Prediction of genetic gains with selection between and within S₂ progenies of papaya using the REML/Blup analysis

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Abstract – The objective of this work was to predict the genetic gains with selection of superior individuals within papaya (*Carica papaya*) progenies using the REML/Blup analysis. Thirty-six S₂ progenies, originated from the Calimosa and Tainung 1 hybrids, and two commercial control checks were evaluated in a randomized complete block design, with four replicates. The following traits were evaluated: heights of plants and first fruit; stem diameter at 12 and 18 months; number of days required for fruiting; number, mass, and average mass of commercial fruit; and number and mass of carpelloid and pentandric fruit. The magnitudes of the genetic parameters indicated that the variability present in most of the characters allows greater genetic gain if the selection is made at the progeny level, and not in individual plants. For selection among progenies, PROT-268, PROT-74, PROT-55, and PROT-22 were the most promising, with the greatest genetic gain for the studied characters. In the selection among and within progenies, the prediction of the gains is higher for the increase in the expression of the number of commercial fruit and for the decrease in the expression of pentandric fruit.

Index terms: *Carica papaya*, agronomic traits, genetic parameters, mixed models, selective accuracy.

Predição de ganhos genéticos com a seleção entre e dentro de progênies S₂ de mamoeiro por meio de análise REML/Blup

Resumo – O objetivo deste trabalho foi predizer os ganhos genéticos em mamoeiro (*Carica papaya*) com a seleção dos indivíduos superiores dentro de progênies, por meio da análise REML/Blup. Foram avaliadas 36 progênies S₂, oriundas dos híbridos Calimosa e Tainung 1, e duas testemunhas comerciais, no delineamento de blocos ao acaso, com quatro repetições. Os caracteres avaliados foram: altura de planta e do primeiro fruto; diâmetro de caule aos 12 e 18 meses; número de dias requeridos para surgimento do primeiro fruto; número, massa e massa média de frutos comerciais; e número e massa de frutos carpeloides e pentândricos. As magnitudes dos parâmetros genéticos estimados indicaram que a variabilidade presente, para a maioria dos caracteres, possibilita maiores ganhos genéticos se a seleção for praticada em progênies e não por plantas individuais. Para a seleção entre progênies, PROT-268, PROT-74, PROT-55 e PROT-22 foram as mais promissoras, com os maiores ganhos genéticos para os caracteres estudados. Na seleção entre e dentro de progênies, a predição dos ganhos é maior para o aumento da expressividade do número de frutos comerciais e para a redução da expressividade do número de frutos pentândricos.

Termos para indexação: *Carica papaya*, caracteres agronômicos, parâmetros genéticos, modelos mistos, acurácia seletiva.

Introduction

Papaya cultivars in Brazil are classified into two groups: Solo and Formosa (Dias et al., 2011). In the Solo group, the average weight of papayas ranges from 300 to 650 g, and the predominant cultivars are Golden and Sunrise Solo. The Formosa group is commonly represented by the commercial hybrids Tainung 1 and Calimosa, with average weight ranging from 1,000 to 1,300 g (Dias et al., 2011; Luz et al., 2015).

Although Brazil is the second largest producer of papaya (FAO, 2013), the country is still dependent on the import of seeds of the Formosa group, which considerably raises the production costs (Marin et al., 2006). Despite this, Brazilian breeding programs have contributed to the development of new cultivars that have both superior agronomic and commercial qualities (Dantas et al., 2015). Although in recent years breeding programs have achieved satisfactory results regarding

the introduction of cultivars with high agricultural ability, overcoming current levels of productivity is a great challenge (Silva, 2008). Therefore, it is necessary to investigate the variability of the species, which has a narrow genetic base, in order to obtain, in a single genotype, the maximum phenotypic qualities that are preferred by producers and consumers.

The search for more efficient selection methodologies is one of the most efficient alternatives to achieve these goals. This is because one of the main challenges faced by the breeding programs is low selective accuracy, which negatively impacts genetic gains (Costa et al., 2008). Therefore, the implementation of more refined genetic-statistical procedures, such as the REML/Blup methodology, is a trend in plant breeding (Maia et al., 2011).

Even under conditions of unbalanced experiments, this approach allows the accurate and unbiased prediction of genetic values, providing additional information that is relevant to the identification of superior genotypes (Ramalho & Araújo, 2011). Moreover, the Blup method allows maximizing selective accuracy, which positively impacts the identification of the best individuals and the gains with selection (Rocha et al., 2009). However, the application of this methodology in papaya breeding is still very scarce. In the literature, the use of REML/Blup has been associated with different purposes, including the estimation of genetic parameters in segregating populations, aiming at the selection of papaya individuals for fruit length and weight, total soluble solids and fruit firmness (Oliveira et al., 2012; Pinto et al., 2013), reduction of physiological spots (Pinto et al., 2013), and resistance to phoma spot (Vivas et al., 2014).

The objective of this work was to predict the genetic gains with selection of superior individuals within papaya progenies using the REML/Blup analysis.

Materials and Methods

The experiment was performed at the Curu experimental field of Embrapa Agroindústria Tropical, located in the municipality of Paraipaba, in the northern region of the state of Ceará, Brazil, in the final stretch of the Curu river basin (3°28'47"S, 39°09'47"W, at 31 m altitude).

The genetic material was obtained from self-fertilized F_1 plants from the Tainung 1 and Calimosa hybrids, from commercial fields in the extreme south of the state Bahia, also in Brazil. The two resulting S_1 populations, 304 plants of Tainung 1 and 342 of Calimosa, were planted in 2009 and evaluated during the period of 2009 to 2011, but covering only one harvest. In these populations, the best individuals for agronomic and fruit quality traits were selected and self-fertilized, generating the S_2 progenies. The latter were evaluated from May 2013 to October 2014.

