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Genetics/ Original Article

Heritability estimated by different methods in four generations of progenies from a pigeon pea cross

Abstract – The objective of this work was to compare different methods to estimate heritability in 30 pigeon pea families from the F_3, F_4, F_5, and F_6 generations, for nine variables. The experimental design was a randomized complete block with three replicates and 20 plants per plot. Broad-sense heritability was estimated by the analysis of variance (ANOVA) [$h^2_{b\text{-}E(MS)}$], restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) ($h^2_{b\text{-}REML}$), parent-offspring regression (h^2_{PO}), and standard deviation unit (h^2_{UP}). The $h^2_{b\text{-}E(MS)}$ and $h^2_{b\text{-}REML}$ estimates were similar for seven of the analyzed variables. For a higher genetic control and easier selection, values of $h^2_{b\text{-}E(MS)}$ and $h^2_{b\text{-}REML}$ >0.70 were estimated for two variables in four generations, two variables in three generations, three variables in two generations, and one variable in one generation. Values of h^2_{UP} and h^2_{PO} >0.70 were obtained for four and five variables, respectively. The estimates via regression or parent-offspring correlation showed some values outside the expected range of 0 to 1. The ANOVA [$h^2_{b\text{-}E(MS)}$] and REML/BLUP [$h^2_{b\text{-}REML}$] methods are the best to estimate pigeon pea heritability.

Index terms: *Cajanus cajan*, expected mean square, genetic parameters, mixed models, parent-offspring regression.

Herdabilidade estimada por diferentes métodos em quatro gerações de progênies de um cruzamento de guandu

Resumo – O objetivo deste trabalho foi comparar diferentes métodos para estimar a herdabilidade em 30 linhagens de guandu das gerações F_3, F_4, F_5 e F_6, para nove variáveis. O delineamento experimental foi em blocos ao acaso, com três repetições e 20 plantas por parcela. Estimou-se a herdabilidade no sentido amplo por meio de análise de variância (ANOVA) [$h^2_{b\text{-}E(MS)}$], máxima verossimilhança restrita/melhor predição linear não viciada (REML/BLUP) ($h^2_{b\text{-}REML}$), regressão pai-filho (h^2_{PO}) e unidade do desvio-padrão (h^2_{UP}). As estimativas de $h^2_{b\text{-}E(MS)}$ e $h^2_{b\text{-}REML}$ foram de magnitude próxima para sete das variáveis analisadas. Para maior controle genético e facilidade na seleção, valores de $h^2_{b\text{-}E(MS)}$ e $h^2_{b\text{-}REML}$ >0,70 foram estimados para duas variáveis em quatro gerações, duas variáveis em três gerações, três variáveis em duas gerações e uma variável em uma geração. Valores de h^2_{UP} e h^2_{PO} >0,70 foram obtidos para quatro e cinco variáveis, respectivamente. As estimativas via regressão ou correlação pai-filho mostraram alguns valores fora da variação esperada de 0 a 1. Os métodos ANOVA [$h^2_{b\text{-}E(MS)}$] e REML/BLUP [$h^2_{b\text{-}REML}$] são os melhores para estimar a herdabilidade em guandu.

Termos para indexação: *Cajanus cajan*, quadrado médio esperado, parâmetros genéticos, modelos mistos, regressão pai-filho.

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Introduction

Pigeon pea [*Cajanus cajan* (L.) Millsp.] is an important pulse in some countries, especially for the populations of tropical and subtropical regions, due to its protein content and ability to withstand drought (Cullis & Kunert, 2017). The species is mainly grown in India, which concentrates 75% of its worldwide production, estimated at 5.6 million per hectare (FAO, 2019).

Despite the advances in global pigeon pea production due to breeding, so far yield gains have been small, and, therefore, increasing them is still one of the main objectives and challenges of the breeders of the species (Saxena et al., 2021a). According to Silva et al. (2018), the estimates and analyses of important genetic parameters to predict yield gains in the selection of superior genotypes have allowed significant advances for several quantitative agronomic traits, with heritability acting as an essential parameter in classical breeding.

