



# Genetic control of quantitative traits and hybrid breeding strategies for cashew improvement

José Jaime Vasconcelos Cavalcanti<sup>1\*</sup>, Marcos Deon Vilela de Resende<sup>2</sup>, João Ribeiro Crisóstomo<sup>1</sup>, Levi de Moura Barros<sup>1</sup>, and João Rodrigues de Paiva<sup>1</sup>

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**ABSTRACT** - Knowledge about genetic parameters and trait control is fundamental for the success of any breeding program. This study aimed to estimate genetic parameters in an interpopulation of cashew using the REML/BLUP methods for vegetative growth, yield and nut quality traits. Results showed that plant height, canopy diameter, kernel weight and nut weight are under strong additive genetic control and do not present heterosis. The heritability of nut number and yield were higher in the broad than in the narrow sense. This indicates dominance and heterosis of these traits that should be adequately exploited in cashew breeding programs. Therefore, the best-suited breeding strategy to exploit heterosis is reciprocal recurrent selection using individual crosses between parents with high mean genotypic performance and high specific combining ability.

**Key words:** *Anacardium occidentale*, heritability, repeatability, heterosis.

## INTRODUCTION

Cashew nuts play an important role in human nutrition as protein and energy source. The crop is mainly grown in tropical countries such as Brazil, India, Vietnam and some others in Africa, where it is a vital income source.

Cashew breeding programs typically comprise the following stages: plant introduction, progeny testing, individual selection and hybrid breeding (Barros et al. 2002). Efforts to improve cashew have strongly emphasized heterosis exploitation whilst trying to minimize the effects of inbreeding depression as well. Breeding strategies have therefore focused on the generation and selection of superior hybrids, combined with the vegetative propagation of elite clones. But the

genetic base of the crop for some traits (particularly disease resistance and quality) still needs to be expanded by targeted introgression of new desirable alleles (Cavalcanti et al. 2000b, Cavalcanti et al. 2003).

Dwarf cashew is well-suited for modern cultivation systems due to its short stature. Considerable efforts have been made to improve this cashew type. However, this choice is not optimal since the greatest variability for most economically desirable traits such as fruit and pseudo-fruit weight and quality is found in the common cashew type. The first cashew dwarf clones were actually derived from a very narrow genetic base - a base population of just 36 plants collected in Maranguape, Ceará State, Brazil, introduced in the Experimental Station of Pacajus, Ceará State, Brazil, in 1956 (Barros et al. 1984). In view of the restricted

<sup>1</sup> Embrapa Agroindústria Tropical, C. P. 3761, 60.511-110, Fortaleza, CE, Brasil. \*E-mail: jaime@cnpat.embrapa.br

<sup>2</sup> Embrapa Florestas, C. P. 319, 83.411-000, Colombo, PR, Brasil

diversity in dwarf types, breeding must include gene introgression from the common into the dwarf genotypes in hybrid programs, coupled with dwarf type breeding and clone selection, to develop elite clones with enhanced yield, quality, disease resistance and physiology.

The success of plant breeding depends on significant levels of genetic variability in the original population and an efficient selection method for the fixation of desirable genetic combinations (Paterniani and Miranda Filho 1987). The efficiency of a breeding method depends on the genetic mechanism involved in the inheritance of the trait to be improved such as the number of genes that influence it, gene actions and effect, genetic heritability, repeatability and associations with other traits. The study of genetic parameters is therefore essential groundwork for the success of any breeding program (Resende 2002).

Particularly, the efficient estimation of genetic parameters is fundamental for that. To date there are few reports about phenotypic and genetic parameters in cashew (Damodaran 1975, Cavalcanti et al. 1997, Paiva et al. 1998, Cavalcanti et al. 2000a, Cavalcanti et al. 2000b, Cavalcanti et al. 2003) and further information about the genetic control of economically important traits in this species is needed to maximize the efficiency of its breeding program.

The statistical procedure BLUP (Best Linear Unbiased Prediction) seems to be the most effective method of genetic value prediction and selection. It adjusts data to the identified environmental effects such as of blocks, years and locations. Simultaneously it predicts individual genetic values by taking the genetic relationship among the candidates for selection into account (Resende 2002). For variance component estimation the method of choice is REML (Residual Maximum Likelihood) as introduced by Patterson and Thompson (1971). The statistical properties of this method are superior in comparison with the ANOVA method.

The objectives of this work were to estimate the additive and dominance genetic variances, narrow and

broad-sense heritability coefficients and repeatability coefficients of repeated measures over time; to predict additive (general combining ability) and dominance (specific combining ability) effects in a cashew interpopulation using the REML/BLUP methods applied to vegetative growth, nut yield and quality traits; and to establish breeding strategies in contribution to the ongoing cashew breeding program in Brazil.