On the basis of the selection among and within the S_1 progenies, 36 individuals of greater agronomic and commercial potential were identified. Of these, 17 were derived from the Calimosa and 19 from the Tainung 1 hybrids (Table 1). The S_2 progenies, plus the two hybrids from which they were generated, were evaluated in a randomized complete block design with four replicates. The experimental plot consisted of five plants. The spacing used was 2.5 m between rows and 2.0 m between plants. Three seedlings were used per pit, to guarantee the presence of at least one hermaphrodite plant. Cultural practices and phytosanitary measures were those recommended for the culture, as described by Martins & Costa (2003).

Plant sex was determined by inspection at the beginning of flowering. Then, thinning was conducted leaving only one plant (hermaphrodite) per pit. Side shoots were removed from plants when they were still small.

To assess the S_2 progenies, the main agronomic/ phenological traits, related to plant architecture and productivity, and commercial traits, such as fruit size and mass, were considered. The following phenological traits were evaluated: height of the first fruit (HFF), in centimeters, determined at the establishment of the first fruit; plant height at 12 months (PH12M) and at 18 months (PH18M), expressed in centimeters, by measuring the distance from the soil level, contiguous to the stem base of the plant, up to the insertion of the youngest leaf; stem diameter at 12 months (SDIA12M) and at 18 months (SDIA18M), in centimeters, calculated at 20 cm from the soil level; and days after planting to fruiting (DAPFR), referring to the period from planting to first harvest, which guided the selection of plants with earlier fruiting.

Regarding productivity, the following traits were evaluated: number of commercial fruits per plant (NCF) and mass of these fruits (CFM), as well as mean commercial fruit mass (MCFM), calculated

using the ratio between NCF and CFM; number of carpelloid fruits per plant (NCARF) and mass of these fruits (CARFM), assessed by counting and weighing carpelloid fruits per plant, respectively; number of pentandric fruits per plant (NPENF) and mass of these fruits (PENFM), obtained by counting and weighing

Table 1. Identification of S₂ progenies of papaya (*Carica papaya*) and commercial hybrids (controls) used in the study.

Number	Progeny/provenance
	Population 1
1	PROC-59
2	PROC-74
3	PROC-76
4	PROC-84
5	PROC-100
6	PROC-106
7	PROC-107
8	PROC-115
9	PROC-122
10	PROC-130
11	PROC-161
12	PROC-179
13	PROC-215
14	PROC-217
15	PROC-222
16	PROC-206
17	PROC-323
	Population 2
18	PROT-13
19	PROT-20
20	PROT-22
21	PROT-23
22	PROT-24
23	PROT-52
24	PROT-53
25	PROT-54
26	PROT-55
27	PROT-68
28	PROT-74
29	PROT-76
30	PROT-135
31	PROT-181
32	PROT-188
33	PROT-234
34	PROT-242
35	PROT-266
36	PROT-268
	Population 3
37	Calimosa
38	Tainung 1

pentandric fruits per plant, respectively. All fruit mass are expressed in grams.

The data were analyzed using mixed models, and the effects were tested using the likelihood ratio test (LRT) for the elaboration of the deviance analysis table. In order to obtain the variance components and estimates of genetic parameters, data were subjected to the deviance analysis, based on the following statistical model: $y = Xr + Za + Wp + Tb + e$, in which y is the vector of phenotypic averages; r is the vector of progenies and controls (considered as random effects); a is the vector of individual additive genetic effects (assumed to be random); p is the plot-effect vector (random); b is the vector of the block effects (fixed); and e is the vector of errors (random). The incidence matrices for the effects of r, a, p, and b are represented by X, Z, W, and T, respectively.

For a better organization and interpretation of the partial results of the analysis, the progenies identified in Table 1 were numbered by individuals. To number each individual, the digit of the unit corresponds to the number of the plant within the plot, the digit of the ten corresponds to the replicate related to the plot, and the remaining digits are from the number of the progeny. For example, individual 1,421 corresponds to plant one, from the second replicate of progeny 14. All analyses were performed using the Selegen software (Resende, 2002).

Results and Discussion

Progenies differed statistically for 7 of the 12 characters studied (Table 2). This indicates that there is genetic variability among these progenies, which allows to obtain gains from selection. Differences were also observed within the progeny for the PH12M, DAPFR, and MCFM characters, indicating the possibility of obtaining genetic gains not only through selection among progenies, but also within progenies.

Among the populations, where the progenies Calimosa and Tainung 1, and the controls (Table 1) are grouped, there were significant differences for HFF, PH18M, DAPFR, NCF, CFM, and MCFM. However, between the progenies obtained and the controls, the differences were only with respect to NCF and MCFM. These results show the existence of genetic variability not only among the evaluated progenies, but also within them. However, the effect among and

within the progenies was not significant for PH18M, SDIA12M, NCARF, and PENFM, indicating that the genotypes within the same progeny or among the progenies evaluated had the same performance. Therefore, it is not feasible to obtain genetic gains through these characters, which were disregarded from the following analyses.

The experimental coefficient of variation (CV) ranged from 6.9 to 223.8%. According to Silva et al. (2008), values of CV less than 20% are determinant of good experimental accuracy for this crop; however, high CVs may be related to the genetic nature of the character. The majority of the characters studied are of polygenic nature, and their expressions are greatly affected by the environment (Maia et al., 2006). The highest values of CV, 223.8 and 121.7, correspond to the number of carpelloid and pentandric fruits, respectively. This is consistent with the results obtained by Damasceno Junior et al. (2008), who observed that the occurrence of fruits with anomalies is a factor strongly associated with environmental variations. These authors studied the occurrence rate of floral anomalies that resulted in anomalous fruits, at different periods, and found that the CVs were superior to the number of abnormal flowers. Moreover, it is worth mentioning that, in the present study, the S_2 progenies were evaluated, that is, the genetic material was not genotypically fixed. Thus, variations in the same progeny are usually observed between experimental plots, because in this generation, there is still reduction of dominance deviations as well as variations caused by additive effects (Silva et al., 2013).