The main methods used to estimate heritability (h^2) fall into three categories (Brown & Caligari, 2008). The first consists of methods based on variance components, such as the expected mean squares of the analysis of variance (ANOVA) and the restricted maximum likelihood (REML) (Hill, 2014). The second comprises methods based on the regression between the offspring and one or both parents, used to estimate narrow-sense heritability (Smith & Kinman, 1965) and the standard unit heritability in terms of standard deviation (Frey & Horner, 1957). The third includes some methods that effectively express heritability achieved as a gain from selection, determining how much of the selection differential applied in previous generations was observed as a response in the progeny (Brown & Caligari, 2008).

Obala et al. (2018) used ANOVA to estimate broad-sense heritability (h^2_b) in pigeon pea, finding values from 0.519 for number of pods per plant to 0.999 for days to flowering, with the h^2_b of 0.519 having particular importance for grain protein content. Studying five pigeon pea generations, Ajay et al. (2012) reported a high heritability and genetic advance in yield-related traits, which are indicative of the high effectiveness of the performed selection. Furthermore, Sharma et al. (2019) used mixed models to evaluate pigeon pea lineages, observing a high broad-sense heritability (>70%) for most traits. However, to date, there are no known studies on heritability estimates for improved pigeon pea populations in Brazil or using different methods to estimate this parameter in the species.

The objective of this work was to compare different methods to estimate heritability in 30 pigeon pea families from the F_3, F_4, F_5, and F_6 generations, for nine variables.

Materials and Methods

The experiment was conducted at the Caatinga experimental field of Embrapa Semiárido, located in the municipality of Petrolina, in the state of Pernambuco, Brazil (09º09'S, 40º22'W, at 365.5 m above sea level). According to Köppen's classification, the climate of the region is of the BSwh' type, i.e., a hot semiarid. The soil of the experimental area was classified as an Ultisol and Oxisol (Soil Survey Staff, 2014), with the following properties according to Claessen (1997): pH 5.0, 3.28 mg dm^{-3} P, 0.22 cmol$_c$ dm^{-3} K, 0.03 cmol$_c$ dm^{-3} Na, 0.60 cmol$_c$ dm^{-3} Mg, 0.00 cmol$_c$ dm^{-3} Al, 1.5 cmol$_c$ dm^{-3} H+Al, sum of bases of 2.5 cmol$_c$ dm^{-3}, cation exchange capacity of 4.3 cmol$_c$ dm^{-3}, porosity of 38.27%, 48.8 g kg^{-1} clay, 225.5 g kg^{-1} silt, and 725.7 g kg^{-1} sand.

For the study, 30 families from different pigeon pea generations from the ICPL 90045 × UW10 cross were randomly selected and evaluated: six families from F_3 and eight families from each of the F_4, F_5, and F_6 generations. Accession ICPL 90045 was developed by International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Patancheru, India) as an extra-early plant, with maturation under 90 days, plant height lower than 100 cm, a 100-grain weight of ~9.0 g, three grains per pod, and pods measuring ~6.0 cm in length. Accession UW10 was developed at The University of the West Indies (St. Augustine, Trinidad and Tobago), with a cycle longer than 100 days, a 100-grain weight of ~11 g, five grains per pod, and pods measuring ~6.2 cm (Santos et al., 2000).

To obtain the seeds of the families evaluated in the F_3, F_4, F_5, and F_6 generations, the plants from the previous generation were protected before anthesis with non-woven fabric bags (TNT) to avoid possible crosses. Two seeds were sown per cell in 200-cell polystyrene trays containing commercial substrate (Maxfertil, Pouso Redondo, SC, Brazil), and the seedlings were transplanted to the field after developing the first true leaves 15 days after sowing.

The experiment was conducted in randomized complete blocks, with three replicates and 20 plants per plot, distributed along two rows with 2.5 m of length, containing five holes each. During the experiment, the plants were irrigated and crop management practices were carried out whenever necessary according to Saxena et al. (2019). No fertilizers were applied.