## MATERIAL AND METHODS

The study was carried out at the Experimental Station of Embrapa Agroindústria Tropical, in Pacajús, state of Ceará, Brazil. The experiment was planted in 1991 and comprised 19 hybrids obtained by controlled crossing between parents of two distinct groups. One of them consisted of dwarf cashew clones (CCP06, CCP76, CCP09 and CCP1001) and the other of common (giant) cashew parents (CP07, CP12, CP77, CP96 and BTON) (Table 1). The experimental layout was a complete randomized block design with three replications and five plants per plot arranged in straight rows spaced 7 x 7 meters.

The evaluated traits were plant height (PH) and canopy diameter (CD) in meters, nut yield (NY) in grams per plant, nut number per plant (NN), nut weight (NW) in gram, kernel weight (KW) in gram, and ratio of kernel weight per nut weight (RKN) = (KW/NW) x 100. Plant height and canopy diameter were evaluated when the trees were 4 and 5 years old, and NY and NN with 3, 4, 5 and 6-year-old trees.

Variance components were estimated by REML and genetic values were predicted by BLUP using the Selegen-Reml/Blup software (Resende 2002). Analyses were carried out using two linear mixed models associated with factorial mating and a randomized complete block design. The first one dealt with individual trait analyses per year of measurement as well as with the trait mean across the years (joint analyses over years). This model was:

$$y = X\beta + X_m g_m + Z_f g_f + Ws + Tp + \epsilon$$

**Table 1.** Hybrids (H) of common x dwarf cashew and their parents

Female parents (dwarf)	Male parents (common)				
	CP 07	CP 12	CP 77	CP 96	BTON
CCP 06	H <sub>1x5</sub>	-	H <sub>1x7</sub>	H <sub>1x8</sub>	H <sub>1x9</sub>
CCP 76	H <sub>2x5</sub>	H <sub>2x6</sub>	H <sub>2x7</sub>	H <sub>2x8</sub>	H <sub>2x9</sub>
CCP 09	H <sub>3x5</sub>	H <sub>3x6</sub>	H <sub>3x7</sub>	H <sub>3x8</sub>	H <sub>3x9</sub>
CCP1001	H <sub>4x5</sub>	H <sub>4x6</sub>	H <sub>4x7</sub>	H <sub>4x8</sub>	H <sub>4x9</sub>

where:

$y$ ,  $\beta$ ,  $g_m$ ,  $g_f$ ,  $s$ ,  $p$  and  $e$ : vector of observed data, vector of block effects (assumed as fixed), vector of general combining ability effects of parents in the male population (assumed as random), vector of general combining ability effects of parents in the female population (assumed as random), vector of specific combining ability (assumed as random), vector of plot effects (assumed as random) and random error effects, respectively.  $X$ ,  $Z_m$ ,  $Z_f$ ,  $W$  and  $T$ : incidence matrices for  $b$ ,  $g_m$ ,  $g_f$ ,  $s$  and  $p$ , respectively.

The distributions and variance structures associated with the terms in the model are:

$$y|\beta, V \sim N(X\beta, V)$$

$$g_m | I\sigma_{g_m}^2 \sim N(0, I\sigma_{g_m}^2)$$

$$g_f | I\sigma_{g_f}^2 \sim N(0, I\sigma_{g_f}^2)$$

$$s | \sigma_s^2 \sim N(0, I\sigma_s^2)$$

$$p | \sigma_p^2 \sim N(0, I\sigma_p^2)$$

$$e | \sigma_e^2 \sim N(0, I\sigma_e^2)$$

$$V = Z_m\sigma_{g_m}^2 Z_m' + Z_f\sigma_{g_f}^2 Z_f' + W\sigma_s^2 W' + T\sigma_p^2 T' + I\sigma_e^2$$

According to this model, the effects of  $g_m$  and  $g_f$  are associated with interpopulation additive genetic effects in the male and female populations, respectively. The effects deal with dominance effects in the crossing between the two populations. Additive and dominance variances and the heritability coefficients were estimated using the following formulae:

$$\hat{\sigma}_a^2 = \frac{2(\hat{\sigma}_{g_m}^2 + \hat{\sigma}_{g_f}^2)}{\hat{\sigma}_y^2} : \text{estimate of the additive genetic variance}$$

in the crossed population.

$$\hat{\sigma}_d^2 = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_y^2} : \text{estimate of the dominance genetic variance in}$$

the crossed population;

$$\hat{\sigma}_y^2 = \hat{\sigma}_{g_m}^2 + \hat{\sigma}_{g_f}^2 + \hat{\sigma}_s^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2 : \text{estimate of the individual}$$

phenotypic variance in the crossed population;

$$\hat{h}_a^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_y^2} = \text{individual narrow-sense heritability;}$$

$$\hat{h}_g^2 = \frac{\hat{\sigma}_a^2 + \hat{\sigma}_d^2}{\hat{\sigma}_y^2} = \text{individual broad-sense heritability;}$$

$$\hat{h}_d^2 = \frac{\hat{\sigma}_d^2}{\hat{\sigma}_y^2} = \text{dominance individual heritability. The}$$

coefficients of determination of random effects were estimated as:

$$\hat{c}_{g_m}^2 = \frac{\hat{\sigma}_{g_m}^2}{\hat{\sigma}_y^2} = \text{coefficient of determination of general}$$

combining ability effects in the male population;

$$\hat{c}_{g_f}^2 = \frac{\hat{\sigma}_{g_f}^2}{\hat{\sigma}_y^2} = \text{coefficient of determination of general}$$

combining ability effects in the female population;

$$\hat{c}_s^2 = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_y^2} = \text{coefficient of determination of specific}$$

combining ability effects in the crossed population;

$$\hat{c}_p^2 = \frac{\hat{\sigma}_p^2}{\hat{\sigma}_y^2} = \text{coefficient of determination of plot effects.}$$

