary to develop efficient models of multiple trait and  
348 multiple environments for selection, in order to take advantage of multiple correlated  
349 features. In this work, was proposed an alternative method to analyze MTME model data  
350 that could be useful for genotype selection, and estimation of genetic parameters in  
351 flooded rice in the context of an abundance of traits and environments.

352 Full-model multi-trait analysis tends to be powerful and provide more accurate  
353 estimates than single-trait analysis because the previous method can take into account the  
354 underlying correlation structure found in a multi-trait dataset. However, Bayesian and  
355 non-Bayesian inferences from the MTME model analysis are complex and  
356 computationally demanding [40]. [28] argue that Bayesian multi-trait analysis is more  
357 appropriate than ANOVA to perform analyzes and select superior genotypes for genetic  
358 improvement since the Bayesian model can capture small genetic differences between  
359 families, while ANOVA cannot. In this study, was explained how to make Bayesian  
360 inference using a multi-trait multi-environment Bayesian model in plant breeding. These  
361 results showed that the approach was efficient in estimating genetic parameters in flooded  
362 rice.

363 The correlation study revealed favorable associations for the traits in studies in  
364 two settings. This result indicates that the selection of genotypes characterized by longer  
365 flowering period favors grain yield in flood-irrigated rice, which is desirable for rice  
366 cultivation since later plants tend to be more productive. However, late cycle cultivars  
367 tend to be more productive in relation to the early cycle, since they obtain an increase in  
368 the amount of photoassimilates that are translocated to grains [3]. This result justifies the  
369 significant correlation between the traits. According to [24], correlations between traits  
370 may be the result of pleiotropy or genetic linkage. Thus, if the undesirable correlations  
371 are caused by genetic linkage, these associations can be broken by recombination caused  
372 by crossing or self-fertilization; consequently, these factors do not necessarily become  
373 major impediments to breeding programs [(Liersch et al., 2016; Radkowski et al., 2017;  
374 Bocianowski et al, 2019).

375 Another point that we would like to highlight is that our proposed model is of  
376 MTME, but with the restriction that an identity matrix is assumed for the variance-  
377 covariance matrix of the environments. However, even with this restrictive assumption in  
378 the variance-covariance matrix of the environments, the model has the advantage of

379 taking into account the terms of interaction x trait, genotype x trait, and the environment  
380 x genotype x trait. Furthermore, it takes into account the correlated traits. The program of  
381 irrigated rice program aims to obtain the desired results in a short period and with  
382 precision, therefore, the choice of the model will be use as breeding strategies.

383

### 384 **Conclusion**

385 The multi-trait and multi-environment Bayesian model was efficient to estimate  
386 genetic parameters for the flood-irrigated rice crop.

387 The estimates of genetic parameters bring new perspectives on the application of  
388 Bayesian methods to solve modeling problems in the genetic improvement of flood-  
389 irrigated rice.

390

### 391 **Compliance with ethical standards**

392 This manuscript is not under consideration for publication elsewhere and has  
393 not been made publicly available online. All authors have approved the submission, and  
394 all the copyrighted individuals are listed. The authors declare that they have no conflicts  
395 of interest.

396

### 397 **References**

- 398 1. Silva Júnior, AC, Silva, MJ, Cruz, CD, Nascimento, M, Azevedo, CF & Soares,  
399 PC. (2020). Patterns recognition methods to study genotypic similarity in flood-  
400 irrigated rice. *Bragantia*, 79(3), 356-363. <https://doi.org/10.1590/1678-4499.20200232>.
- 402 2. Yu, H, Campbell, T, Zhang, Qi, Walia, H, Morota, G. Genomic Bayesian  
403 Confirmatory Factor Analysis and Bayesian Network To Characterize a Wide  
404 Spectrum of Rice Phenotypes. (2019). *G3: GENES, GENOMES, GENETICS*.  
405 vol. 9 n. 6. 1975-1986; <https://doi.org/10.1534/g3.119.400154>.
- 406 3. Silva Júnior AC, Santanna IC, Silva GN, Cruz CD, Nascimento M, Bhereng LL,  
407 Soares PC. (2022). Computational intelligence to study the importance of  
408 characteristics in flood-irrigated rice. *Acta Scientiarum-Agronomy*.
- 409 4. Valente BD, Rosa GJ, de Los Campos G, Gianola D, Silva MA. (2010). Searching  
410 for recursive causal structures in multivariate quantitative genetics mixed models.  
411 *Genetics*;185(2):633–644. <https://doi.org/10.1534/genetics.109.112979>.