The following nine traits were evaluated: number of days to start flowering (NIF); number of days to 50% flowering (NDF); number of days to pod maturation (NDM), with 95% of the pods in the plot showing a typical mature pod color; mature plant height (PH), measured from the base of the plant to the tip of the main stem; mean pod length (PL) of five random pod samples, in millimeters; number of pods per plant (NPP); mean number of grains per pod (NGP) of five randomly sampled pods; 100-seed weight (P100), in grams; and grain yield, defined as the total weight of grains harvested per plant, in grams or kilograms. Selection was performed for all traits evaluated in each generation and was considered: positive, when an increasing mean was obtained for NPP, NGP, P100, and grain yield; and negative, when a decreasing mean was found for NIF, NDF, NDM, PH, and PL.

The data were tested for normality of residuals using the Kolmogorov-Smirnov test and the PROC GLM procedure of the SAS software (SAS Institute Inc., Cary, NC, USA). The variables NPP and grain yield did not meet the normality assumptions and were transformed to square root of x.

For PH, NPP, PL, NGP, P100, and grain yield, the variance components were calculated with the PROC VARCOMP procedure (SAS Institute Inc., Cary, NC, USA) using the expected mean square according to the following model: $Y_{ijk}=\mu+t_i+b_j+e_{ij}+\pi_{ijk}$, , where Y_{ijk} is the value observed in the k-th plant, in the j-th replicate of the i-th treatment; μ is the overall mean; t_i is the random effect of the i-th treatment (i=1, 2, ..., n;); b_j is the random effect of the j-th block (j=1, 2, ..., r); e_{ij} is the random effect of the variation between plots; and π_{ijk} is the random effect of the variation between plants within the plot.

For the remaining traits – NIF, NDF, and NDM –, the parameters were estimated by the expected mean square using the following model: $y_{ij}=m+b_j+t_i+e_{ij}$, , where y_{ij} is the value of the studied trait in treatment i (i =1, 2, ..., I) and in block (or replicate) j (j =1, 2, ..., J); m is the overall mean (of all observations) of the experiment; t_i is the effect of treatment i; and e_{ij} is the error associated with observation y_{ij} or the effect of uncontrolled factors. Individual ANOVAs by generations and a pooled ANOVA with all generations were performed to estimate genetic parameters and to test for phenotypic variance, respectively.

Broad-sense heritability by ANOVA ($h^2_{a\text{-}E(MS)}$), the genetic coefficient of variation between families (CVge), and the environmental coefficient of variation (CVe) were estimated as described by Cruz et al. (2014). According to Vencovsky & Barriga (1992), when the CVge/CVe ratio is equal to or greater than 1.0, there is a favorable condition for selection.

Genetic gain as a percentage of the mean (GG%) was obtained and categorized as: low, from 0–10%; moderate, 10–20%; and high, >20% (Obala et al., 2018), using the following equation:

$$GG\%=\left(kh_a^2\sqrt{\sigma_P^2}\Big/\overline{X}\right)\times 100,$$

where $\overline{X}$ is the mean of the evaluated phenotypes and k is the constant for selection intensity (1.27 at a selection intensity of 25%).

The estimates were obtained by the restricted maximum likelihood/best unbiased linear prediction (REML/BLUP) procedure. The genetic parameters were estimated for: PH, NPP, PL, NGP, P100, and grain yield, which are variables with plant-level data, using model 18 of the SELEGEN-REML/BLUP software (Resende, 2016); and NIF, NDF, and NDM, with model 21 of the same software.

The several selections performed during generation advance made it impossible to estimate the additive and dominance variances and, therefore, narrow-sense heritability, as discussed by Vencovsky & Barriga (1992). Continuous self-fertilization resulted in an increased homozygosity and equal broad- and narrow-sense heritability values (Clo et al., 2019).

The parent-offspring regression method was used to estimate the heritability values (h^2_{PO}) between F_6 and F_3, offspring and parent, respectively. The estimates were obtained according to Smith & Kinman (1965): $h^2_{PO}=b/2r_{op}$, where b is the regression coefficient and $2r_{op}$ is the parent-offspring correlation coefficient (0.5

for F_3). The analyses were performed using the PROC REG procedure (SAS Institute Inc., Cary, NC, USA).

Narrow-sense heritability estimates were obtained by the standard deviation unit method (h^2_{UP}) of Frey & Horner (1957), which shows the correlation between the means of the families of generations F_6 and F_3, offspring and parent, respectively. Heritability was estimated using the PROC CORR procedure (SAS Institute Inc., Cary, NC, USA).