A second model dealt with all observations simultaneously on an individual basis, by the repeatability model:

$$y = Xb + Z_m g_m + Z_f g_f + Ws + Tp + Qc + e$$

where  $c$  is a vector of permanent or constant environmental effects at the individual level. The distribution of this effect was assumed to be  $c | \sigma_c^2 \sim N(0, I\sigma_c^2)$ .

The repeatability coefficient was estimated as:

$$\hat{r} = \frac{\hat{\sigma}_{g_m}^2 + \hat{\sigma}_{g_f}^2 + \hat{\sigma}_s^2 + \hat{\sigma}_p^2 + \hat{\sigma}_c^2}{\hat{\sigma}_{g_m}^2 + \hat{\sigma}_{g_f}^2 + \hat{\sigma}_s^2 + \hat{\sigma}_p^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2} = \text{individual}$$

repeatability coefficient.

## RESULTS AND DISCUSSION

The heritabilities of the estimates of genotypic ( $\hat{h}_g^2$ , individual broad-sense heritability) and additive ( $\hat{h}_a^2$ , individual narrow-sense heritability) were high for PH (89.1 and 86.5%), CD (65.9 and 51.2%), NW (76.9 and 63.2%) and KW (74.3 and 58.8%) at the two different ages, respectively (Tables 2, 3 and 4). On the other hand, the magnitudes of NN and NY did not exceed for 41.1% for  $\hat{h}_g^2$  and 21.2% for  $\hat{h}_a^2$ . Among the nut traits, the lowest magnitude was observed for RKN ( $\hat{h}_g^2 < 53.6\%$  and  $\hat{h}_a^2 < 40.0\%$ ). For all traits, results from joint analyses over years were similar to single year analyses. The estimates remained approximately constant over the years of evaluation (Tables 2, 3 and 4).

Estimates of individual narrow-sense heritability for PH, CD, KW, NW and RKN were higher than the dominance heritability (or degree of determination,  $\hat{h}_d^2$ ), indicating that the additive genetic components are more important for these traits. This was not the case for NN and NY, where there was an alternation of superiority between the additive and dominance effects in the individual analyses, with slight superiority for dominance effect in the global analysis.

Based on the results of the joint analyses over years as the best trait representation, the summary statistics for

**Table 2.** Estimates of genetic parameters for the vegetative growth traits, cashew plant height (PH) and canopy diameter (CD), evaluated in 1995 and 1996

Estimates*	PH		CD	
	1995	1996	1995	1996
$\hat{\sigma}_{g_f}^2$	0.089	0.124	0.022	0.035
$\hat{\sigma}_{g_m}^2$	0.161	0.253	0.276	0.656
$\hat{\sigma}_a^2$	0.501	0.753	0.595	1.383
$\hat{\sigma}_s^2$	0.004	0.026	0.043	0.141
$\hat{\sigma}_p^2$	0.018	0.006	0.114	0.051
$\hat{\sigma}_e^2$	0.306	0.437	0.708	1.410
$\hat{\sigma}_y^2$	0.579	0.845	1.162	2.294
$\hat{c}_g^2$	0.432	0.446	0.256	0.301
$\hat{c}_s^2$	0.008	0.031	0.037	0.062
$\hat{h}_d^2$	0.031±0.05	0.124±0.11	0.147±0.13	0.246±0.17
$\hat{h}_a^2$	0.865±0.22	0.891±0.22	0.512±0.17	0.603±0.18
$\hat{h}_g^2$	0.895	1.000	0.659	0.849
$\hat{c}_p^2$	0.032	0.007	0.098	0.022
CVg (%)	23.224	25.729	17.979	25.087
CVe (%)	9.110	8.481	10.377	10.379
Mean	3.096	3.598	4.871	5.562