- 412 5. Momen M, Campbell MT, Walia H, Morota G. Predicting Longitudinal Traits  
413 Derived from High-Throughput Phenomics in Contrasting Environments Using  
414 Genomic Legendre Polynomials and B-Splines. *G3* (Bethesda, Md.). (2019)  
415 Oct;9(10):3369-3380. <https://doi.org/10.1534/g3.119.400346>.
- 416 6. Burgueño, J., G. de los Campos, K. Weigel, and J. Crossa. (2012). Genomic  
417 prediction of breeding values when modeling genotype-environment interaction  
418 using pedigree and dense molecular markers. *Crop Sci.* 52(2): 707–719.
- 419 7. Heslot, N., D. Akdemir, M. E. Sorrells, and J. L. Jannink. (2014). Integrating  
420 environmental covariates and crop modeling into the genomic selection  
421 framework to predict genotype by environment interactions. *Theor. Appl. Genet.*  
422 127(2): 463–480.
- 423 8. Jarquín, D., J. Crossa, X. Lacaze, P. D. Cheyron, J. Daucourt et al. (2014). A  
424 reaction norm model for genomic selection using high-dimensional genomic and  
425 environmental data. *Theor. Appl. Genet.* 127(3): 595–607.
- 426 9. Montesinos-López, O. A., A. Montesinos-López, P. Pérez-Rodríguez, G. de los  
427 Campos, K. M. Eskridge et al. (2015). Threshold models for genome-enabled  
428 prediction of ordinal categorical traits in plant breeding. *G3* (Bethesda) 5(1): 291–  
429 300.
- 430 10. Silva Júnior AC, Silva MJ, Sousa I, Costa WG, Cruz CD, Nascimento M, Soares  
431 PC. (2021). Fuzzy logic for adaptability and stability studies in irrigated rice  
432 (*Oryza Sativa* L.) genotypes. *Plant Breeding*. <https://doi.org/10.1002/PBR.12973>.
- 433 11. Torres LG, Rodrigues MC, Lima NL, Trindade TFH, Silva FFe, Azevedo CF, et  
434 al. (2018). Multi-trait multi-environment Bayesian model reveals G x E  
435 interaction for nitrogen use efficiency components in tropical maize. *PLoS ONE*  
436 13(6): e0199492. <https://doi.org/10.1371/journal.pone.0199492>.
- 437 12. Malosetti, M., Ribaut, J.M., Vargas, M. et al. (2008). A multi-trait multi-  
438 environment QTL mixed model with an application to drought and nitrogen stress  
439 trials in maize (*Zea mays* L.). *Euphytica*. 161: 241.  
440 <https://doi.org/10.1007/s10681-007-9594-0>.
- 441 13. Peixoto MA, Evangelista JSPC, Coelho IF, Alves RS, Laviola BG, Fonseca e  
442 Silva F, et al. (2021). Multiple-trait model through Bayesian inference applied  
443 to *Jatropha curcas* breeding for bioenergy. *PLoS ONE* 16(3): e0247775.  
444 <https://doi.org/10.1371/journal.pone.0247775>.