Results and Discussion

All variables showed statistical differences, except PL and NGP, for pooled generations (Table 1). The CVs ranged from 8.93% for PL to 32.32% for grain yield, indicating a good to reasonable experimental control for most variables (Zavinon et al., 2019).

The means of NIF, NDF, PH, NPP, and grain yield were lower in generation F_3, with no significant differences for PL and NGP (Figure 1). With the exception of P100, none of the means of the analyzed variables differed significantly between the F_4, F_5, and F_6 generations. With a high selection intensity, it is expected that the genetic gain of selection will be reduced after a few generations; therefore, as observed for the NIF and NDF variables, there is a greater chance that selection will be more effective when practiced in the initial generations for traits controlled by a greater number of genes, such as grain yield (Hallauer et al., 2010; Saxena et al., 2021b).

The present study highlights the high convergence of heritability in the broad-sense (h^2_b) estimated by ANOVA and REML-BLUP in generations F_3, F_4, F_5, and F_6 from the ICPL 90045 × UW10 pigeon pea cross, with similar values for 23 of the 36 estimates obtained by both methods (Figure 2). Among the various methodologies available to estimate the parameter, the one based on ANOVA and mixed models, such as REML-BLUP (You et al., 2016), helps the breeder to choose appropriate strategies to select superior genotypes.

The heritability values obtained for the studied variables differed among generations. For NIF, heritability decreased from generation F_3 to F_4, but showed an increasing trend in F_6, reaching a value close to 1.0. For NDF, heritability values increased from generation F_3 to F_4, decreasing in F_5 and F_6. For NDM, the estimated values of heritability oscillated, decreasing from F_3 to F_4 and increasing from F_4 to F_5, followed by another decrease from F_5 to F_6. The h^2_b estimates, except those obtained for NIF and NDM in F_4, are in agreement with those reported in the literature on the crop (Ajay et al., 2014; Vohra et al., 2015). In pigeon pea, NDF is considered a trait with a high heritability value and has been used in crop improvement programs for germplasm classification (Zavinon et al., 2019).

PH estimates increased from generation F_3 to F_4, with the highest values of 0.83 and 0.84 obtained by ANOVA and REML-BLUP, respectively, followed by a decrease in F_5, with the lowest h^2_b values for this variable, and then a slight increase in F_6. For NPP, there was an increase in the h^2_b values from generation F_4 to F_5, progressing since F_3, which showed a negative value considered equal to zero via the ANOVA and to 0.03 using REML-BLUP, reaching 0.57 in generation

Table 1. Mean squares of number of days to start flowering in the plot (NIF), number of days to 50% flowering in the plot (NDF), number of days to pod maturation (NDM), mature plant height (PH), number of pods per plant (NPP), pod length (PL), number of grains per pod (NGP), 100-seed weight (P100), and grain yield (Yield) for 30 families of the F_3, F_4, F_5 and F_6 generations from the ICPL 90045 × UW10 pigeon pea (*Cajanus cajan*) cross.

Source of variation	Mean squares								
	NIF	NFD	NDM	PH	NPP(1)	PL	NGP	P100	Yield(1)
Blocks	10.21	16.84	70.74	38,964.80	75.28	319.23	7.02	8.04	79.90
Generations	249.28**	159.31**	148.98*	46,359.34**	88.15*	1223.75^{ns}	3.49^{ns}	161.30*	69.44**
Between plots	-	-	-	1,887.65**	13.20^{ns}	262.37**	1.34**	16.59**	3.27^{ns}
Within plots	15.41	13.44	37.81	619.09	6.80	28.93	0.25	1.76	2.67
Mean	55.36	61.64	103.28	101.60	9.18	60.24	3.75	9.98	5.05
CV (%)	7.09	5.95	5.95	24.49	28.39	8.93	13.29	13.28	32.32

(1)Data transformed by square root of x. ** and *Significant by the F-test, at 1 and 5%, respectively. ^{ns}Nonsignificant.