\* Estimates of  $\hat{\sigma}_{g_m}^2$ : general combining ability variance among male parents;  $\hat{\sigma}_{g_f}^2$ : general combining ability variance among female parents;  $\hat{\sigma}_a^2$ : estimate of additive genetic variance;  $\hat{\sigma}_s^2$ : specific combining ability variance;  $\hat{\sigma}_p^2$ : phenotypic variance;  $\hat{\sigma}_e^2$ : error variance;  $\hat{\sigma}_y^2$ : individual phenotypic variance;  $\hat{c}_g^2$ : coefficient of determination of general combining ability effects;  $\hat{c}_s^2$ : coefficient of determination of specific combining ability effects;  $\hat{h}_d^2$ : dominance individual heritability;  $\hat{h}_a^2$ : individual narrow-sense heritability;  $\hat{h}_g^2$ : individual broad-sense heritability;  $\hat{c}_p^2$ : coefficient of determination of plot effects; CVg: coefficient of genetic variance; and CVe: coefficient of environmental variance

yield and nut quality traits were (i) individual narrow-sense heritability: 0.11, 0.13, 0.71 and 0.71 for NN, NY, NW and KW, respectively; and (ii) individual broad-sense heritability: 0.35, 0.31, 0.87 and 0.84 for NN, NY, NW and KW, respectively. These confirm that the genetic control of the quality traits NW and KW is mainly additive as well as the genetic control of the vegetative traits PH and CD. The dominance effects in these traits tended to be null as can be seen from the standard deviations associated with the dominance heritabilities ( $\hat{h}_d^2$ ) in Tables 2 and 4, with magnitudes as high as or in some cases superior to the dominance heritability estimates. These traits are therefore probably not heterotic and simpler selection methods can be used for their improvement. On the other hand, the broad-sense heritabilities of the yield traits NN and NY were much higher than narrow-sense heritabilities. This shows that these traits are probably heterotic and can therefore be adequately exploited in cashew breeding programs for yield.

To our knowledge these heritability estimates are the first reported in literature for cashew and therefore highly important for cashew breeding programs around

the world. Their magnitudes agree with expected values for these traits based on other studies on cashew genetics. Using fixed model approaches for the genetic effects, Damodaran (1975) and Cavalcanti et al. (2000b) also inferred the presence of heterosis in cashew yield traits.

Heritability represents the relative ratio of genetic and environmental influences on the phenotypic expression of the traits and indicates the degree of difficulty or ease of improvement (Resende 2002). It plays a main role in the prediction of genetic values. Therefore, it expresses the reliability of the phenotypic value as estimator of the genotypic value, since the higher the heritability, the higher the genetic gain for selection (Falconer and Mackay 1996). According to this estimate, more or less complex selection methods are defined and applied (Resende 2002). In this sense, it is easier to obtain genetic gains for PH, CD, KW and NW than for RKN, NN and NY since the inheritance of the latter traits is complex and, consequently, requires more intricate breeding methods.

The narrow-sense heritability considers only the genetic additive variance that is associated with the additive

**Table 3.** Estimates of genetic parameters for the yield traits, cashew nut number (NN) and yield (NY) evaluated from 1994 to 1997

Estimates*	Nut number				Yield				Joint Analyses over Years	
	1994	1995	1996	1997	1994	1995	1996	1997	NN	NY
$\hat{\sigma}_{by}^2$	11.81	352.44	1103.85	373.81	14092.98	64558.85	78052.14	99330.63	528.22	66961.30
$\hat{\sigma}_{bm}^2$	68.54	2343.11	1171.57	4722.74	1436.44	53724.61	1502.15	245320.14	701.50	2195.61
$\hat{\sigma}_a^2$	160.70	5391.10	4550.83	10193.10	31058.84	236566.91	159108.57	689301.55	2459.43	138313.82
$\hat{\sigma}_e^2$	974.22	1614.09	2092.01	334.66	41272.30	60564.08	69406.99	27335.35	1409.00	45440.77
$\hat{\sigma}_p^2$	73.86	192.51	3462.21	8854.18	28636.38	26868.59	124573.26	363707.06	1109.35	66278.18
$\hat{\sigma}_d^2$	10343.86	29898.39	23558.23	58798.78	558543.6	1448839.61	1313230.26	2510710.90	19467.34	853616.11
$\hat{\sigma}_g^2$	11472.29	34400.53	31387.87	73084.18	643981.6	1654555.74	1586764.80	3246404.08	23215.41	1034491.97
$\hat{\sigma}_c^2$	0.007	0.078	0.072	0.070	0.024	0.071	0.050	0.106	0.053	0.067
$\hat{\sigma}_s^2$	0.085	0.047	0.067	0.005	0.064	0.037	0.044	0.008	0.061	0.044
$\hat{h}_d^2$	0.340±0.19	0.188±0.14	0.267±0.17	0.018±0.04	0.256±0.17	0.146±0.13	0.175±0.14	0.034±0.06	0.243±0.16	0.176±0.14
$\hat{h}_a^2$	0.014±0.03	0.157±0.09	0.145±0.09	0.139±0.09	0.048±0.05	0.143±0.09	0.100±0.07	0.212±0.11	0.106±0.07	0.134±0.09
$\hat{h}_g^2$	0.354	0.344	0.412	0.158	0.305	0.289	0.275	0.246	0.349	0.309
$\hat{c}_p^2$	0.006	0.006	0.110	0.121	0.044	0.016	0.079	0.112	0.048	0.064
R										
$r_m$										
Accuracy										
CVg (%)	42.396	39.878	47.735	27.376	37.710	33.967	34.698	29.811	34.210	28.088
CVe (%)	30.808	28.784	37.970	36.602	31.898	27.621	32.672	31.040	26.893	24.169
Mean	150.249	272.945	238.110	392.260	1174.461	2037.204	1904.594	2997.752	263.010	2014.244

