

# Theobroma Grandiflorum Breeding Optimization Based on Repeatability, Stability and Adaptability Information

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## Research Article

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## ***Theobroma grandiflorum* breeding optimization based on repeatability, stability and adaptability information**

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### **Declarations**

All authors contributed to the study conception and design. Saulo Fabrício da Silva Chaves, Rafael Moysés Alves, Rodrigo Silva Alves, Alexandre Magno Sebbenn, Marcos Deon Vilela de Resende and Luiz Antônio dos Santos Dias performed material preparation, data collection and analysis. Saulo Fabrício da Silva Chaves wrote the first draft of the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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### **Conflicts of interests**

There are no conflicts of interests in this article.

### **Availability of data and material**

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

### **Code availability**

Not applicable

## 1 *Theobroma grandiflorum* breeding optimization based on repeatability, stability and adaptability information

2

3 **Abstract:** The cultivation of *Theobroma grandiflorum* in the Brazilian Amazon is mainly conducted by family farmers  
4 who use a range of different management strategies. Thus, breeding programs of the species must address the challenge  
5 of developing cultivars that are adapted to and stable in a variety of cultivation environments. In this context, this study  
6 aimed to estimate the optimum number of harvests for genetic selection of *T. grandiflorum* progenies and identify the  
7 most promising ones in terms of productivity, stability, and adaptability. The trials were implemented in three  
8 environments, using a randomized complete block design, with 25 full-sib progenies, five replications, and three plants  
9 per plot. The traits mean number of fruits/plant, mean fruit production/plant, and rate of infection with witches' broom  
10 (*Moniliophthora pernicioso*) were evaluated over 11 harvests. The Restricted Maximum Likelihood/Best Linear Unbiased  
11 Prediction (REML/BLUP) mixed model method was used to estimate genetic parameters and predict genetic values,  
12 which were then applied to assess stability and adaptability. The results show that there is genetic variability among the  
13 studied *T. grandiflorum* progenies and that accurate genetic selection aiming at recombination is effective after three  
14 harvests, for recombination, or eleven harvests for identification of recommended progenies. Six progenies were selected  
15 that met the requirements for productivity, stability, and adaptability to different cultivation environments. These results  
16 can be used to optimize and advance *T. grandiflorum* breeding programs.

17

18 **Key words:** repeated measures, genotype x environment interaction, genotype x measure interaction, REML/BLUP, fruit  
19 tree breeding.

20

## 21 INTRODUCTION

22 The allogamous tree *Theobroma grandiflorum* (Willd. Ex Spreng.) Schum. (Malvaceae family), commonly  
23 known as cupuassu tree, is native to Southeast Pará and Northwest Maranhão States in the Brazilian Amazon (Alves et  
24 al., 2003). Due to the movement of indigenous peoples throughout the interior of the Amazon region, the species is now  
25 dispersed across all Amazonian states (Alves et al. 2007), and plantations of *T. grandiflorum* have been established in 97  
26 (67%) of the 144 municipalities in Pará State (Pará 2020). These plantations are generally small-scale seed orchards of  
27 less than one hectare, planted by family farmers (Homma, 2014). The expansion of the crop and its adaptation to different  
28 environments in Pará is an indicator of the genetic plasticity of the species (Alves et al. 2007).

29 The economic importance of *T. grandiflorum* has grown in recent years as the main products derived from the  
30 tree, including its seeds and the pulp covering them, have attracted increased attention in national and international  
31 markets (Silva et al. 2020). The pulp, with high acidity and strong aroma, is used to produce juices, sweets, and jellies,  
32 among other food products (Pugliese et al., 2013). The almonds, which have antioxidant properties, are used in the

33 pharmaceutical and cosmetic industries (Oliveira and Genovese 2013), as well as to produce cupuassu chocolate, a  
34 product known as “cupulate” (Genovese and Lannes 2009). The municipality of Tomé Açu, Northeast Pará, was a pioneer  
35 in the cultivation of this fruit tree. The region has become a model for production as farmers have organized an agricultural  
36 cooperative that processes all cupuassu products, which is essential for expanding its production and use in the region  
37 (Alves et al. 2014). To ensure the development and sustainability of the crop, communities have continuously sought  
38 research support, particularly in terms of developing varieties that are well adapted to local conditions.

39 At the end of the 1980s, Embrapa Amazonia Oriental initiated a *T. grandiflorum* breeding program and  
40 developed genetic resources to produce genotypes with high levels of fruit production and tolerance to the fungus  
41 *Moniliophthora perniciosa*, etiological agent of the witches’ broom disease, a pathogen that can affect the cultivation of  
42 all species of the *Theobroma* genus, including *T. grandiflorum* and *T. cacao* (Gramacho et al. 2016; Patrocínio et al.  
43 2017). However, the previously developed genotypes have inconsistent fruit production when subjected to different  
44 environments.

45 Currently, the Restricted Maximum Likelihood/Best Linear Unbiased Prediction (REML/BLUP) mixed model  
46 method is the standard for analyses of genotype x environment (GE) interaction (Coelho et al. 2020; Evangelista et al.  
47 2021) and repeated measures (Resende et al. 2014; Ferreira et al. 2020). There are numerous reasons for its use, including  
48 the fact that it enables the simultaneous estimates of variance components and prediction of genetic values. The method  
49 also deals well with unbalanced data, describes the heterogeneity of genetic covariances and residual variances across  
50 environments, and models spatial trends (Resende 2016).

51 The evaluation of different genotypes in a variety of environments enables the quantification of the GE  
52 interaction effect (Resende 2015) and the analysis of genotypic stability and adaptability (Chipeta et al. 2017).  
53 Understanding stability and adaptability enables the identification of productive, stable, and adaptable genotypes (Silva  
54 et al., 2019). However, evaluating GE interaction is one of the most costly aspects of a breeding program (Dias et al.,  
55 2018), especially for perennial fruit trees such as *T. grandiflorum*, where the breeding cycle can last up to 15 years (Alves  
56 et al. 2021). This may explain why studies on GE interaction in *T. grandiflorum* are extremely rare.

57 Variation throughout years can create different environments, which, in turn, will influence genotypes differently  
58 (Jaimez et al. 2020). The evaluation of genotypes across several harvests is crucial in perennial fruit trees as it enables  
59 the quantification of the genotype x measurement (GM) interaction effect and estimates of the repeatability coefficient to  
60 determine the optimal number of harvests necessary to conduct effective genetic selection (Resende 2015; Ferreira et al.,  
61 2020).

62 In this context, this study aimed to estimate the optimum number of harvests for genetic selection of *T.*  
63 *grandiflorum* progenies and identify the most promising progenies in terms of productivity, stability, and adaptability.

## 64 MATERIAL AND METHODS

## 65 Experimental data

66 Full-sib *T. grandiflorum* progeny tests were established in three farms in Northeastern Pará State, Brazil; two  
 67 located in the municipality of Tomé Açu and one in the municipality of São Francisco do Pará, approximately 210 km  
 68 apart. The three environments represent a sample of the different cultivation systems used to produce *T. grandiflorum* in  
 69 Pará. This experimental system enables the evaluation and selection of genotypes for conditions similar to those in which  
 70 they are often cultivated. The differences between the three environments are mainly the different cropping systems used  
 71 for each trial, in terms of temporary and definitive shading or full sun, and spacing.