F_5 and later decreasing in F_6. When evaluating the parents and progenies of the F_1, F_2, and F_3 generations of four pigeon pea crosses, Ajay et al. (2012) found high heritability values. According to these authors, the association of high h^2_b and genetic advance values is indicative of the possibility of a successful selection in later generations. In the present work, high heritability estimates in the broad sense were obtained for PH and NPP, highlighting the presence of the additive gene action.

Among the analyzed variables, only PL showed a continuous increase in h^2_b throughout the advance of all evaluated generations, with the lowest value in F_3 and peak of 0.83 in F_6; the greatest difference between the obtained estimates was due to the used model, i.e., the ANOVA and REML-BLUP, resulting in values of 0.24 and 0.05, respectively. In addition, NGP presented the smallest variation in h^2_b estimates between generations, with the highest value in F_4.

For P100, the highest value among all h^2_b estimates was observed in generation F_4, decreasing in F_5 and F_6, which showed the lowest value for this variable. For grain yield, the value for h^2_b was the lowest in generation F_3 and the highest in F_4, followed by successive decreases in F_5 and F_6. These values are higher than those found by Zavinon et al. (2019) for pigeon pea grain yield.

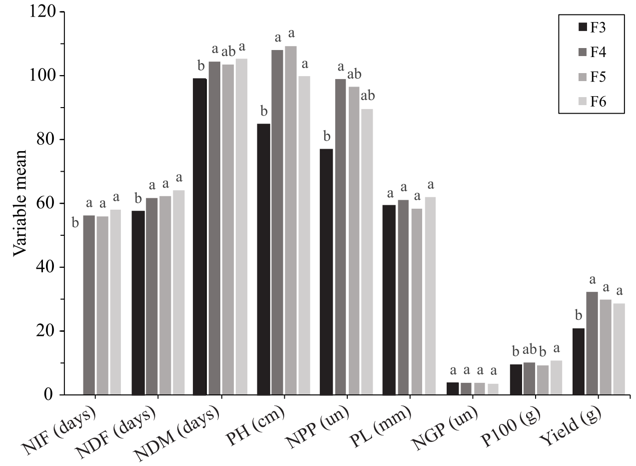

Figure 1. Heritability means obtained for the following variables evaluated in generations F_3, F_4, F_5, and F_6 from the ICPL 90045 × UW10 pigeon pea (Cajanus cajan) cross: number of days to start flowering in the plot (NIF), number of days to 50% flowering in the plot (NDF), number of days to 95% pod maturation (NDM), mature plant height (PH), number of pods per plant (NPP), pod length (PL), number of grains per pod (NGP), 100-seed weight (P100), and grain yield (Yield). Means followed by equal letters do not differ by the Bonferroni test, at 5% probability.

The CVge estimated by the ANOVA and REML were similar (Figure 3 A and B). CVge values higher than those of CVe were only found for: NDF in generations F_4, F_5, and F_6; PH in F_3, F_4, and F_6; and P100 in F_3, F_4, and F_5. A CVge/CVe ratio equal to or greater than 1.0 was obtained for NDM, grain yield, NIF, and PL in generations F_5, F_4, F_5, and F_6, respectively. For NPP and NGP, the ratio was <1.0 and >1.0, respectively. A CVge/CVe ratio greater than 1.0 favors selection for trait improvement in general, allowing the breeder to make inferences about genetic variability and expected genetic gain with selection (Lopes et al., 2017).

GG% was considered low for most variables (Obala et al., 2018), being <10% for all of them in generation F_3 (Figure 3 C) and also for NIF, NDF, NDM, and PL in all generations; high values of >20% were only obtained for grain yield in F_5. A moderate GG% of 10–20% was found for: NPP in generation F_5, grain yield in F_4, NGP in F_4 and F_6, P100 in F_4 and F_5, and PH in F_4 to F_6. According to Obala et al. (2018), the association of h^2_b with other parameters, such as CVge and GG%, results in a greater reliability for estimating the expected genetic gain in phenotypic selection. In the present study, grain yield showed a high genetic gain with selection and low heritability estimates, stressing the importance of parameter association in the breeding process.