\* Estimates of  $\hat{\sigma}_{gm}^2$ : general combining ability variance among male parents;  $\hat{\sigma}_{fy}^2$ : general combining ability variance among female parents;  $\hat{\sigma}_g^2$ : estimate of additive genetic variance;  $\hat{\sigma}_s^2$ : specific combining ability variance;  $\hat{\sigma}_p^2$ : phenotypic variance;  $\hat{\sigma}_e^2$ : error variance;  $\hat{\sigma}_d^2$ : individual phenotypic variance;  $\hat{\sigma}_a^2$ : coefficient of determination of general combining ability effects;  $\hat{\sigma}_c^2$ : coefficient of determination of specific combining ability effects;  $\hat{h}_d^2$ : dominance individual heritability;  $\hat{h}_a^2$ : individual narrow sense heritability;  $\hat{h}_g^2$ : individual broad-sense heritability;  $\hat{c}_p^2$ : coefficient of determination of plot effects; R: repeatability at individual level;  $r_m$ : repeatability at means (across four measures) level; CVg: coefficient of genetic variance; and CVe: coefficient of environmental variance

**Table 4.** Estimates of genetic parameters for the quality traits, cashew nut weight (NW), kernel weight (KW) and ratio KW/NW (RKN) evaluated in 1995 and 1996

Estimates*	NW			KW			RKN			Joint Analyses over Years		
	1995	1996	1995	1996	1995	1996	1995	1996	NW	AW	KKN	
	$\hat{\sigma}_{\sigma_y}^2$	0.9892	0.7063	0.0919	0.0707	0.2807	0.0674	0.8516	0.0812	0.8516	0.0812	0.2403
$\hat{\sigma}_{\sigma_{\text{gen}}}^2$	1.1807	1.0648	0.0617	0.0406	0.9324	2.6849	1.1055	0.0506	1.1055	0.0506	1.8034	
$\hat{\sigma}_{\sigma}^2$	4.3398	3.5421	0.3071	0.2225	2.4263	5.5046	3.9142	0.2637	3.9142	0.2637	4.0875	
$\hat{\sigma}_s^2$	0.1469	0.3112	0.0025	0.0224	0.6418	0.1505	0.2295	0.0123	0.2295	0.0123	0.0986	
$\hat{\sigma}_p^2$	0.4726	0.5099	0.0295	0.0333	0.0270	0.0471	0.4585	0.0274	0.4585	0.0274	0.0249	
$\hat{\sigma}_e^2$	3.6138	3.0054	0.2408	0.2111	7.4313	10.8072	2.8965	0.1989	2.8965	0.1989	6.7119	
$\hat{\sigma}_y^2$	6.4032	5.5976	0.4263	0.3780	9.3132	13.7571	5.5416	0.3704	5.5416	0.3704	8.8791	
$\hat{c}_g^2$	0.3389	0.3164	0.3601	0.2943	0.1303	0.2001	0.3532	0.3559	0.3532	0.3559	0.2302	
$\hat{c}_p^2$	0.0229	0.0556	0.0058	0.0592	0.0689	0.0109	0.0414	0.0332	0.0414	0.0332	0.0111	
$\hat{h}_d^2$	0.0917±0.10	0.2224±0.16	0.0232±0.05	0.2368±0.16	0.2757±0.18	0.0438±0.07	0.1657±0.14	0.1326±0.12	0.1657±0.14	0.1326±0.12	0.0444±0.07	
$\hat{h}_r^2$	0.6778±0.20	0.6328±0.10	0.7203±0.20	0.5885±0.18	0.2605±0.12	0.4001±0.15	0.7063±0.20	0.7119±0.20	0.7063±0.20	0.7119±0.20	0.4604±0.16	
$\hat{h}_g^2$	0.7695	0.8552	0.7435	0.8253	0.5362	0.4439	0.8720	0.8445	0.8720	0.8445	0.5048	
$\hat{c}_s^2$	0.0738	0.0911	0.0692	0.0880	0.0029	0.0034	0.0827	0.0740	0.0827	0.0740	0.0028	
R												
r <sub>m</sub>												
Accuracy												
CVg (%)	23.239	23.709	21.218	21.193	7.968	8.520	23.410	21.148	23.410	21.148	7.424	
CVe (%)	11.446	11.422	10.501	10.422	4.386	5.124	10.849	9.799	10.849	9.799	4.100	
Mean	9.552	9.228	2.654	2.636	28.045	29.004	9.390	2.645	9.390	2.645	<b>28.518</b>	