72 Each *T. grandiflorum* progeny test was installed in consortium with other tree species, all of which were planted  
 73 in February 2005. The field arrangement affected conditions of luminosity and competition over and under the soil. In  
 74 trial 1, *T. grandiflorum* was maintained in shade during the productive phase, while in the other two trials (trials 2 and 3)  
 75 the trees were kept in full sun (Table 1). In trial 1, *T. grandiflorum* progenies were part of an agroforestry system (AFS),  
 76 together with *Passiflora edulis* Sims. (passion fruit) and *Swietenia macrophylla* King. (Brazilian mahogany), at initial  
 77 densities of 400, 800, and 100 plants/ha, respectively. After the third year, the passion fruit was removed from the AFS  
 78 as it had completed its cycle. Therefore, through all production stages, *T. grandiflorum* was shaded with *S. macrophylla*.  
 79 Trial 2 was also installed as an AFS and consisted of *T. grandiflorum* progenies, *Piper nigrum* L. (Black pepper), and  
 80 *Bertholletia excelsa* Bonpl. (Brazil nut), at densities of 303, 1800, and 75 plants/ha, respectively. As *B. excelsa* developed  
 81 a very prolific crown, producing too much shade for *T. grandiflorum* in the first years, it was removed from the AFS in  
 82 the fifth year. *Piper nigrum* cultivation occurred over the first seven years of the trial. Thus, after *P. nigrum* tree mortality  
 83 in the seventh year, *T. grandiflorum* was left in full sun. In trial 3, *T. grandiflorum* progenies were intercropped with  
 84 *Musa* spp. (banana tree), both with a density of 400 plants/ha. As in trial 2, after the fifth year, the *Musa* spp. was removed  
 85 from the AFS, with *T. grandiflorum* progenies remaining in full sun until the end of the study (Table 1). It is important to  
 86 highlight that these different field arrangements, involving full sun and temporary and definitive shading, were designed  
 87 to reproduce a similar environment to what farmers cultivate cupuassu tree in the state of Pará.

88 **Table 1.** Characteristics of the trials with 25 full-sib *Theobroma grandiflorum* progenies in Northeast Pará State, Brazil.  
 89

Characteristic	Trial 1	Trial 2	Trial 3
Soil type	Yellow latosol (Oxisol)	Yellow latosol (Oxisol)	Yellow latosol (Oxisol)
Soil texture	Loam	Clayey	Loam
Annual precipitation (mm)	2300	2300	2432
Average temperature (°C)	26.4	26.4	26.6
Latitude	02°26'03.0" S	02°25'57.8" S	01°07'01.1" S
Longitude	48°18'37.6" W	48°23'39.7" W	47°44'26.6" W

Altitude (m)	45	45	46
<i>T. grandiflorum</i> spacing (m)	5 x 5	5.5 x 6	5 x 5
Provisional shading and spacing (m)	<i>Passiflora edulis</i> (5 x 2.5)	<i>Piper nigrum</i> [(2 x 2) x 4]	<i>Musa</i> spp. (5 x 5)
Definitive shading and spacing (m)	<i>Swietenia macrophylla</i> (10 x 10)	<i>Bertholletia excelsia</i> (11 x 12) <sup>1</sup>	None
System type	Agroforestry	Full sun	Full sun
Initial density (including all species) (plants)	1300	2178	800
Final density (reproductive phase) <sup>2</sup> (plants)	500	441	400
Planting date	February, 2005	February, 2005	February, 2005

<sup>1</sup>: removed from the experimental field after the fifth year; <sup>2</sup>: excluding *Theobroma grandiflorum* mortality.

90  
91 The progeny test, carried out in three trials, was established using a randomized complete block design, with 25  
92 *T. grandiflorum* full-sib progenies, five replications, and three plants per plot. The 25 full-sib progenies were obtained  
93 through controlled pollination. Phenotypic data were measured over 11 consecutive annual harvests, based on a total plot.  
94 The harvest opening coincides with the beginning of the rainy season and extends over the entire period of about six  
95 months. Therefore, each harvest was divided into four evaluations with 45-day intervals between them. Response  
96 variables included the mean number of fruits/plant (NF) and mean fruit production (kg/plant), obtained by multiplying  
97 the NF by the average weight of the fruit of each genotype. We also assessed tolerance to witches' broom disease (*M.*  
98 *perniciosa*) based on the rate of symptomatic plants per progeny (WB, %). Plants were deemed symptomatic when at  
99 least one branch presented misshapen phyllotaxis, compared to a normal branch, and after one month appeared desiccated  
100 (Alves et al. 2009). For selection, a tolerance threshold of 30% was adopted as the maximum rate of symptomatic plants  
101 per progeny.

## 102 Statistical analyses

103 Due to the unbalance caused by the mortality of some trees, which is common in long-term trials involving  
104 perennial crops, the mixed model method was adopted for statistical analysis. With such an approach, the variance  
105 components and genetic parameters are estimated by the restricted maximum likelihood (REML) (Patterson and  
106 Thompson 1971), and genetic values are predicted by the best linear unbiased prediction (BLUP) (Henderson 1975). The  
107 mixed linear model associated with the analysis of progeny, with a complete randomized block design, three locations, at  
108 the plot level, and with repeated measures, is defined as:

$$109 y = Xf + Zg + Qge + Tgm + Wgem + Sp + e;$$

110 where,  $y$  is the vector of phenotypic data;  $f$  is the vector of the effects of the combination repetition-environment-  
111 measurement (assumed to be fixed), added to the general mean;  $g$  is the vector of genotypic effects (assumed to be  
112 random),  $g \sim \text{NID}(0, \sigma_g^2)$ , where  $\sigma_g^2$  is the genotypic variance;  $ge$  is the vector of genotypes  $\times$  environments (GE)

113 interaction effects (assumed to be random),  $ge \sim \text{NID}(0, \sigma_{ge}^2)$ , where  $\sigma_{ge}^2$  is the GE interaction variance;  $gm$  is the vector  
 114 of genotypes  $\times$  measurements (GM) interaction effects (random),  $gm \sim \text{NID}(0, \sigma_{gm}^2)$ , where  $\sigma_{gm}^2$  is the GM interaction  
 115 variance;  $gem$  is the vector of the triple genotypes  $\times$  environments  $\times$  measurements (GEM) interaction effects (random),  
 116  $gem \sim \text{NID}(0, \sigma_{gem}^2)$ , where  $\sigma_{gem}^2$  is the GEM interaction variance;  $p$  is the vector of the permanent plot effects within  
 117 locations (assumed to be random),  $p \sim \text{NID}(0, \sigma_{perm}^2)$ , where  $\sigma_{perm}^2$  is the permanent plot effect variance; and  $e$  is the  
 118 vector of residuals (random),  $e \sim \text{NID}(0, \sigma_e^2)$ , where  $\sigma_e^2$  is the residual variance. The capital letters ( $X, Z, Q, T, W$  e  $S$ )  
 119 represent the incidence matrices for the correspondents' effects.