- 445 14. Volpato L, Alves RS, Teodoro PE, Vilela de Resende MD, Nascimento M,  
446 Nascimento ACC, et al. (2019). Multi-trait multi-environment models in the  
447 genetic selection of segregating soybean progeny. PLoS ONE 14(4): e0215315.  
448 <https://doi.org/10.1371/journal.pone.0215315>.
- 449 15. Montesinos-López, OA, Montesinos-López A, Montesinos-López JC, Crossa J,  
450 Luna-Vázquez FJ, Salinas-Ruiz JA. (2018). Bayesian Multiple-Trait and  
451 Multiple-Environment Model Using the Matrix Normal Distribution. Phys.  
452 Methods Stimul. Plant Mushroom Dev. 19.
- 453 16. Van Tassel CP, Van Vleck LD. (1996). Multiple-trait Gibbs sampler for animal  
454 models: flexible programs for Bayesian and likelihood-based (co)variance  
455 component inference. J Anim Sci. 74:2586–2597. pmid:8923173.  
456 <https://doi.org/10.2527/1996.74112586x>.
- 457 17. Hadfield J. MCMC Methods for Multi-Response Generalized Linear Mixed  
458 Models: The MCMCglmm R Package. J Stat Softw. 2010; 33:1–22.  
459 <https://doi.org/10.18637/jss.v033.i02>.
- 460 18. Geweke J. Evaluating the accuracy of sampling-based approaches to the  
461 calculation of posterior moments. In: Bernardo JM, Berger JO, Dawid AP, Smith  
462 AFM, editors. Bayesian Statistics 4. Oxford University Press; 1992. pp 625–631.
- 463 19. Smith BJ. boa: an R package for MCMC output convergence assessment and  
464 posterior inference. J Stat Softw. 2007; 21:1–37.  
465 <https://doi.org/10.18637/jss.v021.i11>.
- 466 20. Plummer M, Best N, Cowles K, Vines K. CODA: Convergence diagnosis and  
467 output analysis for MCMC. R news. 2006; 6:7–11.
- 468 21. Sorensen DA, Gianola D. Likelihood, Bayesian and MCMC methods in  
469 quantitative genetics: statistics for biology and health. Springer-Verlag; 2002.
- 470 22. Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A. Bayesian Measures of  
471 Model Complexity and Fit. J R Stat Soc Ser B. Statistical Methodol. 2002;64: 583–  
472 639.
- 473 23. Piepho HP. Allowing for the structure of a designed experiment when estimating  
474 and testing trait correlations. J Agric Sci. 2018;156: 59–70.
- 475 24. Falconer DS, Mackay TFC. 1996. Introduction to quantitative genetics.  
476 Edinburgh, SC: Addison Wesley Longman.
- 477 25. Cruz, CD; Regazzi, AJ; Carneiro, PCS. (2012). Modelos biométricos aplicados ao  
478 melhoramento genético. UFV. Viçosa.

- 479 26. Ventura HT, Silva FF, Varona L, de Figueiredo EAP, Costa EV, da Silva LP, et  
480 al. Comparing multi-trait Poisson and Gaussian Bayesian models for genetic  
481 evaluation of litter traits in pigs. *Livestock Science*. 2015;176:47–53.
- 482 27. Rolf MM, Garrick DJ, Fountain T, Ramey HR, Weaber RL, Decker JE, et al.  
483 Comparison of Bayesian models to estimate direct genomic values in multi-breed  
484 commercial beef cattle. *Genetics Selection Evolution*. 2015;47(1):23.
- 485 28. Junqueira VS, Azevedo Peixoto Ld, Galvêas Laviola B, Lopes Bhering L,  
486 Mendonça S, et al. (2016) Correction: Bayesian Multi-Trait Analysis Reveals a  
487 Useful Tool to Increase Oil Concentration and to Decrease Toxicity in *Jatropha*  
488 *curcas* L.. *PLOS ONE* 11(8): e0161046.  
489 <https://doi.org/10.1371/journal.pone.0161046>.
- 490 29. Gianola D, Fernando RL. Bayesian Methods in Animal Breeding Theory. *J Anim*  
491 *Sci*. 1986;63: 217–244.
- 492 30. Mora, F. & Serra, N. (2014). Bayesian estimation of genetic parameters for  
493 growth, stem straightness, and survival in *Eucalyptus globulus* on an Andean  
494 Foothill site. *Tree Genetics & Genomes*.10: 711. [https://doi.org/10.1007/s11295-](https://doi.org/10.1007/s11295-014-0716-2)  
495 [014-0716-2](https://doi.org/10.1007/s11295-014-0716-2).
- 496 31. Duhnen A, Gras A, Teyssèdre S, Romestant M, Claustres B, Daydé J, et al.  
497 Genomic selection for yield and seed protein content in Soybean: A study of  
498 breeding program data and assessment of prediction accuracy. *Crop Sci*. 2017;57:  
499 1325–1337.
- 500 32. Van de Schoot, R., Depaoli, S., King, R. *et al.* Bayesian statistics and  
501 modelling. *Nat Rev Methods Primers* 1, 1 (2021).  
502 <https://doi.org/10.1038/s43586-020-00001-2>.
- 503 33. Resende MDV, Duda LL, Guimarães PRB, Fernandes JSC. Análise de modelos  
504 lineares mistos via inferência Bayesiana. *Rev Mat Estat*. 2001;19: 41–70.  
505 Available: [http://jaguar.fcav.unesp.br/RME/fasciculos/v19/A3\\_Artigo.pdf](http://jaguar.fcav.unesp.br/RME/fasciculos/v19/A3_Artigo.pdf).
- 506 34. Guimarães, P. H. R., Melo, P. G. S., Cordeiro, A. C. C., Torga, P. P., Rangel, P.  
507 H. N., Castro, A. P. Index selection can improve the selection efficiency in a rice  
508 recurrent selection population. *Euphytica* (2021) 217:95.  
509 <https://doi.org/10.1007/s10681-021-02819-7>.
- 510 35. Sari, W. K., Nualsri, C., Junsawang, N., Soonsuwon, W. Combining ability and  
511 heritability for yield and its related traits in Thai upland rice (*Oryza sativa* L.).  
512 *Agr. Nat. Resour*. Vol. 54 No. 3 (2020)