\* Estimates of  $\hat{\sigma}_{\sigma_{\text{gen}}}^2$ : general combining ability variance among male parents;  $\hat{\sigma}_{\sigma_y}^2$ : general combining ability variance among female parents;  $\hat{\sigma}_s^2$ : estimate of additive genetic variance;  $\hat{\sigma}_p^2$ : specific combining ability variance;  $\hat{\sigma}_e^2$ : phenotypic variance;  $\hat{\sigma}_e^2$ : error variance;  $\hat{\sigma}_y^2$ : individual phenotypic variance;  $\hat{c}_g^2$ : coefficient of determination of general combining ability effects;  $\hat{c}_s^2$ : coefficient of determination of specific combining ability effects;  $\hat{h}_d^2$ : dominance individual heritability;  $\hat{h}_r^2$ : individual narrow sense heritability;  $\hat{h}_g^2$ : individual broad-sense heritability;  $\hat{c}_p^2$ : coefficient of determination of plot effects; R: repeatability at individual level; r<sub>m</sub>: repeatability at means (across four measures) level; CVg: coefficient of genetic variance; and CVe: coefficient of environmental variance

effects, which is effectively transmitted during the selection process for sexual propagation. The broad-sense heritability capitalizes on both additive and dominance genetic variances. This is important for perennial species of vegetative propagation where the genotype is fully inherited (Ramalho et al. 1990). This is the case of cashew, when clonal selection is used.

The high heritability values established for PH, CD, KW and NW in this study indicate a greater probability of presence of a small number of genes controlling them and/or, a smaller environmental effect influencing the trait.

Repeatability reflects the phenotypic correlation between repeated measurements in the same individual over time (Resende 2002). The values for NN and NY repeatability estimates on individual level were low (around 0.30) (Table 3). On the other hand, the magnitudes for NW, KW and RKN were high (around 0.85), so high reliability can be obtained in each one of the measurements.

Taking the evaluation over four consecutive years into consideration, the repeatability rises to over 0.61 for NN and NY and to around 0.95 for NW and KW. These repeatabilities of means across several years represent the coefficient of determination of the true genotypic values of the individuals. The square root of these estimates expresses the selection accuracy, according to the number of repeated measures. Accuracy is generally defined as the proximity between predicted and true genetic values of individuals (Resende 2002a). The accuracy estimates considering all repeated annual measures were high (>0.78%) for NN, NY, NW, KW and RKN (Tables 3 and 4), showing that the number of annual evaluations was sufficient.

The number of repeated measures can be determined based on accuracy. Therefore, four evaluations would be necessary to achieve an accuracy of 80% for NN and NY and only one for NW, KW and RKN. This information is relevant for time and cost reductions in the evaluations of cashew breeding experiments.

The contributions of the general and specific combining abilities as a proportion of the total phenotypic variance can be inferred from the respective coefficients of determination  $\hat{\epsilon}_g^2$  and  $\hat{\epsilon}_s^2$  (Tables 2, 3 and 4).  $\hat{\epsilon}_g^2$  is related to narrow-sense individual heritabilities, whereas  $\hat{\epsilon}_s^2$  is only related to dominance individual heritability. The coefficient of determination of the general combining ability (GCA) is equivalent to half of the individual narrow-sense heritability and the determination coefficient of the specific combining ability is equivalent to one quarter of the dominance individual heritability. The highest

contributions were for PH, CD, KW, NW and RKN, in a range from 13 to 44.6% of the phenotypic variance, while NN and NY presented 0.7 to 10.6% only (Tables 2, 3 and 4). On the other hand, the values of variances of the specific combining ability (SCA) were low, not exceeding 8.5% of the phenotypic variance. These values indicate the importance of GCA and SCA in the genetic variability, with predominance of CGC for PH, CD, KW, NW and RKN.

GCA is related to the mean performance of a parent in a series of hybrid combinations and is associated with the additive effect of alleles and epistatic actions of the additive type. On the other hand, SCA informs which hybrid combinations are relatively superior or inferior to what would be expected on the basis of GCA and is associated with dominance effects of genes and epistasis (Cruz and Vencovsky 1989). Significant GCA and SCA were also observed by Wunnachit et al. (1992) when studying nut yield in adult plants and Cavalcanti et al. (1997) who studied early nut yield. Cavalcanti et al. (2000b) used a methodology of Miranda Filho and Geraldi (1984) for partial diallel analysis and identified importance for GCA of NN, NY, PH, CD, KW, NW, and RKN. These results corroborate the significance of mean parent effects and heterosis; while SCA was only significant for NN and NY, in accordance with the results for the corresponding parameter, i.e. specific heterosis. These results are consistent with the ones found here.

The analyses of  $g$  (genetic GCA) effects demonstrated different contributions of the parents to the mean of the traits in question (Table 5). For PH and CD, we only considered values for the age of five years. Parents BTON (among the common parents) and CCP06 and CCP09 (among dwarfs) presented the highest negative  $g$  effect for PH and CD, demonstrating a higher presence of favorable alleles to reduce plant vigor, which is desirable for this crop. On the other hand, parents CCP1001 (of the dwarfs) and CP96 (common cashew) presented the highest contributions to increase the expression of PH and CD.