The coefficients of heritability of the progeny ranged from 1.6 to 83.9% for PH12M and HFF, respectively (Table 3). PH12M and HFF were evaluated at entirely different periods, and PH12M was susceptible to a greater environmental effect. However, for the majority of the characters, the coefficients of heritability of the progenies varied from medium to high magnitude, which could lead to the selection of superior progenies with high selective accuracy (Resende & Duarte, 2007). Therefore, the prediction information of the genetic values to be used in the selection process is precise. Additionally, it has a substantial fraction of the additive genetic variance, which tends to facilitate the identification and selection of progenies with proper phenotypes (Pimentel et al., 2014). For selection within progenies, individual heritability in the strict sense was low for all characters. Regarding mass selection, the coefficients of heritability also presented low magnitude. These results indicate the possibility of obtaining individuals with the same or similar behavior in the next generation, and also the prospect of practicing a satisfactory selection of progenies and not individual plants. There is well shown by the low values observed for the selective accuracy when analyzed with these heritabilities. Pinto et al. (2013) described individual and average values of heritability for several plant and fruit traits, and found that, for averages, the values were up to seven-fold higher than those of individual heritability.

The selective accuracy reflects the quality of the information of the procedures used in the prediction of genetic values. This measure is associated with

Table 2. Likelihood ratio and F-values for progeny effects, difference between progeny (P) and control (C), variation within progenies and populations composed by different progenies, in 36 S_2 progenies of papaya (*Carica papaya*) and in two commercial hybrids (controls).

Effect[1]	HFF	PH12M	PH18M	SDIA12M	SDIA18M	DAPFR	NCF	CFM	MCFM	NCARF	CARFM	NPENF	PENFM
Between	211.01***	1.38ns	0.34ns	2.39ns	60.23***	79.55***	7.42***	45.47***	40.35***	0.07ns	40.42***	4.82**	0.76ns
P vs. C	0.18ns	0.13ns	1.60ns	1.16ns	1.77ns	0.02ns	9.79*	0.12ns	105.38**	0.51ns	0.86ns	0.82ns	2.70ns
Within	1.11ns	63.88***	0.02ns	0.03ns	1.72ns	3.86**	0.02ns	4.57**	0.07ns	0.13ns	0.06ns	0.00ns	0.02ns
Population	16.77***	0.01ns	0.00ns	0.00ns	4.26**	3.58*	10.78***	7.82***	8.03***	0.00ns	0.00ns	2.06ns	0.21ns
Average	134.5	474.8	491.3	56.8	58.6	127.3	109.2	41.9	1.2	22.3	1.4	0.6	228.5
CV (%)	10.1	78.1	16.3	20.7	6.9	11.3	53.4	30.3	24.2	223.8	80.1	121.7	10.7

[1]Values obtained by the likelihood ratio test (LRT), except for the effect of progeny vs. control, for which the F-values are displayed, tested with 1 and 111 degrees of freedom. nsNonsignificant. ***, **, and *Significant by the chi-square test, at 1, 5, and 10% probability, respectively, with 1 degree of freedom. PH12M, plant height (PH) at 12 months; PH18M, at 18 months; SDIA12M, stem diameter (SD) at 12 months; and SDIA18M, at 18 months; DAPFR, days after planting to fruiting; NCF, number of commercial fruit; CFM, mass of commercial fruit; MCFM, mean commercial fruit mass; NCARF, number of carpelloid fruit; CARFM, carpelloid fruit mass; NPENF, number of pentandric fruit; and PENFM, pentandric fruit mass.

the selection precision and refers to the correlation between the predicted and the actual genetic values of progenies (Pimentel et al., 2014). The higher the selective accuracy of the evaluation of a progeny, the higher the genetic value predicted for it. Therefore, the estimates obtained for the characters SDIA18M, DAPFR, and HFF should be indicated. However, for the NCF character, the estimate varied from low to moderate magnitude. This reiterates the particularity of each character (Marin, 2004), providing the evidence that the complexity of the expression of a particular trait is directly proportional to the complexity of the selection process associated with it.

Individual coefficients of heritability of low magnitude within the progenies may be understood as additional information to heritabilities between progenies, when the individual Blup method is used

(Pimentel et al., 2014). Selective accuracy was higher than 75% for most of the characters studied, with the exception of PH12M, NCF, and NPENF. Moreover, for the characters in which the accuracy was high, individual coefficients of heritability were greater than 15%, which represents a considerable magnitude.

The assessment of individuals by Blup analysis presented higher implication for information based exclusively on progeny selection. This is supported by the contribution to selection within progenies, evidenced by the increase in accuracy values, when comparing the progeny selection accuracy with the accuracy in the combined selection among progenies, using the individual Blup. The efficiency of information use within progenies was greater than one unit for all traits, and it was obtained as the ratio of the accuracy in the combined selection, among and within

Table 3. Variance components and genetic parameters estimated in 36 S$_2$ progenies of papaya (*Carica papaya*) and in two commercial hybrids (controls)[1].

Parameter	HFF	PH12M	SDIA18M	DAPFR	NCF	CFM	MCFM	CARFM	NPENF
Additive variance between progenies	247.220	549.337	14.296	160.092	176.427	52.982	0.029	0.792	0.067
Environmental variance between plots	33.449	137,284.217	4.852	59.292	128.543	46.275	0.004	0.047	0.013
Variance between blocks	273.771	19.992	12.167	51.968	1,819.859	41.885	0.114	0.000	0.055
Phenotypic variance within plot	753.962	1777.160	56.745	740.944	16,360.166	573.201	0.367	5.825	2.781
Total phenotypic variance	1,308.402	139,630.706	88.060	1,012.296	18,484.996	714.343	0.513	6.664	2.916
Additive variance within progeny	123.610	274.668	7.148	80.046	88.214	26.491	0.014	0.396	0.033
Individual heritability (IH) in the strict sense – mass (%)	18.9	0.4	16.2	15.8	1.0	7.4	5.6	11.9	2.3
IH in the strict sense within progeny (%)	16.4	15.5	12.6	10.8	0.5	4.6	3.9	6.8	1.2
Heritability at the average level (%)	83.9	1.6	78.0	75.5	17.2	56.9	59.8	72.3	31.9
Accuracy in individual selection – mass (%)	43.5	6.3	40.3	39.8	9.8	27.2	23.7	34.5	15.1
Accuracy in progeny selection (%)	91.6	12.5	88.3	86.9	41.5	75.4	77.3	85.0	56.5
Accuracy in the combined selection between and within progenies – Blup (%)	96.0	30.5	91.8	90.0	41.8	76.9	78.6	87.0	57.0
Efficiency of Blup selection between and within populations	1.048	2.438	1.040	1.035	1.008	1.020	1.016	1.023	1.009
Coefficient of determination of plot effects (%)	0.026	0.983	0.055	0.059	0.007	0.065	0.008	0.007	0.005
Individual coefficient of additive genetic variance (%)	11.686	4.936	6.457	9.945	12.162	17.374	14.730	64.754	41.678
Coefficient of experimental variance (%)	10.089	78.137	6.874	11.321	53.394	30.278	24.159	80.081	121.735
Coefficient of relative variance	1.158	0.063	0.939	0.878	0.228	0.574	0.610	0.809	0.342
General average	134.543	474.803	58.555	127.233	109.216	41.897	1.153	1.375	0.600