120 The significance of the random effects of the statistical model was tested by the likelihood ratio test (LRT), given  
 121 by the following equation (Wilks 1938):

$$122 \quad LRT = -2(\text{Log}L - \text{Log}L_R);$$

123 where,  $\text{Log}L$  is the logarithm of the maximum point of the residual likelihood function ( $L$ ) of the complete model; and  
 124  $\text{Log}L_R$  is the logarithm of the maximum point of the residual likelihood function ( $L_R$ ) of the reduced model (without the  
 125 effect under test). The chi-square statistic with one degree of freedom and a probability level equal to 1% was used to test  
 126 the LRT significance.

127 From the variance components ( $\sigma_g^2, \sigma_{ge}^2, \sigma_{gm}^2, \sigma_{gem}^2, \sigma_{perm}^2$ , and  $\sigma_e^2$ ), we estimated (Resende et al. 2014):

$$128 \quad \text{Phenotypic variance: } \hat{\sigma}_p^2 = \sigma_g^2 + \sigma_{ge}^2 + \sigma_{gm}^2 + \sigma_{gem}^2 + \sigma_{perm}^2 + \sigma_e^2;$$

$$129 \quad \text{Mean phenotypic variance: } \overline{\hat{\sigma}_p^2} = \sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_{gm}^2}{m} + \frac{\sigma_{perm}^2}{b} + \sigma_e^2,$$

130 where  $e$ ,  $m$ , and  $b$  are the number of environments, measurements, and blocks, respectively;

$$131 \quad \text{Individual broad-sense heritability: } \hat{h}_g^2 = \frac{\sigma_g^2}{\hat{\sigma}_p^2};$$

$$132 \quad \text{Mean broad-sense heritability: } \hat{h}_{mg}^2 = \frac{\sigma_g^2}{\overline{\hat{\sigma}_p^2}};$$

$$133 \quad \text{Accuracy of genotype selection: } r_{gg} = \sqrt{\hat{h}_{mg}^2};$$

$$134 \quad \text{Coefficient of determination of GE interaction effects: } c_{ge}^2 = \frac{\sigma_{ge}^2}{\hat{\sigma}_p^2};$$

$$135 \quad \text{Coefficient of determination of GM interaction effects: } c_{gm}^2 = \frac{\sigma_{gm}^2}{\hat{\sigma}_p^2};$$

$$136 \quad \text{Coefficient of determination of GEM interaction effects: } c_{gem}^2 = \frac{\sigma_{gem}^2}{\hat{\sigma}_p^2};$$

$$137 \quad \text{Coefficient of determination of plot effects: } c_{perm}^2 = \frac{\sigma_{perm}^2}{\hat{\sigma}_p^2};$$

$$138 \quad \text{Coefficient of individual repeatability: } \rho = \frac{\sigma_g^2 + \sigma_{gm}^2 + \sigma_{perm}^2}{\hat{\sigma}_p^2};$$

139 Genotypic correlation among environments:  $r_{ge} = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{ge}^2}$ ;

140 Genotypic correlation among measurements:  $r_{gm} = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{gm}^2}$ ; and

141 Genotypic correlation among environments and measurements:  $r_{gem} = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{gr}^2 + \sigma_{gm}^2 + \sigma_{gem}^2}$ .

142 To determine the optimal number of harvests for genetic selection, accuracy was calculated considering the use  
143 of  $m$  harvests ( $r_m$ ) (Resende et al. 2014):

$$144 \quad r_m = \sqrt{\frac{m\rho}{m\rho + 1 - \rho}}$$

145 We also considered the efficiency (E) of the use of  $m$  harvests in relation to the use of only one harvest (Resende et al.  
146 2014):

$$147 \quad E = \sqrt{\frac{m}{[1 + (m - 1)\rho]}}$$

148 To select progenies with greater adaptability, stability, and productivity, the Harmonic Mean of Relative  
149 Performance of Genotypic Values (HMRPGV) method was used. This method provides a genotypic value that is affected  
150 negatively by instability and positively by adaptability (Resende 2004):

$$151 \quad \text{HMRPGV} = \frac{n}{\sum_j^n \frac{1}{\text{RPGV}_i}},$$

152 where,  $n$  is the number of environments;  $\text{RPGV}_{ij}$  is the Relative Performance of Genotypic Values, estimated as

$$153 \quad \text{RPGV}_i = \frac{\sum \frac{GV_{ij}}{\mu}}{m},$$

154 where,  $GV_{ij}$  is the genotypic value of the  $i^{\text{th}}$  genotype in the  $j^{\text{th}}$  environment, and  $\mu$  is the phenotypic mean of the  $j^{\text{th}}$   
155 environment. All statistical analyses were performed using the SELEGEN REML/BLUP software (Resende 2016).

## 156 RESULTS

157 The genotypic effects were significant for both the mean number of fruits/plant and mean fruit production/plant,  
158 indicating genetic variability among progenies. Furthermore, the presence of GE and GEM interaction was verified for  
159 these traits. As expected for polygenic traits, there was a high level of influence of uncontrolled environmental factors,  
160 which is reflected in the residual variance that corresponds to the largest proportion of phenotypic variance (Table 2).

161 **Table 2.** Estimates of the components of variance and genetic parameters for mean number of fruits/plant and mean fruit  
162 production/plant, evaluated in 25 full-sib progenies of *Theobroma grandiflorum*.

---

Component/ parameter	Mean number of fruits/plant	Mean fruit production/plant (kg)
-------------------------	--------------------------------	-------------------------------------

$\sigma_g^2$	4.20**	4.38**
$\sigma_{gm}^2$	0.40	0.37
$\sigma_{ge}^2$	1.38**	7.91**
$\sigma_{gem}^2$	3.42**	8.44**
$\sigma_{perm}^2$	3.45**	13.95**
$\sigma_e^2$	25.13	68.23
$\hat{\sigma}_p^2$	34.56	94.85
$\hat{h}_g^2 \pm$ standard error	$0.12 \pm 0.02$	$0.04 \pm 0.01$
$\hat{h}_{mg}^2$	0.87	0.59
$r_{gg}$	0.93	0.77
$c_{ge}^2$	0.04	0.08
$c_{gm}^2$	0.01	0.004
$c_{gem}^2$	0.09	0.09
$c_{perm}^2$	0.09	0.15
$\rho \pm$ standard error	$0.26 \pm 0.02$	$0.27 \pm 0.02$
$r_{ge}$	0.769	0.356
$r_{gm}$	0.913	0.920
$r_{gem}$	0.447	0.207
$\mu$	11.36	17.90

163  $\sigma_g^2$ : genotypic variance;  $\sigma_{gm}^2$ : variance of genotype x measurement interaction (GM);  $\sigma_{ge}^2$ : variance of genotype x  
164 environment interaction (GE);  $\sigma_{gem}^2$ : variance of genotype x environment x measurement interaction (GEM);  $\sigma_{perm}^2$ :  
165 variance of permanent plot effects;  $\sigma_e^2$ : residual variance;  $\hat{\sigma}_p^2$ : phenotypic variance;  $\hat{h}_g^2$ : individual broad-sense heritability;  
166  $\hat{h}_{mg}^2$ : mean broad-sense heritability;  $r_{gg}$ : accuracy of genotype selection;  $c_{ge}^2$ : coefficient of determination of GE  
167 interaction effects;  $c_{gm}^2$ : coefficient of determination of GM interaction effects;  $c_{gem}^2$ : coefficient of determination of GEM  
168 interaction effects;  $c_{perm}^2$ : coefficient of determination of plot effects;  $\rho$ : coefficient of individual repeatability;  $r_{ge}$ :  
169 genotypic correlation among environments;  $r_{gm}$ : genotypic correlation among measurements;  $r_{gem}$ : genotypic correlation  
170 among environments and measurements; and  $\mu$ : general mean. \*\*: significant at  $P < 0.01$ , by chi-square test.