The heritability values estimated by the standard deviation unit method (h^2_{UP}) were higher than those obtained by the parent-offspring regression (h^2_{PO}) for six of the nine variables evaluated in generations F_3 and F_6 (Table 2), as observed for NPP and PL. The values estimated by h^2_{UP} and h^2_{PO} for NDF and PH were similar via the ANOVA and REML. However, unlike for h^2_b, the proportion of h^2_{UP} and h^2_{PO} estimates higher than 0.70 was low. The greatest difference between the values estimated by the two used methods was found for NDM, whose h^2_{UP} was approximately nine times higher than that of h^2_{PO}. Among the studied variables, PH showed the highest value for h^2_{UP} and h^2_{PO}.

For NGP, the h^2_{UP} estimate was high, above 1.0 (Table 2). Grain yield also showed a h^2_{PO} higher than 1.0, with a h^2_{UP} estimate of 0.80. For Cavalli-Sforza

& Feldman (1976), heritability values higher than 1.0 occur when the intensity of selection is so high that selection variance becomes small and phenotypic variance becomes smaller than genetic variance. In this context, Frey & Horner (1957) proposed a modification in the procedure to estimate heritability by regression, according to which, regardless of the environmental effects, the estimated value will be close to 1.0, as found in the present study.

Similarly to NPP in generation F_3, two negative h^2_{PO} values were estimated for P100 using the ANOVA; REML was the only method that did not result in negative estimates (Tables 1 and 2). According to Maia et al. (2016), this is a characteristic of the REML methodology, which shows a non-negativity restriction for the estimates of the variance components. Moreover, PH and NPP presented h^2_b estimates higher than 80 and 90%, respectively. These results suggest a greater probability of success in early selection for traits with high h^2_b values, e.g., PH, NGP, P100, and NDF in all evaluated generations (Figure 2), estimated both by the ANOVA and REML/BLUP. This observation was confirmed by the high h^2_{UP} and h^2_{PO} estimates obtained for NDF, NGP, and PH (Table 2).

