

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

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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) ¹	None
System type	Agroforestry	Full sun	Full sun
Initial density (including all species) (plants)	1300	2178	800
Final density (reproductive phase) ² (plants)	500	441	400
Planting date	February, 2005	February, 2005	February, 2005

¹: removed from the experimental field after the fifth year; ²: 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:

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

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 σ_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 σ_{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 σ_{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 σ_{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 σ_{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 σ_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 σ_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; 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^{th} genotype in the j^{th} environment, and μ is the phenotypic mean of the j^{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)
-------------------------	--------------------------------	-------------------------------------

σ_g^2	4.20**	4.38**
σ_{gm}^2	0.40	0.37
σ_{ge}^2	1.38**	7.91**
σ_{gem}^2	3.42**	8.44**
σ_{perm}^2	3.45**	13.95**
σ_e^2	25.13	68.23
$\hat{\sigma}_p^2$	34.56	94.85
$\hat{h}_g^2 \pm$ standard error	0.12 ± 0.02	0.04 ± 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 ± 0.02	0.27 ± 0.02
r_{ge}	0.769	0.356
r_{gm}	0.913	0.920
r_{gem}	0.447	0.207
μ	11.36	17.90

163 σ_g^2 : genotypic variance; σ_{gm}^2 : variance of genotype x measurement interaction (GM); σ_{ge}^2 : variance of genotype x
164 environment interaction (GE); σ_{gem}^2 : variance of genotype x environment x measurement interaction (GEM); σ_{perm}^2 :
165 variance of permanent plot effects; σ_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; ρ : 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 μ : 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 (ρ) 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 9th and 10th, 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 * μ), 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 ¹	Mean number of fruits/plant				Prog ¹	Mean fruit production/plant (kg)				
	($\mu + g$)	($\mu + g + gem$)	(HMRPGV * μ)	Gain		($\mu + g$)	($\mu + g + gem$)	(HMRPGV * μ)	Gain	WB (%)
36	15.25	15.67	15.70	3.89	36	21.13	23.08	23.10	3.23	37.3
37	14.61	14.96	15.03	3.57	5	19.98	21.24	21.58	2.66	11
11	13.71	13.96	13.85	3.16	37	19.84	21.01	20.97	2.42	25.8
5	13.49	13.73	13.63	2.91	11	19.41	20.32	20.57	2.09	11
49	13.09	13.28	13.20	2.67	23	19.56	20.55	20.43	2.23	29
23	12.95	13.13	13.11	2.49	49	19.14	19.89	20.10	1.95	20
6	12.25	12.35	12.31	2.26	21	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	25	18.01	18.08	17.91	1.24	23.5

25	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
21	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 ¹progenies 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.

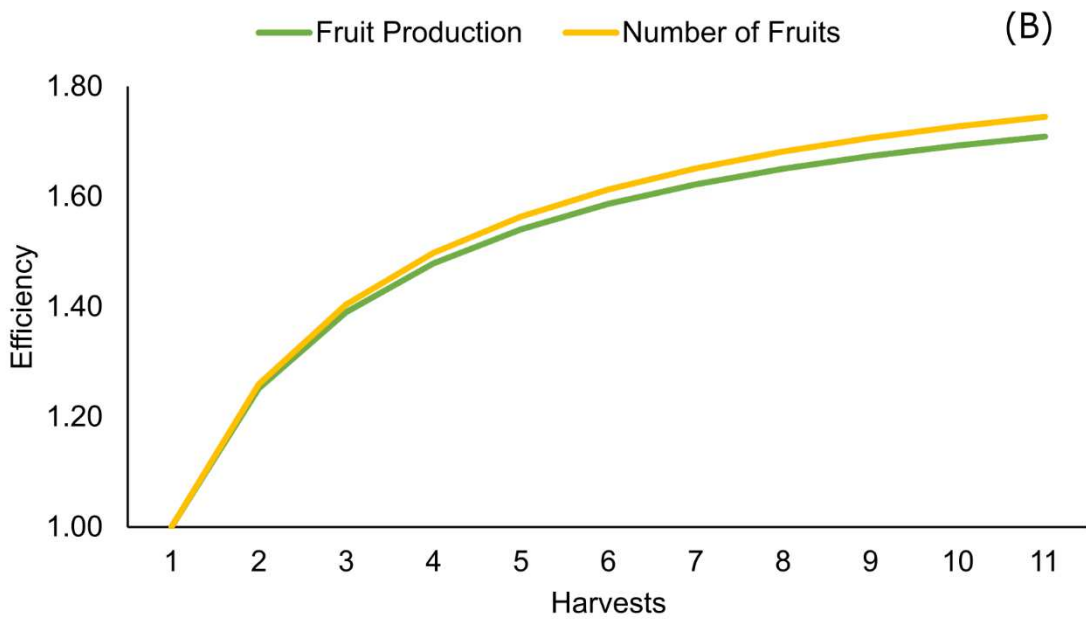
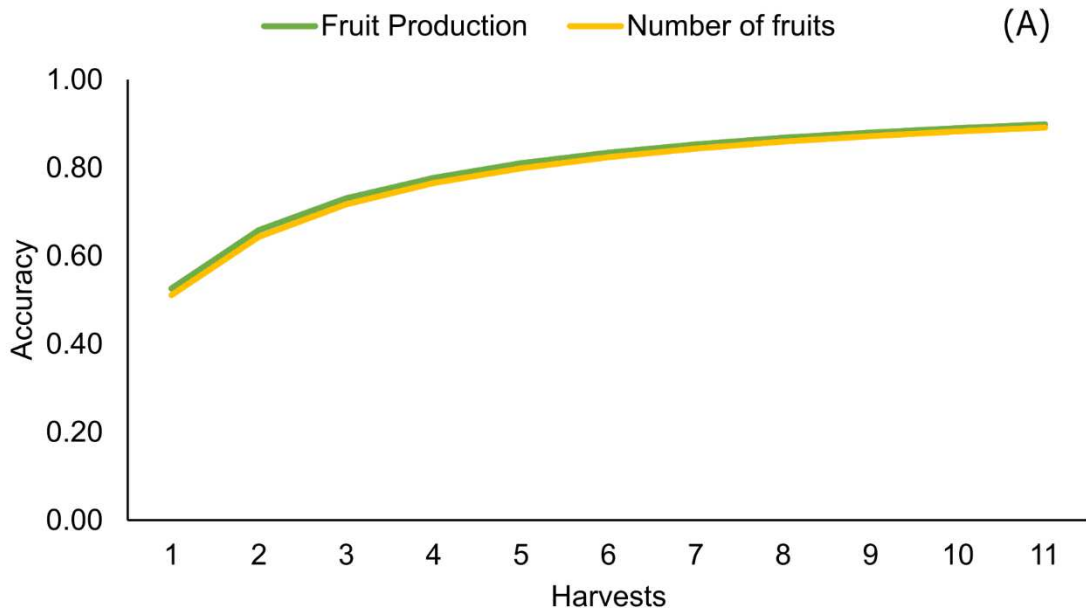
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408

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

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