171 Only mean broad-sense heritability of genotypes ( $\hat{h}_{mg}^2$ ) can be considered high. Both mean and individual broad-  
172 sense heritability ( $\hat{h}_g^2$ ) were higher for mean number of fruits/plant than for mean fruit production/plant. Selective accuracy  
173 ( $r_{gg}$ ) followed the same pattern. The coefficient of repeatability ( $\rho$ ) showed similar magnitudes for mean number of  
174 fruits/plant and mean fruit production/plant, a positive aspect in selection when considering both traits simultaneously  
175 since the optimal number of measurements will coincide. With the use of a greater number of measurements, compared  
176 to only one measurement, the selective accuracy increases (Fig 1). With the use of data from three harvests, the selective  
177 accuracy exceeds 0.70; with the use of 11 harvests, the selective accuracy exceeds 0.90 (Fig 1A). The efficiency associated

178 with the use of  $m$  measures indicates smaller increments as the number of harvests increases (Fig 1B). These increments  
179 become almost constant as of the ninth harvest, with only 2% increase compared to the previous harvest.

180 The coefficient of determination of GE interaction effects ( $c_{ge}^2$ ), GM interaction effects ( $c_{gm}^2$ ), and plot effects  
181 ( $c_{perm}^2$ ) were all low for both traits (ranging from 0.004 to 0.15). The genotypic correlations across environments ( $r_{ge}$ ) and  
182 environments and measurements ( $r_{gm}$ ) were higher for mean number of fruits/plant, while the genotypic correlation across  
183 measurements ( $r_{gm}$ ) was slightly higher for mean fruit production/plant.

184 For mean number of fruits/plant, the coincidence was high (90%) between HMRPGV, genotypic values ( $\mu + g$ ),  
185 and genotypic values plus the mean effect of the GE interaction ( $\mu + g + gem$ ), considering the selection of the 10 best  
186 progenies. This demonstrates that the most productive progenies are also the most adapted and stable. The selection of  
187 the ten best progenies (36, 37, 11, 5, 49, 23, 6, 43, 19, and 25) provided a predicted selection gain of 2.61 fruits/plant (~  
188 23% compared to the general mean) (Table 3).

189 For mean fruit production/plant (kg), which is the trait of greatest economic importance, there was an 80%  
190 coincidence between  $\mu + g$ ,  $\mu + g + gem$ , and HMRPGV. Progenies 56 and 43, despite having higher values for  $\mu + g$  and  
191  $\mu + g + gem$  compared to genotypes 25 and 38 (ranked 9<sup>th</sup> and 10<sup>th</sup>, respectively), did not show satisfactory stability. The  
192 selection of the ten best progenies (36, 5, 37, 11, 23, 49, 21, 6, 25, and 38) led to a predicted selection gain of 2.03 kg per  
193 plant (~ 11.3% compared to the general mean; Table 3). However, for genetic selection, the incidence rate of witches'  
194 broom must be taken into account. Considering a rate of 30% symptomatic plants per progeny as a tolerance threshold,  
195 progenies 36, 6, and 38 should not be selected. Thus, the choice of the seven remaining progenies (5, 37, 11, 23, 49, 21,  
196 and 25, in bold) provided a predicted selection gain of 2.05 kg (~ 11.4% in relation to the general mean).

197  
198 **Table 3.** Genotypic values ( $\mu + g$ ), genotypic values plus the average GE interaction effect ( $\mu + g + gem$ ), Harmonic  
199 Mean of the Relative Performance of Genotypic Values multiplied by the General Mean (HMRPGV \*  $\mu$ ), and genetic gain  
200 with selection (Gain), for mean number of fruits/plant, mean fruit production/plant, and incidence rate of witches' broom  
201 (WB, %), evaluated in 25 full-sib progenies (Prog) of *Theobroma grandiflorum*.

Prog <sup>1</sup>	Mean number of fruits/plant				Mean fruit production/plant (kg)					
	( $\mu + g$ )	( $\mu + g + gem$ )	(HMRPGV * $\mu$ )	Gain	Prog <sup>1</sup>	( $\mu + g$ )	( $\mu + g + gem$ )	(HMRPGV * $\mu$ )	Gain	WB (%)
36	15.25	15.67	15.70	3.89	36	21.13	23.08	23.10	3.23	37.3
<b>37</b>	14.61	14.96	15.03	3.57	<b>5</b>	19.98	21.24	21.58	2.66	11
<b>11</b>	13.71	13.96	13.85	3.16	<b>37</b>	19.84	21.01	20.97	2.42	25.8
<b>5</b>	13.49	13.73	13.63	2.91	<b>11</b>	19.41	20.32	20.57	2.09	11
<b>49</b>	13.09	13.28	13.20	2.67	<b>23</b>	19.56	20.55	20.43	2.23	29
<b>23</b>	12.95	13.13	13.11	2.49	<b>49</b>	19.14	19.89	20.10	1.95	20
6	12.25	12.35	12.31	2.26	<b>21</b>	18.54	18.93	18.92	1.76	8.3
43	12.13	12.21	11.97	2.08	6	18.41	18.72	18.81	1.61	32.7
19	11.54	11.56	11.59	1.46	<b>25</b>	18.01	18.08	17.91	1.24	23.5