[1]HFF, height of the first fruit; PH12M, plant height at 12 months; SDIA18M, stem diameter at 18 months; DAPFR, days after planting to fruiting; NCF, number of commercial fruit; CFM, mass of commercial fruit; MCFM, mean commercial fruit mass; CARFM, carpelloid fruit mass; and NPENF, number of pentandric fruit.

progenies, to the accuracy in progeny selection. Under these conditions, individual Blup selection provides additional gains (Pimentel et al., 2014). These gains should range from 0.8% (if the selection is practiced directly through NCF) to 144% (if performed through PH12M).

Individual coefficient of additive genetic variance quantifies the dispersion of the additive values around the general average. Therefore, high values are more appropriate for populations to be susceptible to genetic

progress. The highest percentages were observed in the characters referring to production, although there were deviations of 4.94 and 64.75% for the traits PH12M and CARFM, respectively. Production, however, must be analyzed in combination with the coefficient of environmental variance. Moreover, another important parameter obtained by the ratio among the variables, i.e. the coefficient of relative variance, denotes a favorable condition for selection, when values resulting from this computation are equal to or higher than one

Table 4. Additive genetic effect (a), additive genetic value (u+a), and accumulated genetic gain (AG) estimated for 36 S_2 progenies (Prg) of papaya (*Carica papaya*)[1].

Order	HFF				PH12M				SDIA18M				DAPFR			
	Prg	a	u+a	AG(%)	Prg	a	u+a	AG(%)	Prg	a	u+a	AG(%)	Prg	a	u+a	AG(%)
1	1	-31.343	134.43	-0.1	27	-1.906	474.81	0.0	9	8.694	67.25	8.7	4	-21.443	127.44	0.2
2	3	-30.896	135.28	0.7	18	-1.501	474.86	0.1	14	8.016	66.91	8.4	1	-20.128	128.03	0.8
3	4	-26.613	136.16	1.6	32	-1.366	474.95	0.1	12	7.591	66.66	8.1	10	-17.662	128.61	1.4
4	10	-25.599	136.96	2.4	6	-1.264	475.00	0.2	8	6.634	66.29	7.7	11	-13.558	129.15	1.9
5	11	-24.413	137.79	3.2	36	-1.157	475.04	0.2	7	6.379	66.02	7.5	2	-13.232	129.61	2.4
6	6	-23.545	138.62	4.1	5	-1.086	475.08	0.3	2	4.759	65.57	7.0	26	-12.971	130.08	2.8
7	17	-22.275	139.49	4.9	20	-0.997	475.13	0.3	15	3.952	65.13	6.6	12	-11.835	130.57	3.3
8	16	-20.493	140.37	5.8	28	-0.990	475.17	0.4	17	3.711	64.77	6.2	17	-11.470	131.06	3.8
9	15	-18.684	141.24	6.7	29	-0.969	475.22	0.4	10	3.448	64.46	5.9	15	-10.400	131.57	4.3
10	2	-16.296	142.12	7.6	3	-0.808	475.27	0.5	22	3.447	64.22	5.7	16	-9.682	132.08	4.8
11	26	-16.063	142.97	8.4	30	-0.806	475.32	0.5	19	3.218	64.00	5.4	3	-9.443	132.60	5.4
12	13	-11.908	143.88	9.3	31	-0.754	475.37	0.6	11	2.850	63.78	5.2	7	-7.314	133.15	5.9
13	7	-10.329	145.52	11.0	13	-0.697	475.42	0.6	1	2.810	63.59	5.0	32	-6.935	133.66	6.4
14	5	-10.278	146.40	11.9	14	-0.675	475.47	0.7	25	2.304	63.40	4.8	21	-2.579	134.19	7.0
15	12	-8.549	147.37	12.8	35	-0.499	475.53	0.7	24	2.050	63.21	4.7	29	-2.216	134.59	7.4
16	14	-4.496	148.34	13.8	4	-0.409	475.59	0.8	34	1.860	63.04	4.5	5	-1.148	135.45	8.2
17	32	-2.589	149.21	14.7	17	-0.390	475.64	0.8	5	1.783	62.88	4.3	9	-0.624	135.89	8.7
18	20	-2.475	150.07	15.5	10	-0.294	475.71	0.9	13	1.234	62.71	4.2	20	0.008	136.36	9.1
19	8	-1.723	151.02	16.5	26	-0.197	475.77	1.0	16	1.150	62.55	4.0	13	0.179	136.84	9.6
20	18	-0.423	152.03	17.5	25	-0.192	475.83	1.0	35	0.752	62.39	3.8	8	1.255	137.36	10.1
21	9	0.491	153.08	18.5	1	-0.180	475.91	1.1	30	0.106	62.21	3.7	31	1.961	137.88	10.7
22	29	2.469	154.21	19.7	24	-0.130	475.99	1.2	18	-0.021	62.04	3.5	36	2.043	138.43	11.2
23	27	2.710	155.36	20.8	8	-0.096	476.17	1.4	33	-0.064	61.89	3.3	30	2.376	139.04	11.8
24	36	10.194	156.65	22.1	11	-0.090	476.28	1.5	23	-0.076	61.75	3.2	18	2.737	139.71	12.5
25	31	11.149	157.57	23.0	15	-0.056	476.42	1.6	3	-0.287	61.61	3.1	28	3.480	141.31	14.1
26	22	12.041	158.56	24.0	22	0.001	476.57	1.8	21	-0.438	61.47	2.9	24	4.264	142.27	15.0
27	30	12.982	159.65	25.1	2	0.011	476.74	1.9	31	-0.506	61.35	2.8	6	6.528	143.35	16.1
28	28	13.597	160.86	26.3	34	0.146	476.96	2.2	29	-1.153	61.09	2.5	23	8.570	144.41	17.2
29	24	13.652	162.27	27.7	21	0.198	477.21	2.4	28	-1.205	60.97	2.4	27	9.389	145.49	18.3
30	21	15.222	164.03	29.5	23	0.204	477.52	2.7	26	-1.408	60.84	2.3	22	9.494	146.75	19.5
31	23	19.992	168.56	34.0	7	0.205	477.94	3.1	6	-1.858	60.71	2.2	35	10.605	148.43	21.2
32	35	25.696	171.37	36.8	33	0.214	478.53	3.7	4	-1.997	60.59	2.0	33	17.124	150.54	23.3
33	25	31.213	174.15	39.6	19	0.369	479.41	4.6	27	-2.187	60.46	1.9	25	21.889	152.09	24.9
34	33	34.080	176.95	42.4	9	0.460	480.82	6.0	36	-3.348	60.31	1.8	34	22.687	153.08	25.8
35	19	36.010	181.11	46.6	12	0.742	483.60	8.8	32	-4.890	60.13	1.6	14	25.549	154.66	27.4
36	34	57.125	191.67	57.1	16	16.855	491.66	16.9	20	-6.218	59.92	1.4	19	29.298	156.53	29.3