- 513 36. Catolos Margaret, Sandhu Nitika, Dixit Shalabh, Shamsudin Noraziya A. A.,  
514 Naredo Ma E. B., McNally Kenneth L., Henry Amelia, Diaz Ma G., Kumar  
515 Arvind. Genetic Loci Governing Grain Yield and Root Development under  
516 Variable Rice Cultivation Conditions. *Front. Plant Sci.*, 16 October 2017 |  
517 <https://doi.org/10.3389/fpls.2017.01763>.
- 518 37. Bhandari, A., Bartholomé, J., Cao, T.-V., Kumari, N., Frouin, J., Kumar, A.,  
519 Ahmadi, N. (2019). Selection of trait-specific markers and multi-environment  
520 models improve genomic predictive ability in rice. *PLoS ONE*, 14(5).  
521 <https://doi.org/10.1371/journal.pone.0208871>.
- 522 38. Sangaré, J. R., Konaté, A. K., Cissé, F., Sanni, A. Assessment of genetic  
523 parameters for yield and yield related-traits in an intraspecific rice (*Oryza sativa*  
524 L.) population. *J. Plant Breed. Genet.* 05 (02) 2017. 45-56.
- 525 39. Xu, Y., Wang, X., Ding, X. et al. Genomic selection of agronomic traits in hybrid  
526 rice using an NCH population. *Rice* 11, 32 (2018).  
527 <https://doi.org/10.1186/s12284-018-0223-4>.
- 528 40. Mathew, B., Holand, A.M., Koistinen, P. et al. Reparametrization-based  
529 estimation of genetic parameters in multi-trait animal model using Integrated  
530 Nested Laplace Approximation. *Theor Appl Genet* 129, 215–225 (2016).  
531 <https://doi.org/10.1007/s00122-015-2622-x>.
- 532 41. Liersch A, Bocianowski J, Woś H, Szała L, Sosnowska K, Cegielska-Taras T,  
533 Nowosad K, Bartkowiak-Broda I. (2016). Assessment of genetic relationships in  
534 breeding lines and cultivars of *Brassica napus* and their implications for breeding  
535 winter oilseed rape. *Crop Sci.* 56(4):1540– 1549.
- 536 42. Radkowski A, Sosin-Bzducha E, Radkowska I. (2017). Effects of silicon foliar  
537 fertilization of meadow plants on the nutritional value of silage fed to dairy cows.  
538 *J Elem.* 22(4):1311–1322.
- 539 43. Bocianowski, J; Nowosad, K; Szulc, P; Tratwal, A; Bakinowska, E & Piesik,  
540 D. (2019). Genetic parameters and selection of maize cultivars using Bayesian  
541 inference in a multi-trait linear model, *Acta Agriculturae Scandinavica, Section B*  
542 — Soil & Plant Science, 69:6, 465-478.  
543 <https://doi.org/10.1080/09064710.2019.1601764>.