<b>25</b>	11.57	11.59	11.57	1.57	38	17.84	17.81	17.83	1.14	33.8
38	11.58	11.60	11.56	1.71	52	18.35	18.63	17.75	1.48	37.5
52	11.62	11.65	11.55	1.88	43	18.18	18.35	17.66	1.36	69.8
8	11.19	11.17	11.18	1.33	9	17.71	17.60	17.46	1.03	37.8
4	11.10	11.07	11.06	1.22	8	17.66	17.51	17.38	0.94	8.7
1	10.92	10.87	10.80	1.11	22	17.42	17.13	17.01	0.70	37.7
<b>21</b>	10.75	10.69	10.72	0.91	20	17.55	17.34	16.97	0.86	19.7
9	10.80	10.74	10.67	1.00	4	17.20	16.79	16.69	0.63	22.3
20	10.37	10.26	10.29	0.80	19	17.11	16.64	16.62	0.55	15.8
22	10.15	10.02	10.06	0.70	13	17.49	17.25	16.43	0.78	72.8
17	9.90	9.74	9.78	0.49	1	17.11	16.64	16.13	0.49	28.7
13	9.96	9.80	9.54	0.59	17	16.56	15.76	15.66	0.40	37.5
30	9.51	9.31	9.25	0.39	30	16.45	15.57	15.59	0.32	44.3
40	8.99	8.73	8.76	0.27	40	15.97	14.82	14.44	0.22	26.7
29	8.69	8.40	8.42	0.15	29	15.70	14.37	14.41	0.12	17
28	7.85	7.47	7.42	0.00	28	15.09	13.40	13.23	0.00	13.5
Means	11.36	11.36	11.32	1.54		17.90	17.90	17.75	1.21	28.89

202 <sup>1</sup>progenies are listed in decreasing order in terms of results for mean number of fruits/plant and mean fruit  
 203 production/plant, respectively. Selected progenies are in bold.

## 204 **DISCUSSION**

205 LRT shows genetic variability among progenies for both the traits mean number of fruits/plant and mean fruit  
 206 production/plant. Although the GE and GEM interactions were significant, the genotypic correlation among environments  
 207 ( $r_{ge}$ ) was high (0.77) only for mean number of fruits/plant, according to the classification proposed by (Resende and  
 208 Alves 2020). These results indicate that for this trait the performance of progenies is moderately similar among the trials  
 209 and some of the same progenies can be selected for them all.

210 The significance of the GE interaction associated with low genotypic correlation among environments ( $r_{ge} =$   
 211 0.356) for mean fruit production/plant indicate that the cultivation system of *T. grandiflorum* can have a significant  
 212 influence on the productive performance of different genotypes in different environments. Given that the varied needs of  
 213 the stakeholders and intended end users must be considered when developing cultivars, it is important to highlight that  
 214 the vast majority of producers in Northeast Pará use cultivation systems similar to those studied herein. Therefore, it is  
 215 essential to select genotypes that have satisfactory adaptability, stability, and productivity in a range of management  
 216 scenarios (Diouf et al. 2020). In studying *T. cacao*, Salazar et al. (2018) found that the level of shade, one of the  
 217 distinguishing characteristics of each environment studied herein, can have an effect on photosynthesis and, thus,  
 218 productive capacity.

219 Based on the coefficient of determination of the GE interaction ( $c_{ge}^2$ ) and genotypic correlation among  
 220 environments ( $r_{ge}$ ), mean fruit production/plant was more heavily influenced by the environment than mean number of  
 221 fruits/plant. In a previous study (Resende and Alves 2020), the authors highlight that a useful indicator is the ratio between

222 the variances attributed to the GE interaction and the genotype ( $P = \sigma_{ge}^2 / \sigma_g^2$ ). Variables with  $P < 0.5$ , as is the case with  
223 mean number of fruits/plant (0.33), will not be problematic for selection; while traits with  $P > 0.5$ , such as mean fruit  
224 production/plant (1.80), tend to generate problems due to the complex GE interaction, especially when the intention is to  
225 carry out indirect selection.

226 Such a pattern is expected since mean fruit production/plant is a quantitative trait composed of two other traits  
227 that are also polygenic: the mean number of fruits/plant and the mean fruit weight. Traits of this nature are influenced by  
228 the activity of numerous genes, combined with significant environmental effects (Kumar et al. 2017). This highlights the  
229 impact the type of management can have on the phenotypic manifestation of the evaluated traits, especially mean fruit  
230 production/plant. This fact, combined with the variability resulting from the species' self-incompatibility (Venturieri  
231 2011), is reflected in uncertainties about the cultivation of genetic materials that have not been evaluated in a range of  
232 environments and emphasizes the importance of studies of this nature.

233 On the other hand, the GM interaction was not significant. According to Ferreira et al. (2020), this result is an  
234 indication that there is consistency in the performance of genotypes across the years of evaluation. This was confirmed  
235 by the high values of the genotypic correlation through measurements for both mean number of fruits/plant and mean  
236 fruit production/plant ( $> 0.90$ ). The GM interaction is mainly related to the reaction of progenies to climate change and  
237 its consequences. The development of improved genetic materials must take into account the variation of the climate  
238 between and within years, aiming to increase the resilience of the cultivars offered to producers (Atlin et al. 2017). The  
239 genotypes evaluated in this study fulfil this requirement. When evaluating both components mentioned above jointly  
240 through the triple interaction (GEM), differential behavior was observed across trials and years. However, given the non-  
241 significance of GM, it appears that most of the GEM interaction is due to the GE interaction.

242 According to the classification presented by Resende (2015), individual broad-sense heritability showed a low  
243 magnitude ( $\hat{h}_g^2 < 0.15$ ) for both traits. In contrast, estimates of mean heritability showed a high magnitude ( $\hat{h}_{mg}^2 > 0.50$ ).  
244 The low individual broad-sense heritability ( $\hat{h}_g^2$ ) refers to the quantitative nature of both traits, as discussed above, making  
245 the process of selection more complex (Sousa et al. 2019). Through the interpretation of these heritability values, along  
246 with the high mean heritability ( $\hat{h}_{mg}^2$ ) for both traits, we can infer that priority should be given to the selection of progenies,  
247 rather than the selection of ortets. This is due to the relationship between heritability and genetic gains with selection, in  
248 which the latter is a direct function of the former. Thus, heritability estimates can reveal the selection efficacy, before it  
249 is done (Schmidt et al., 2019). Therefore, smaller-scale heritabilities, as observed at the individual level, can jeopardize  
250 the genetic gains. A previous study (Bezerra et al. 2020) considered this fact to recommend the selection of full-sib  
251 families in guava (*Psidium guajava* L.) to achieve greater genetic gains. Another attribute of heritability is related to  
252 selection accuracy. According to Resende and Duarte (2007), values above 0.7 are considered high, as is the case for

253 mean fruit production/plant, and above 0.9 they are considered very high, as is the case with mean number of fruits/plant.  
254 The selective accuracy, or the correlation between the true and predicted genotypic value, enables us to infer the selection  
255 precision (Resende 2002; Cavalcante et al. 2017).