[1]Genetic value obtained with the general average, and accumulated gain estimated based on the progeny average. HFF, height of the first fruit; PH12M, plant height at 12 months; SDIA18M, stem diameter at 18 months; and DAPFR, days after planting to fruiting.

unit (Resende & Duarte, 2007; Canuto et al., 2015). Therefore, easier gains will be obtained through HFF.

In order to generate more information about the experimental accuracy, the coefficients of determination of plot effects were estimated. In Resende (2002), ideal estimates are those with magnitudes below 10%; this indicates that the observed phenotypic variation was only slightly affected by environmental variation. This could be confirmed by the minor differences detected between the phenotypic variance within the progenies and the total one. Therefore, for most of the characters, high reliability estimates were generated.

In the analysis of the ten best progenies, four (36, 28, 26, and 20) stood out for most of the evaluated characters (Tables 4 and 5). For example, progeny 28 was one of the most promising for PH12M, NCF, CFM, NCARF, and NPENF. Among these features, progeny 36 did not stand out for NPENF. However, it

Table 5. Additive genetic effect (a), additive genetic value (u+a), and accumulated genetic gain (AG, %), estimated for 36 S₂ progenies (Prg) of papaya (*Carica papaya*)[1].

Order	NCF				CFM				MCFM				CARFM				NPENF			
	Prg	a	u+a	AG	Prg	a	u+a	AG	Prg	a	u+a	AG	Prg	a	u+a	AG	Prg	a	u+a	AG
1	36	11.364	141.50	32.3	28	14.161	56.06	14.2	31	-0.467	1.49	0.3	14	-0.857	1.37	0.0	24	-0.338	0.55	-0.1
2	31	10.603	136.08	26.9	20	12.884	55.42	13.5	25	-0.426	1.43	0.3	11	-0.826	1.40	0.0	27	-0.322	0.56	-0.1
3	32	9.073	132.52	23.3	36	10.931	54.55	12.7	23	-0.385	1.38	0.2	8	-0.789	1.42	0.0	30	-0.317	0.57	-0.1
4	34	7.224	129.84	20.6	30	10.421	54.00	12.1	20	-0.370	1.34	0.2	27	-0.728	1.45	0.1	28	-0.306	0.58	0.0
5	25	3.695	127.42	18.2	26	8.631	53.03	11.1	7	-0.333	1.32	0.2	26	-0.707	1.47	0.1	21	-0.302	0.58	0.0
6	29	2.601	125.47	16.3	32	7.676	52.53	10.6	16	-0.320	1.29	0.1	5	-0.661	1.49	0.1	22	-0.285	0.59	0.0
7	26	1.680	123.85	14.6	25	6.164	51.97	10.1	22	-0.318	1.27	0.1	29	-0.587	1.52	0.1	18	-0.262	0.60	0.0
8	28	0.188	122.41	13.2	21	5.869	51.51	9.6	21	-0.309	1.25	0.1	28	-0.568	1.54	0.2	20	-0.252	0.61	0.0
9	23	-0.821	121.13	11.9	18	5.178	51.06	9.2	19	-0.295	1.24	0.1	24	-0.548	1.59	0.2	35	-0.244	0.61	0.0
10	19	-2.065	119.97	10.8	34	4.605	50.65	8.8	36	-0.288	1.23	0.1	36	-0.496	1.62	0.2	33	-0.232	0.62	0.0
11	35	-3.157	118.90	9.7	31	4.105	50.26	8.4	34	-0.268	1.21	0.1	2	-0.469	1.65	0.3	25	-0.226	0.63	0.0
12	21	-4.224	117.90	8.7	22	4.086	49.93	8.0	29	-0.246	1.20	0.0	12	-0.468	1.67	0.3	26	-0.184	0.64	0.0
13	33	-5.646	116.95	7.7	24	3.721	49.62	7.7	5	-0.246	1.19	0.0	34	-0.446	1.71	0.3	23	-0.164	0.65	0.0
14	20	-6.419	116.06	6.8	33	3.632	49.35	7.5	26	-0.233	1.18	0.0	30	-0.374	1.74	0.4	32	-0.153	0.66	0.0
15	18	-6.692	115.27	6.1	19	3.524	49.11	7.2	32	-0.232	1.17	0.0	33	-0.367	1.77	0.4	19	-0.145	0.66	0.0
16	30	-6.761	114.56	5.3	23	2.747	48.84	6.9	28	-0.221	1.16	0.0	19	-0.353	1.80	0.4	5	-0.122	0.67	0.1
17	24	-9.211	113.79	4.6	5	2.209	48.58	6.7	9	-0.221	1.15	0.0	32	-0.338	1.84	0.5	34	-0.120	0.68	0.1
18	22	-9.327	113.10	3.9	4	1.146	48.29	6.4	17	-0.211	1.14	0.0	22	-0.199	1.88	0.5	36	-0.119	0.69	0.1
19	27	-11.470	112.36	3.1	27	0.884	48.01	6.1	35	-0.193	1.13	0.0	1	-0.144	1.92	0.5	1	-0.106	0.70	0.1
20	4	-35.133	110.62	1.4	1	0.379	47.74	5.8	18	-0.185	1.12	0.0	31	-0.136	1.96	0.6	29	-0.105	0.71	0.1
21	3	-37.825	108.92	-0.3	10	0.058	47.48	5.6	14	-0.173	1.11	0.0	13	-0.109	2.00	0.6	2	-0.096	0.72	0.1