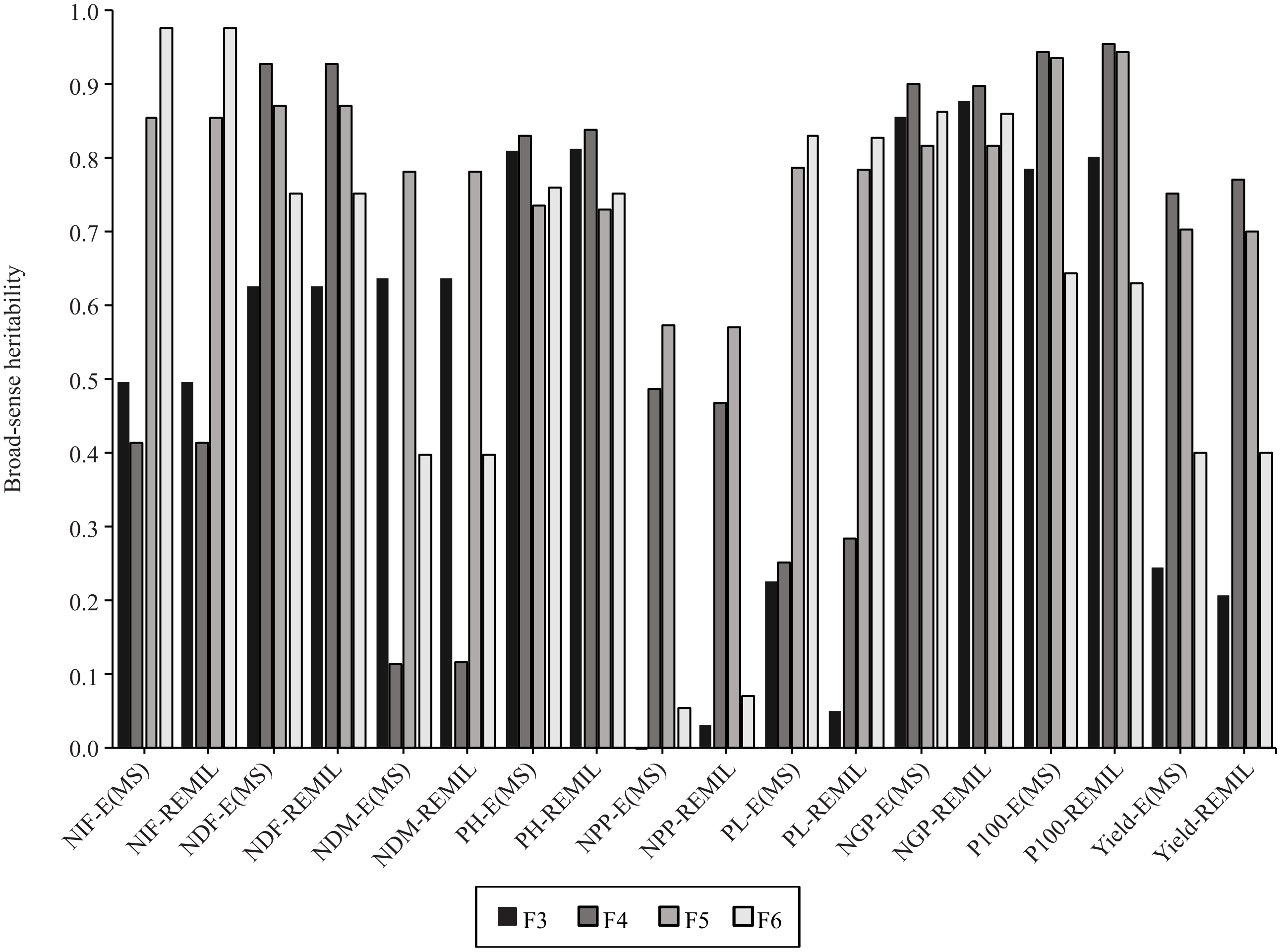

Figure 2. Estimates of broad-sense heritability based on the expected mean square analysis of variance [E(MS)] and restricted maximum likelihood (REML) for the following variables evaluated in generations F_3, F_4, F_5, and F_6 from the ICPL 90045 × UW10 pigeon pea (*Cajanus cajan*) cross: number of days to start flowering in the plot (NIF), number of days to 50% flowering in the plot (NDF), number of days to 95% pod maturation (NDM), mature plant height (PH), number of pods per plant (NPP), pod length (PL), number of grains per pod (NGP), 100-seed weight (P100), and grain yield (Yield).