256 Heritability is also related to the repeatability coefficient, which is the maximum value that individual broad-  
257 sense heritability can achieve (Resende 2002). Estimating the repeatability coefficient using the mixed model method has  
258 greater flexibility when compared to ANOVA, as it can be used even when the assumptions required for the analysis of  
259 variance are not met (Ferreira et al. 2020). Previous research has highlighted the importance of this parameter for perennial  
260 species, which have a long breeding cycle (Sánchez et al. 2017). In that study, the authors obtained a repeatability  
261 coefficient of 0.35 for fruit production in *Annona muricata* L., classifying it as moderate, based on (Resende 2002).  
262 Taking into account this same classification, the estimates of repeatability coefficients for both traits studied herein were  
263 of low magnitude ( $< 0.3$ ), which indicates that the evaluation of several harvests is necessary for genetic selection. To  
264 achieve an accuracy of 0.70, the minimum value for selection aiming at recombination (Resende and Duarte, 2007), data  
265 from three consecutive initial harvests are enough, which is consistent with what was found for yield components in *T.*  
266 *cacao* (Carvalho et al. 2002; Mustiga et al. 2018). If the objective is only to recombine and advance the cycle, subsequent  
267 measurements are unnecessary as they would offer limited increases in efficiency (Fig 1B) but require more time and  
268 incur higher costs related to the measurement of each harvest. If the intention is to identify genetic materials for  
269 cultivation, the evaluation of 11 harvests is recommended, since conducting such measurements can offer a selective  
270 accuracy of 0.90, a value suggested by Resende and Duarte (2007). Within the *Theobroma* genus, analyses similar to the  
271 present study have only been conducted for *T. cacao* (Carvalho et al. 2002; Dias et al. 1998) and have offered substantial  
272 and fundamental results for breeding programs. For *T. grandiflorum*, the results presented herein will enable optimization  
273 of the breeding period, increasing gains by decreasing the time of field assessment from 15 to six years, considering the  
274 three years needed for initial establishment (juvility period). Studies of this nature are rare for *T. grandiflorum*, thus  
275 demonstrating the pioneering nature of this work.

276 The use of HMRPGV proved to be a viable alternative for *T. grandiflorum*, as it allows us to infer the adaptability  
277 and stability of genotypic values. We found high levels of coincidence between the best genotypes in HMRPGV and  $\mu +$   
278  $g$ , what indicates the efficiency of the method (Evangelista et al. 2021). Comparing both studied traits, it is clear that there  
279 is no perfect match as to the best genotypes. This is due to the low levels of correlation between the number of fruits and  
280 the average weight of fruits, that is, plants that produce heavy fruits and in large quantities are exceptions. The  
281 identification of these genotypes is essential for advancing the improvement of the species (Alves et al. 2021). In this  
282 context, progenies 36, 37, 11, 5, 49, 23, 6, and 25 are the most suitable, as they stand out for both traits simultaneously.

283 Combining the analysis of productive traits with the resistance to witches' broom (*M. pernicioso*) disease,  
284 progenies 6, 36, and 38 were excluded, as they did not present satisfactory tolerance, and thus, can increase the pathogen

285 pressure on resistant individuals. Thus, of the 25 studied progenies, 5, 37, 11, 23, 49, 21, and 25 were selected. Breeding  
 286 programs for *T. grandiflorum* must always take into account the plants' reaction to the fungus since it is the main pathogen  
 287 that affects the cultivation of both *T. grandiflorum* and *T. cacao* (Mournet et al. 2020). Therefore, through breeding of  
 288 the species, genetic materials can be developed that combine high levels of productivity and resistance to *M. pernicioso*,  
 289 thus reducing production costs related to phytosanitary pruning and the application of fungicide. This, in turn, can mitigate  
 290 the risks and effects of chemical contamination for humans, animals, and the environment (Willoquet et al. 2017).

## 291 CONCLUSIONS

292 Data from three or 11 harvests should be used in selection aiming at recombination or identification of genotypes  
 293 for selection, respectively.

294 Seven progenies (5, 37, 11, 23, 49, 21 and 25) were identified and selected with high adaptability, stability,  
 295 productivity, and resistance to witches' broom disease.

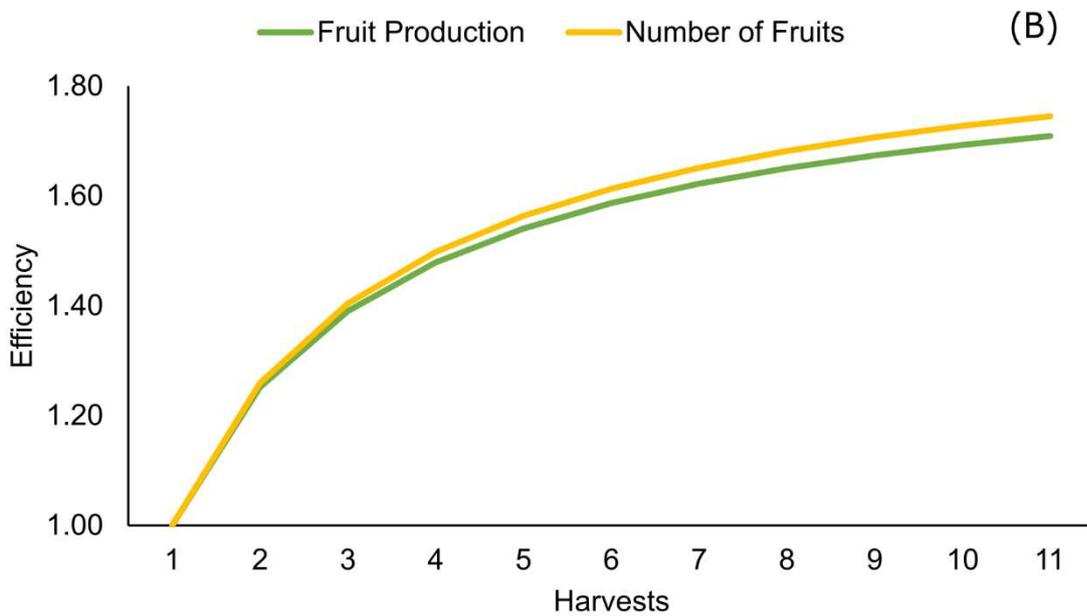
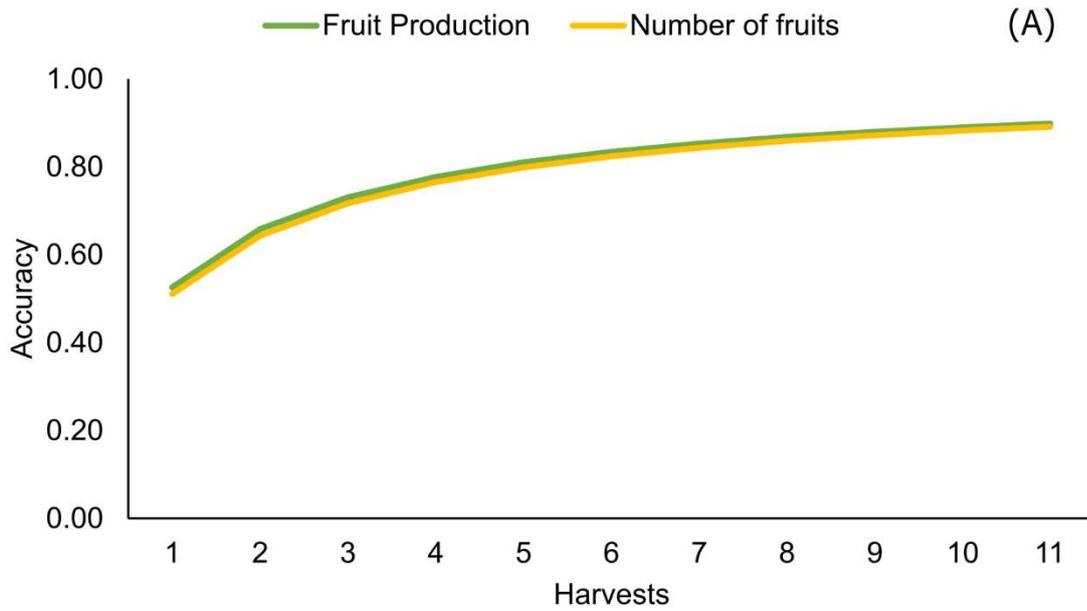
## 296 REFERENCES