22	12	-38.129	107.34	-1.9	29	-0.140	47.23	5.3	10	-0.133	1.11	0.0	17	-0.097	2.05	0.7	31	-0.092	0.73	0.1
23	16	-38.178	105.89	-3.3	12	-1.427	46.95	5.0	1	-0.120	1.10	-0.1	7	0.005	2.10	0.7	10	-0.059	0.74	0.1
24	15	-38.283	104.55	-4.7	2	-3.368	46.61	4.7	33	-0.114	1.09	-0.1	25	0.207	2.15	0.8	8	-0.058	0.75	0.1
25	5	-39.323	103.26	-6.0	35	-4.257	46.26	4.4	27	-0.112	1.08	-0.1	10	0.243	2.19	0.8	15	-0.047	0.77	0.1
26	9	-39.626	102.06	-7.2	15	-4.272	45.94	4.0	30	-0.104	1.08	-0.1	35	0.252	2.24	0.9	6	-0.043	0.78	0.2
27	7	-39.735	100.94	-8.3	11	-5.314	45.61	3.7	13	-0.083	1.07	-0.1	15	0.332	2.29	0.9	12	-0.039	0.80	0.2
28	11	-39.908	99.88	-9.3	3	-5.645	45.29	3.4	24	-0.056	1.06	-0.1	9	0.387	2.35	1.0	14	0.003	0.82	0.2
29	2	-39.952	98.89	-10.3	6	-6.086	44.97	3.1	3	-0.048	1.06	-0.1	6	0.479	2.42	1.0	7	0.040	0.84	0.2
30	1	-40.019	97.97	-11.3	13	-9.365	44.24	2.3	6	-0.042	1.05	-0.1	18	0.483	2.49	1.1	17	0.064	0.86	0.2
31	17	-40.518	97.08	-12.1	17	-9.407	43.88	2.0	11	-0.037	1.04	-0.1	4	0.736	2.68	1.3	11	0.072	0.88	0.3
32	13	-40.973	96.23	-13.0	16	-11.080	43.50	1.6	8	-0.008	1.04	-0.1	16	0.796	2.80	1.4	9	0.138	0.94	0.3
33	6	-41.785	95.41	-13.8	7	-11.645	43.12	1.2	4	0.006	1.03	-0.1	23	0.903	2.96	1.6	13	0.229	0.98	0.4
34	10	-42.134	94.62	-14.6	9	-11.865	42.76	0.9	12	0.031	1.02	-0.1	21	1.108	3.18	1.8	4	0.359	1.02	0.4
35	8	-43.231	93.85	-15.4	8	-12.580	42.39	0.5	2	0.112	1.01	-0.1	3	1.680	3.53	2.2	16	0.404	1.04	0.4
36	14	-44.855	93.07	-16.1	14	-16.563	41.95	0.0	15	0.183	1.00	-0.1	20	2.632	4.01	2.6	3	0.435	1.05	0.4

[1]Genetic value obtained with the general average, and accumulated gain estimated based on the progeny average. NCF, number of commercial fruit; CFM, mass of commercial fruit; MCFM, mean commercial fruit mass; CARFM, carpelloid fruit mass; and NPENF, number of pentandric fruit.

was among the best for MCFM, which did not occur with progeny 28. Similar results were also observed involving progenies 26 and 20. These four progenies were promising with regard to CFM. Estimates show that these progenies have the highest frequency of favorable alleles for most of the evaluated traits. Thus, these progenies stand out with potential for breeding.

Alves & Resende (2008), in a similar study on cupuaçu [*Theobroma grandiflorum* (Willd. ex Spreng.) K. Schum] cultivation, when ordering progenies based on the accumulated genetic gain to increase fruit production, verified the possibility of obtaining considerable gains with the selection of the first five progenies of the rankings. In the literature, there are few studies that involve the prediction of genetic gains in fruit species through mixed models, especially with regard to the analysis of a high number of concomitant traits. Oliveira et al. (2012) and Pinto et al. (2013), using mixed models for segregating populations of papaya, obtained satisfactory results, while estimating genetic parameters aiming at the selection of papaya individuals for fruit length and weight, total soluble solids, and fruit firmness.

In order to select potential individuals within the best progenies, a ranking of the 20 most promising individuals within and among the progenies was established (Tables 6 and 7). Obviously, this classification was made considering the purpose of the

Table 6. Additive genetic effect (a), individual additive genetic value (u + a), and accumulated genetic gain (AG, %), estimated with the selection of 10 and 20% of the best genotypes (plant) within and among 36 S$_2$ progenies of papaya (*Carica papaya*)[1].