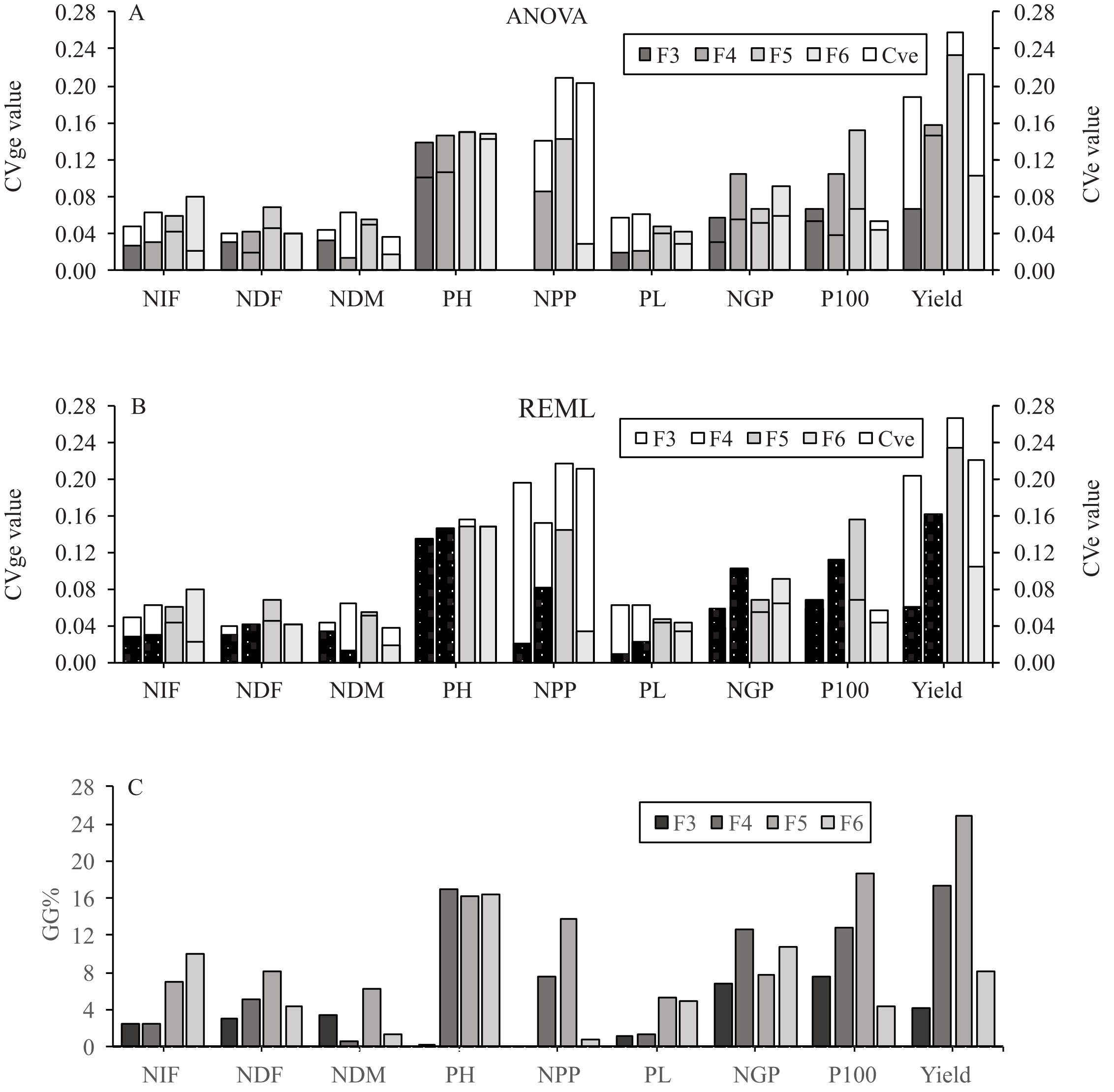

Figure 3. Estimates of the genetic coefficient of variation (CVge) and environmental coefficient of variation (CVe) for the following variables evaluated in generations F_3, F_4, F_5, and F_6 from the ICPL 90045 × UW10 pigeon pea (*Cajanus cajan*) cross: number of days to start flowering in the plot (NIF), number of days to 50% flowering in the plot (NDF), number of days to 95% pod maturation (NDM), mature plant height (PH), number of pods per plant (NPP), pod length (PL), number of grains per pod (NGP), 100-seed weight (P100), and grain yield (Yield), using: A, the analysis of variance (ANOVA); B, restricted maximum likelihood (REML); and C, genetic gain as a percentage of the mean (GG%).

Table 2. Heritability estimates obtained by the standard deviation unit method (h^2_{UP}) and parent-offspring regression (h^2_{PO}) using data from generations F_3 and F_6 from the ICPL 90045 × UW10 pigeon pea (*Cajanus cajan*) cross(1).

Heritability	NIF	NDF	NDM	PH	NPP(2)	PL	NGP	P100	Yield(2)
h^2_{UP}	0.11	0.93	0.92	0.97	0.43	0.49	0.92	-0.51	0.80
h^2_{PO}	0.05	0.75	0.10	0.85	0.25	0.31	1.44	-0.18	1.04

(1)NIF, number of days to start flowering in the plot; NDF, number of days to 50% flowering in the plot; NDM, number of days to pod maturation; PH, mature plant height; NPP, number of pods per plant; PL, pod length; NGP, number of grains per pod; P100, 100-seed weight; and Yield, grain yield per plant. (2)Data transformed by square root of x.

Conclusions

1. The broad-sense heritability estimates obtained by the analysis of variance (ANOVA) and restricted maximum likelihood (REML) methods for the evaluated families of different pigeon pea (*Cajanus cajan*) generations are similar in terms of magnitude.
2. The estimates obtained by the regression or parent-offspring correlation are precise for estimating heritability in pigeon pea.
3. The broad-sense heritability values estimated for the four studied pigeon pea generations are similar or close via the ANOVA and REML/best linear unbiased prediction, showing that both methods are appropriate for studies on this species.

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