- 297 Alves RM, Sebbenn AM, Artero AS, Clement C, Figueira A (2003) Mating system in a natural population of *Theobroma*  
 298 *grandiflorum* (Willd. ex Spreng.) Schum., by microsatellite markers. *Genet. Mol. Biol* 26(3):373-379. doi:  
 299 10.1590/S0100-29452013000300019
- 300 Alves RM, Sebbenn AM, Artero AS, Clement C, Figueira A (2007) High levels of genetic divergence and inbreeding in  
 301 populations of cupuassu (*Theobroma grandiflorum*). *Tree Genetics. Genomes* 3(4):289-298. doi: 10.1007/s11295-  
 302 006-0066-9
- 303 Alves RM, Resende MDV, Bandeira BDS, Pinheiro TM, Farias DCR (2009) Evolução da vassoura-de-bruxa e avaliação  
 304 da resistência em progênies de cupuaçuzeiro. *Rev. Bras. Frutic* 31(4):1022-1032. doi: 10.1590/S0100-  
 305 29452009000400015
- 306 Alves RM, Filgueiras GC, Homma AKO (2004) Aspectos socioeconômicos do cupuaçuzeiro na Amazônia: do  
 307 extrativismo a domesticação. In: Santana AC (ed). *Mercado, cadeias produtivas e desenvolvimento rural na Amazônia*.  
 308 1st ed. UFRA, Belém, pp. 197–223.
- 309 Alves RM, Chaves SFS, Alves RS, Santos TG, Araújo DG, Resende MDV (2021) Cupuaçu tree genotype selection for  
 310 an agroforestry system environment in the Amazon. *Pesq. Agropec. Bras* 56:e02139. doi: 10.1590/S1678-3921.
- 311 Atlin GN, Cairns JE, Das B (2017) Rapid breeding and varietal replacement are critical to adaptation of cropping systems  
 312 in the developing world to climate change. *Glob. Food Sec* 12:31-37. doi: 10.1016/j.gfs.2017.01.008
- 313 Bezerra CM, Ribeiro RM, Viana AP, Cavalcante NR, Silva FAD, Ambrósio M, Amaral Junior ATD (2020) Guava  
 314 breeding via full-sib family selection: conducting selection cycle and divergence between parents and families. *Crop*  
 315 *Breed. Appl. Biotechnol* 20(1):e256520112. doi: 10.1590/1984-70332020v20n1a12

- 316 Carvalho CGP, Cruz CD, Almeida CMVC, Machado PFR (2002) Yield repeatability and evaluation period in hybrid  
317 cocoa assessment. *Crop Breed. Appl. Biotechnol* 2(1):149-156. doi: 10.12702/1984-7033.v02n01a19
- 318 Cavalcante NR, Krause W, Viana AP, Silva CA, Porto KXX, Martinez RAS (2017) Anticipated selection for  
319 intrapopulation breeding of passion fruit. *Acta Sci. Agron* 39(2):143-148. doi: 10.4025/actasciagron.v39i2.31022
- 320 Chipeta MM, Melis R, Shanahan P, Sibiya J, Benesi RMI (2017) Genotype x environment interaction and stability  
321 analysis of cassava genotypes at different harvest times. *J. Anim. Plant Sci* 27:901–919.
- 322 Coelho IF, Peixoto MA, Evangelista JSPC, Alves RS, Sales S, Resende MDV et al (2020) Multiple-trait, random  
323 regression, and compound symmetry models for analyzing multi-environment trials in maize breeding. *PLoS ONE*  
324 15(11):e0242705. doi: 10.1371/journal.pone.0242705
- 325 Dias LAS, Kageyama PY (1998) Repeatability and minimum harvest period of cacao (*Theobroma cacao* L.) in Southern  
326 Bahia. *Euphytica* 102(1): 29-35. doi: 10.1023/A:1018373211196
- 327 Dias PC, Xavier A, Resende MDV, Barbosa MHP, Bierkaski FA, Estopa RA (2018) Genetic evaluation of *Pinus taeda*  
328 clones from somatic embryogenesis and their genotype x environment interaction. *Crop Breed. Appl. Biotechnol*  
329 18:55–64. doi: 10.1590/1984-70332018v18n1a8
- 330 Diouf I, Derivot L, Koussevitzky S, Carretero Y, Bitton F, Moreau L, Causse M (2020) Genetic basis of phenotypic  
331 plasticity and genotype × environment interactions in a multi-parental tomato population. *J. Exp. Bot* 71(18):5365-  
332 5376. doi: 10.1093/jxb/eraa265
- 333 Evangelista JSPC, Alves RS, Peixoto MA, Resende MDV, Teodoro PE, Silva FL, Bhering LL (2021) Soybean  
334 productivity, stability, and adaptability through mixed model methodology. *Cienc. Rural* 51(2):e20200406. doi:  
335 10.1590/0103-8478cr20200406
- 336 Ferreira FM, Alves RS, Elizeu AM, Benites FRG, Resende MDV, Souza Sobrinho F, Bhering LL (2020) Estimates of  
337 repeatability coefficients and optimum number of measures for genetic selection of *Cynodon* spp. *Euphytica* 216(5):1-  
338 11. doi: 10.1007/s10681-020-02605-x
- 339 Genovese MI, Lannes SCS (2009) Comparison of total phenolic content and antiradical capacity of powders and  
340 "chocolates" from cocoa and cupuassu. *Food Sci. Technol* 29:810–814. doi: 10.1590/S0101-20612009000400017
- 341 Gramacho KP, Luz EDMN, Silva FS, Lopes UV, Pires JL, Pereira L (2016) Pathogenic variability of *Moniliophthora*  
342 *perniciosa* in three agroecological zones of the cacao region of Bahia, Brazil. *Crop Breed. Appl. Biotechnol* 16:7–13.  
343 doi: 10.1590/1984-70332016v16n1a2
- 344 Henderson CR (1975) Best linear unbiased estimation and prediction under a selection model. *Biometrics* 31:423-447.  
345 doi: 10.2307/2529430
- 346 Homma AKO (2014) Extrativismo vegetal na Amazônia: história, ecologia, economia e domesticação. 2<sup>nd</sup> ed, Embrapa:  
347 Brasília.