Order	HFF				PH12M				SDIA18M				DAPFR			
	Gen.[2]	a	u+a	AG	Gen.	a	u+a	AG	Gen.	a	u+a	AG	Gen.	a	u+a	AG
1	125	-37.578	96.97	0.5	2233	-55.108	419.69	0.0	943	10.494	69.05	10.5	141	-25.368	101.87	0.3
2	333	-37.150	97.39	0.6	1234	-17.768	457.03	0.1	925	10.257	68.81	10.4	144	-24.288	102.95	0.3
3	324	-36.639	97.90	0.6	721	-15.246	459.56	0.1	914	9.759	68.31	10.2	343	-24.119	103.11	0.4
4	122	-36.103	98.44	0.7	531	-13.993	460.81	0.2	734	9.684	68.24	10.0	113	-23.384	103.85	0.4
5	145	-35.895	98.65	0.8	1025	-13.271	461.53	0.2	1213	9.673	68.23	10.0	215	-23.323	103.91	0.5
6	133	-35.756	98.79	0.8	613	-12.108	462.70	0.2	1421	9.452	68.01	9.9	212	-23.323	103.91	0.5
7	144	-35.731	98.81	0.9	921	-11.900	462.90	0.3	924	9.123	67.68	9.8	245	-23.237	104.00	0.5
8	342	-35.023	99.52	0.9	634	-11.492	463.31	0.3	942	9.109	67.66	9.7	243	-23.237	104.00	0.6
9	312	-34.704	99.84	1.0	2824	-11.296	463.51	0.3	1443	9.072	67.63	9.6	241	-23.237	104.00	0.6
10	311	-34.704	99.84	1.0	543	-11.208	463.60	0.3	931	8.818	67.37	9.5	445	-23.132	104.10	0.6
11	131	-34.608	99.93	1.1	1344	-11.095	463.71	0.4	1243	8.794	67.35	9.5	342	-23.039	104.19	0.7
12	334	-34.362	100.18	1.2	131	-11.002	463.80	0.4	1225	8.705	67.26	9.4	242	-22.913	104.32	0.7
13	113	-34.133	100.41	1.2	1824	-10.800	464.00	0.4	1422	8.696	67.25	9.4	441	-22.700	104.53	0.8
14	344	-33.547	101.00	1.3	1035	-10.111	464.69	0.4	1432	8.573	67.13	9.3	442	-22.376	104.86	0.8
15	114	-32.821	101.72	1.3	243	-10.087	464.72	0.5	1442	8.568	67.12	9.3	444	-22.052	105.18	0.8
16	123	-32.660	101.88	1.4	1325	-9.670	465.13	0.5	825	8.451	67.01	9.2	443	-22.052	105.18	0.9
17	414	-32.543	102.00	1.5	2813	-9.661	465.14	0.5	921	8.367	66.92	9.2	145	-22.019	105.21	0.9
18	1023	-32.201	102.34	1.5	3234	-9.506	465.30	0.5	1235	8.350	66.91	9.1	341	-21.958	105.28	1.0
19	314	-32.080	102.46	1.6	423	-9.183	465.62	0.5	1215	8.287	66.84	9.1	313	-21.798	105.44	1.0
20	115	-31.837	102.71	1.6	1012	-9.180	465.62	0.6	812	8.224	66.78	9.0	311	-21.798	105.44	1.0
Selection pressure[3]																
10%		-30.676	103.87	2.1	-	-10.149	464.65	0.6	-	8.441	67.00	9.2	-	-19.985	107.25	1.4
20%		-27.258	107.29	3.8	-	-7.514	467.29	1.1	-	7.234	65.79	8.5	-	-16.861	110.37	2.4
$\bar{X}_G$		-	134.54	-	-	-	474.80	-	-	-	58.56	-	141	-	127.23	-
$\bar{X}_{WC}$		-	133.48	-	-	-	474.83	-	-	-	59.98	-	144	-	127.13	-

[1]Genetic value obtained with the general average, and accumulated gain estimated based on the progeny average. [2]In the numbering of each individual, its unit number corresponds to the number of the plant within the plot, the tens digit corresponds to the replicate related to the plot, and the remaining digits are derived from the number of the progeny. For example, individual 1421 corresponds to plant one, of the second replicate of progeny 14. [3]The selection pressures of 10 and 20% correspond to the averages of the 72 and 144 genotypes, respectively, which were better ranked to the characters. $\bar{X}_G$, general average; and $\bar{X}_{WC}$, average without the controls. HFF, height of the first fruit; PH12M, plant height at 12 months; SDIA18M, stem diameter at 18 months; and DAPFR, days after planting to fruiting.

program for increasing or reducing the expression of the character. However, none of the individuals stood out in this ranking among all analyzed characters, probably due to the lack of correlation among those. However, based on the data obtained, it was observed that among the individuals, 16 (113, 141, 145, 311, 342, 921, 1421, 1422, 1432, 1442, 1443, 2424, 3125, 3134, 3142, and 3144) stood out by being among the top 20 in at least two distinct characters simultaneously. The progenies evaluated in the present study are still segregating. Thus, it is risky to indicate one particular individual that may be suitable for assessing the value for cultivation or use. Therefore, it is more plausible to promote selection in subsequent cycles or to apply lenient selection indices, so that promising

individuals, although not fixed genotypically yet, are not immediately penalized/disregarded. In this way, two selection conditions were simulated considering intensities of 10 and 20% (Tables 6 and 7). The gains that each intensity represents were predicted based on the average genetic value of the populations and the average genetic value of the selected individuals.

Among the characters that were evaluated for the purpose of increasing expression, NCF generated the highest average gains – 28.8 and 23.0%, respectively – with both selection intensity of 10 and 20%. However, when the goal is to reduce the expression of characters with unfavorable phenotypes, it is recommended to identify the individuals that provide the greatest negative gains. Among the characters that were

Table 7. Additive genetic effect (a), individual additive genetic value (u+a), and accumulated genetic gain (AG, %) estimated with the selection of 10 and 20% of the best genotypes (plant) within and among 36 S₂ progenies of papaya (*Carica papaya*)[1].