For the yield-related traits NN and NY, it was observed that CCP1001 and CCP09 among the dwarf parents, and CP96 (NN) and CP77 (NY) among the common parents presented the highest  $g$  effect (Table 5), contributing to increase the expression of these traits. For the quality-related traits, the parents CP12 and CP77 (common) and CCP09 and CCP76 (dwarf) attained the highest  $g$  values and were outstanding for the increase in nut and kernel weight they provided. For RKN, parent CP96 (common) and CCP09 (dwarf) presented the highest contributions to increase this trait (Table 5).

**Table 5.** Estimates of general (*g*) and specific (*s*) combining ability and genetic gain (*g*) for cashew plant height (PH), canopy diameter (CD), nut number (NN), yield (NY), nut weight (NW), kernel weight (KW) and ratio KW/NW (RKN) over years

Parent	PH		CD		NN		NY		NW		KW		RKN	
	<i>g</i>	<i>g</i> %	<i>g</i>	<i>g</i> %	<i>g</i>	<i>g</i> %	<i>g</i>	<i>g</i> %	<i>g</i>	<i>g</i> %	<i>g</i>	<i>g</i> %	<i>g</i>	<i>g</i> %
1. CCP06	-0.31	0.00	-0.19	0.00	-7.80	1.89	-274.73	0.00	-1.16	0.00	-0.35	0.00	-0.07	0.88
2. CCP76	0.13	7.58	0.09	1.67	2.64	4.33	132.54	8.55	0.57	6.91	0.11	7.67	-0.35	0.00
3. CCP09	-0.23	2.91	-0.04	0.89	-14.95	0.00	-69.68	4.55	0.73	7.75	0.29	11.07	0.57	1.99
4. CCP1001	0.41	11.41	0.09	1.70	20.11	7.65	211.87	10.52	-0.13	4.13	-0.06	4.38	-0.15	0.41
5. CP07	-0.07	5.51	-0.66	4.52	19.12	7.27	3.15	0.32	-0.94	2.62	-0.23	0.00	0.15	3.93
6. CP12	0.41	11.50	0.51	9.98	-6.33	3.85	5.24	0.39	1.04	11.07	0.25	9.56	-0.19	2.40
7. CP77	0.08	8.06	0.55	10.39	-8.32	2.10	10.67	0.53	0.96	10.66	0.18	8.19	-0.82	1.08
8. CP96	0.38	11.00	0.61	10.96	17.62	6.98	-0.72	0.23	-0.98	0.00	-0.09	4.31	2.09	7.35
9. BTON	-0.79	0.00	-1.00	0.00	-22.10	0.00	-18.34	0.00	-0.08	6.82	-0.11	2.16	-1.23	0.00
Hybrid*	<i>s</i>	<i>g</i> %	<i>s</i>	<i>g</i> %	<i>s</i>	<i>g</i> %	<i>s</i>	<i>g</i> %	<i>s</i>	<i>g</i> %	<i>s</i>	<i>g</i> %	<i>s</i>	<i>g</i> %
H <sub>4x8</sub>	0.01	1.53	0.28	5.76	58.22	22.14	106.36	6.48	-0.34	0.35	-0.08	0.24	0.01	0.30
H <sub>2x5</sub>	0.09	2.53	-0.01	2.67	28.41	10.80	145.55	7.23	-0.04	1.66	0.02	1.65	0.13	0.59
H <sub>4x5</sub>	0.02	1.87	-0.03	2.42	18.34	6.97	30.54	4.24	-0.08	0.98	-0.03	0.78	-0.03	0.17
H <sub>2x9</sub>	0.02	1.64	0.14	3.94	17.12	6.51	41.06	4.80	-0.07	1.28	-0.05	0.62	-0.12	0.11
H <sub>1x5</sub>	0.10	2.67	0.05	3.13	13.58	5.16	37.29	4.51	0.00	2.16	-0.03	0.90	-0.18	0.00
H <sub>4x6</sub>	0.05	2.02	0.13	3.72	11.87	4.51	128.10	6.88	0.05	2.84	0.02	2.12	0.02	0.33
H <sub>1x8</sub>	0.09	2.58	0.22	5.16	9.55	3.63	51.28	5.15	0.02	2.47	0.02	1.92	0.08	0.41
H <sub>3x9</sub>	0.08	2.43	0.11	3.37	8.09	3.07	6.49	3.91	-0.16	0.59	-0.06	0.44	-0.04	0.15
H <sub>4x7</sub>	0.06	2.10	0.13	3.54	3.99	1.52	141.99	7.14	0.38	4.39	0.07	2.62	-0.18	0.03
H <sub>3x7</sub>	0.06	2.28	0.16	4.58	-0.51	-0.20	102.89	6.20	-0.03	1.89	0.02	1.77	0.20	0.71
H <sub>2x7</sub>	0.02	1.74	0.36	6.46	-7.05	-2.68	87.85	5.90	0.44	4.71	0.07	2.70	-0.17	0.07
H <sub>3x6</sub>	0.06	2.18	0.15	4.21	-9.23	-3.51	65.87	5.52	0.24	3.53	0.05	2.38	-0.01	0.27
H <sub>1x7</sub>	-0.13	0.33	-0.52	0.00	-13.12	-4.99	-112.81	1.78	-0.60	0.00	-0.11	0.00	0.09	0.48
H <sub>2x6</sub>	-0.07	0.81	-0.18	1.45	-15.35	-5.84	-86.06	2.78	-0.07	1.12	-0.01	1.20	-0.03	0.19
H <sub>2x8</sub>	-0.03	1.35	0.05	2.92	-16.08	-6.11	-98.49	2.27	-0.11	0.73	-0.01	1.36	0.03	0.37
H <sub>3x8</sub>	-0.03	1.18	-0.42	0.53	-16.29	-6.19	-73.98	3.33	0.23	3.31	0.05	2.48	-0.01	0.24
H <sub>3x5</sub>	-0.21	0.00	-0.15	1.76	-21.93	-8.34	-148.54	1.24	-0.08	0.86	-0.02	1.05	0.08	0.44
H <sub>1x9</sub>	-0.12	0.57	-0.34	1.00	-30.82	-11.72	-162.15	0.73	0.26	3.85	0.07	2.65	-0.02	0.21
H <sub>4x9</sub>	-0.06	0.99	-0.13	2.08	-38.77	0.00	-263.24	0.00	-0.05	1.46	0.01	1.53	0.11	0.53