- 348 Jaimez RE, Vera DI, Mora A, Loor RG, Bailey BA (2020) A disease and production index (DPI) for selection of cacao  
349 (*Theobroma cacao*) clones highly productive and tolerant to pod rot diseases. *Plant Pathol* 69:698-712. doi:  
350 10.1111/ppa.13156.
- 351 Kumar J, Gupta DS, Gupta S, Dubey S, Gupta P, Kumar S (2017) Quantitative trait loci from identification to exploitation  
352 for crop improvement. *Plant Cell Rep* 36(8):1187-1213. doi: 10.1007/s00299-017-2127-y
- 353 Mournet P, Albuquerque PSB, Alves RM, Silva-Werneck JO, Rivallan R, Marcellino LH, Clément D (2020) A reference  
354 high-density genetic map of *Theobroma grandiflorum* (Willd. ex Spreng) and QTL detection for resistance to witches'  
355 broom disease (*Moniliophthora perniciosa*). *Tree Geneti. Genomes* 16(6):1-13. doi: 10.1007/s11295-020-01479-3
- 356 Mustiga GM, Gezan SA, Phillips-Mora W, Arciniegas-Leal A, Mata-Quirós A, Motamayor JC (2018) Phenotypic  
357 description of *Theobroma cacao* L. for yield and vigor traits from 34 hybrid families in Costa Rica based on the  
358 genetic basis of the parental population. *Front. Plant. Sci* 9:808. doi: 10.3389/fpls.2018.00808.
- 359 Oliveira TB, Genovese MI (2013) Chemical composition of cupuassu (*Theobroma grandiflorum*) and cocoa (*Theobroma*  
360 *cacao*) liquors and their effects on streptozotocin-induced diabetic rats. *Food Res. Int* 51:929–935. doi:  
361 10.1016/j.foodres.2013.02.019
- 362 Para [Internet] Secretaria de Estado de Desenvolvimento Agropecuário e da Pesca: Indicadores Agropecuários 2020 [cited  
363 2021 Apr 21]. Available from: <http://www.sedap.pa.gov.br/content/cupua%C3%A7u>
- 364 Patrocinio NGRB, Ceresini PC, Gomes LZ, Resende ML, Mizubbuti ESG, Gramacho KP (2017) Population structure  
365 and migration of the witches' broom pathogen *Moniliophthora perniciosa* from cacao and cultivated and wild  
366 solanaceous hosts in southeastern Brazil. *Plant Pathol* 66: 900–911. doi: 10.1111/ppa.12636
- 367 Patterson HD, Thompson R (1971) Recovery of inter-block information when block sizes are unequal. *Biometrika* 58:545-  
368 554. doi: 10.1093/biomet/58.3.545
- 369 Pugliese AG, Tomas-Barberan FA, Truchado P, Genovese MI (2013) Flavonoids, proanthocyanidins, vitamin C, and  
370 antioxidant activity of *Theobroma grandiflorum* (Cupuassu) pulp and seeds. *J. Agric. Food Chem* 61:2720–2728. doi:  
371 10.1021/jf304349u
- 372 Resende MDV (2002) *Genética biométrica e estatística no melhoramento de plantas perenes*. 1st ed. Embrapa Informação  
373 Tecnológica: Brasília.
- 374 Resende MDV (2004) *Métodos estatísticos ótimos na análise de experimentos de campo*. Embrapa Florestas:Colombo.
- 375 Resende MDV, Duarte JB (2007) Precisão e controle de qualidade em experimentos de avaliação de cultivares. *Pesqui.*  
376 *Agropecu. Trop* 37(3):182-194.
- 377 Resende MDV, Silva FF, Azevedo CF (2014) *Estatística Matemática, Biométrica e Computacional*. 1st ed. Suprema:  
378 Visconde do Rio Branco.
- 379 Resende MDV (2015) *Genética quantitativa e de populações*. 1st ed. Suprema: Visconde do Rio Branco.

- 380 Resende MDV (2016) Software Selegen-REML/BLUP: a useful tool for plant breeding. *Crop Breed. Appl. Biotechnol*  
381 16:330–339. doi: 10.1590/1984-70332016v16n4a49
- 382 Resende MDV, Alves RS (2020) Linear, Generalized, Hierarchical, Bayesian and Random Regression mixed models in  
383 genetics/genomics in plant breeding. *Funct. Plant. Breed. J.* 2:1–31. doi: 10.35418/2526-4117/v2n2a1
- 384 Salazar JCS, Melgarejo LM, Casanoves F, Rienzo JA, DaMatta FM, Armas C (2018) Photosynthesis limitations in cacao  
385 leaves under different agroforestry systems in the Colombian Amazon. *PLoS ONE* 13(11):e0206149. doi:  
386 10.1371/journal.pone.0206149
- 387 Sánchez CFB, Alves RS, Garcia A, Teodoro PE, Peixoto LA, Silva LA, Bhering LL, Resende MDV (2017) Estimates of  
388 repeatability coefficients and the number of the optimum measure to select superior genotypes in *Annona muricata* L.  
389 *Genet. Mol. Res* 16(3):gmr16039753. doi: 10.4238/gmr16039753
- 390 Schmidt P, Hartung J, Bennowitz J, Piepho H (2019) Heritability in plant breeding on a genotype-difference basis.  
391 *Genetics* 212:991-1008. doi: 10.1534/genetics.119.302134
- 392 Silva EM, Nunes EWLP, Costa JM, Ricarte AO, Nunes GHS, Aragão FAZ (2019) Genotype x environment interaction,  
393 adaptability and stability of ‘Piel de Sapo’ melon hybrids through mixed models. *Crop Breed. Appl. Biotechnol*  
394 19:402–411. doi: 10.1590/1984-70332019v19n4a57
- 395 Silva LMR, Sousa PHM, Sabino LBS, Prado GM, Torres LBV, Maia GA, Figueiredo RW, Ricardo NMPS (2020)  
396 Brazilian (North and Northeast) fruit by products. In: Campos-Vega R, Oomah BD, Vergara-Castañeda HA, eds. *Food*  
397 *Wastes and By-products: Nutraceutical and Health Potential*. John Wiley and Sons, New Jersey, pp. 127–158.
- 398 Sousa TV, Caixeta ET, Alkimim ER, Oliveira ACB, Pereira AA, Sakiyama NS, Zambolim L, Resende MDV (2019)  
399 Early selection enabled by the implementation of genomic selection in *Coffea arabica* breeding. *Front. Plant Sci*  
400 9:1934. doi: 10.3389/fpls.2018.01934
- 401 Venturieri GA (2011) Flowering levels, harvest season and yields of cupuassu (*Theobroma grandiflorum*). *Acta Amaz*  
402 41:143–152. doi: 10.1590/S0044-59672011000100017
- 403 Wilks SS (1938) The Large-Sample Distribution of the Likelihood Ratio for Testing Composite Hypotheses. *Ann Math*  
404 *Stat* 9:60–62. doi: 10.1214/aoms/1177732360
- 405 Willocquet L, Savary S, Yuen J (2017) Multiscale phenotyping and decision strategies in breeding for resistance. *Trends*  
406 *Plant Sci* 22(5):420–432. doi: 10.1016/j.tplants.2017.01.009
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408

409 **Fig 1. Accuracy (A) and efficiency (B) of selection as a function of the number of measures.**

410