Order	NCF				CFM				MCFM				CARFM				NPENF			
	Gen.[2]	a	u+a	AG	Gen.	a	u+a	AG	Gen.	a	u+a	AG	Gen.	a	u+a	AG	Gen.	a	u+a	AG
1	3633	13.981	123.20	42.0	2832	16.058	57.95	16.1	3142	0.282	1.44	0.41	1425	-0.905	0.47	0.0	2435	-0.343	0.277	-0.1
2	3144	13.651	122.87	41.2	2842	15.561	57.46	15.8	3144	0.282	1.43	0.41	1424	-0.905	0.47	0.0	2434	-0.343	0.277	-0.1
3	3142	13.641	122.86	40.5	2814	15.487	57.38	15.7	3134	0.244	1.40	0.40	1423	-0.905	0.47	0.0	2433	-0.343	0.277	-0.1
4	3622	13.575	122.79	39.8	2825	15.458	57.35	15.6	2542	0.215	1.37	0.40	1422	-0.905	0.47	0.0	2432	-0.343	0.277	-0.1
5	3134	13.104	122.32	39.1	2815	15.418	57.31	15.6	3125	0.212	1.37	0.39	1421	-0.905	0.47	0.0	2431	-0.343	0.277	-0.1
6	3615	13.096	122.31	38.4	2811	15.122	57.02	15.5	3112	0.187	1.34	0.39	1445	-0.889	0.49	0.0	2415	-0.342	0.278	-0.1
7	3612	13.080	122.30	37.8	2831	15.053	56.95	15.5	3114	0.179	1.33	0.38	1444	-0.889	0.49	0.0	2414	-0.342	0.278	-0.1
8	3125	12.707	121.92	37.2	2042	15.011	56.91	15.4	2535	0.176	1.33	0.38	1443	-0.889	0.49	0.0	2413	-0.342	0.278	-0.1
9	3233	11.600	120.82	36.6	2823	14.924	56.82	15.3	3141	0.176	1.33	0.37	1442	-0.889	0.49	0.0	2412	-0.342	0.278	-0.1
10	3632	11.495	120.71	36.0	2812	14.860	56.76	15.3	3131	0.176	1.33	0.37	1414	-0.886	0.49	0.0	2411	-0.342	0.278	-0.1
11	3635	11.431	120.65	35.5	2824	14.682	56.58	15.2	3115	0.175	1.33	0.36	1411	-0.886	0.49	0.0	2425	-0.342	0.278	-0.1
12	3614	11.398	120.61	35.0	2043	14.500	56.40	15.2	3125	0.174	1.33	0.36	1433	-0.885	0.49	0.0	2424	-0.342	0.278	-0.1
13	3642	11.276	120.49	34.5	2841	14.366	56.26	15.1	3113	0.172	1.33	0.36	1432	-0.885	0.49	0.0	2423	-0.342	0.278	-0.1
14	3621	11.272	120.49	34.0	2844	14.258	56.15	15.1	3111	0.171	1.32	0.35	1431	-0.885	0.49	0.0	2422	-0.342	0.278	-0.1
15	3225	11.204	120.42	33.5	2045	14.211	56.11	15.0	3122	0.171	1.32	0.35	1123	-0.877	0.50	0.0	2421	-0.342	0.278	-0.1
16	3641	11.201	120.42	33.1	2822	14.102	56.00	14.9	3133	0.168	1.32	0.35	1122	-0.877	0.50	0.0	2445	-0.339	0.280	-0.1
17	3631	11.107	120.32	32.6	2033	14.094	55.99	14.9	3132	0.168	1.32	0.34	1121	-0.877	0.50	0.0	2444	-0.339	0.280	-0.1
18	3643	11.066	120.28	32.2	2843	14.093	55.99	14.8	3123	0.165	1.32	0.34	1145	-0.860	0.51	0.0	2443	-0.339	0.280	-0.1
19	3644	10.980	120.20	31.8	2833	13.923	55.82	14.8	3124	0.152	1.31	0.33	1144	-0.860	0.51	0.0	2442	-0.339	0.280	-0.1
20	3625	10.938	120.15	31.4	2014	13.884	55.78	14.8	2521	0.143	1.30	0.33	1143	-0.860	0.51	0.0	2441	-0.339	0.280	-0.1
Selection pressure[3]																				
10%		9.932	119.15	28.8	-	12.890	54.79	14.2	-	0.100	1.25	0.30	-	-0.833	0.54	0.0	-	-0.328	0.29	-0.1
20%		6.202	115.42	23.0	-	10.402	52.30	12.8	-	0.039	1.19	0.23	-	-0.756	0.62	0.1	-	-0.310	0.31	0.0
$\overline{X}_G$	-		109.22	-	-	-	41.90	-	-	-	1.15	-	-	-	1.37	-	-	-	0.000	-
$\overline{X}_{ST}$	-		88.83	-	-	-	41.61	-	-	-	0.97	-	-	-	1.37	-	-	-	0.549	-

[1]Genetic value obtained with the general average. and accumulated gain estimated based on the progeny average. [2]In the numbering of each individual, its unit number corresponds to the number of the plant within the plot, the tens digit corresponds to the replicate related to the plot, and the remaining digits are derived from the number of the progeny. For example, individual 1421 corresponds to plant one, of the second replicate of progeny 14. [3]The selection pressures of 10 and 20% correspond to the averages of the 72 and 144 genotypes, respectively, which were better ranked to the characters. $\overline{X}_G$, general average; and $\overline{X}_{ST}$, average without the controls. NCF, number of commercial fruit; CFM, mass of commercial fruit; MCFM, mean commercial fruit mass; CARFM, carpelloid fruit mass; and NPENF, number of pentandric fruit.

evaluated for this purpose, NPENF generated the lowest average gains for the two selection intensities: -0.1% for 10% intensity and for 20% intensity; the accumulated gain was null.

Conclusions

1. The variability observed for most of the characters allows greater genetic gains if selection is made at the progeny level, and not in individual papaya (*Carica papaya*) plants.

2. In progeny selection, PROT-268, PROT-74, PROT-55, and PROT-22 are the most promising for the breeding process.

3. The prediction of the gains is higher for the increase in the expression of the number of commercial fruits and for the decrease in the expression of the number of pentandric fruits.

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