\*: H<sub>4x8</sub> = hybrid originated from the cross between parents 4 and 8, for example



The SCA estimates ( $s$ ) identified the hybrids with highest contributions:  $H_{2 \times 5}$ ,  $H_{4 \times 5}$  and  $H_{2 \times 8}$  for NN and  $H_{2 \times 5}$ ,  $H_{4 \times 6}$  and  $H_{4 \times 7}$  for NY (Table 5). In relation to NW and KW, the hybrid combinations with the best performances were  $H_{2 \times 7}$ ,  $H_{4 \times 7}$  and  $H_{3 \times 9}$ , and for RKN were  $H_{2 \times 5}$ ,  $H_{3 \times 7}$  and  $H_{4 \times 9}$ . These results indicate presence of important genetic divergences and considerable degree of complementation in the loci with dominance among the parents of these hybrids. These results show expressive genetic variability, suitable for exploitation in the improvement program.

The selection of individual hybrid combinations is of great importance for any breeding program. For long-term breeding, the selection strategy should consider the types of gene action controlling the yield traits. This study corroborated the presence of dominance and strong heterosis for yield traits. So an adequate breeding strategy should be delineated to improve both heterosis and general combining abilities. This strategy is the reciprocal recurrent selection (RRS) as introduced by Comstock et al. (1949) and used successfully in several breeding programs of annual (Gallais 1989) and perennial plants

(Baudouin et al. 1997, Resende 2002). RRS can be practiced using individual crosses between parents with high genotypic mean performance and high specific combining ability (Resende 2002). This study indicated at least four crosses in which parents are promising for RRS (Table 5).

## CONCLUSIONS

Plant height, canopy diameter, kernel weight and nut weight are under strong additive genetic control and probably not heterotic, so simpler selection methods can be used for their improvement.

The heritability of the traits nut number and yield was much higher in the broad than in the narrow sense.

Reciprocal recurrent selection is the most suitable breeding strategy for cashew improvement.

Individual repeatabilities were of the order of 30% for nut number and yield and 85% for kernel weight and nut weight. One annual measurement for kernel weight and nut weight and four for nut number and yield warrant a high selection accuracy.

# Controle genético de caracteres quantitativos e estratégias de hibridações para o melhoramento do cajueiro

**RESUMO** - O conhecimento sobre parâmetros genéticos agindo no controle dos caracteres é fundamental para o sucesso de qualquer programa de melhoramento. Este estudo teve como objetivo obter estimativas de parâmetros genéticos numa interpopulação de cajueiro usando os métodos REML/BLUP aplicados às características de vigor vegetativo, produção e da castanha. Os resultados revelaram que altura de planta, diâmetro do caule, peso da castanha e peso da amêndoa estão sob forte controle genético aditivo, não sendo provável exibirem heterose. O número de castanhas e a produção mostraram herdabilidades mais altas no sentido amplo que no sentido restrito. Isto indica que tais caracteres apresentam dominância e heterose, a qual deve ser adequadamente explorada no programa para melhoramento. Portanto, a estratégia adequada para melhor explorar a heterose é a seleção recorrente recíproca que pode ser praticada usando cruzamentos individuais entre pais com elevado desempenho genético em cruzamento e alta capacidade específica de combinação.

**Palavras-chave:** *Anacardium occidentale*, herdabilidade, repetibilidade, heterose.

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