Parental selection in diallel crosses of *Jatropha curcas* using mixed models

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ABSTRACT. Diallel crosses in an unbalanced scheme were carried out in Jatropha to (i) evaluate the additive and non-additive genetic components; (ii) select parents through the general combining ability; (iii) estimate the specific combining ability used in the crosses; and (iv) verify the existence of the maternal effect and inbreeding depression. The experiment was carried out in a complete diallel scheme with four progenitors, unbalanced for the number of crosses. The experimental design consisted of a randomized block, with 5 replications and 3 plants per plot. The following characteristics were evaluated: stem diameter (SD), number of branches (NB), plant height (PH), canopy projection on the row (CPR), canopy projection between rows (CPB), mass of hundred grains (MHG) and grain yield (GY). Estimates of variances were obtained using the method of restricted maximum likelihood, while breeding values were estimated by the best linear unbiased prediction. It was concluded that the additive effect was predominant in the genetic control for SD, CPR, and CPB; the dominance effect was predominant for PH, NB, and GY; there was a cytoplasmic effect and nuclear genes of the female parent for all evaluated traits; parents 107 and 190 are promising for reducing the size and increasing the grain yield; there was inbreeding depression for SD and GY; and the favorable crosses for increasing GY were 190x107 and 190x190.

Keywords: combining ability, REML, BLUP, plant breeding.

Introduction

Currently, with the high demand for energy and the intense pollution generated by petroleum derivatives, Jatropha (*Jatropha curcas* L.) has been a target for research worldwide in order to achieve large-scale oil production for biodiesel and biokerosene production (Duras, Laviola, & Alves, 2011). Its production potential ranges between 1,200 and 1,500 kg ha⁻¹ oil from the 4th year of cultivation (Laviola et al., 2014). However, though it is a promising species, the lack of varieties with high yield, wide adaptability, and phenotypic stability, which ensure such potential, still make this species unpromising for large-scale planting (Dias et al., 2007). Because it is a perennial oleaginous with a long cycle, one of the most important steps in the search for genotypes with greater agronomic and
industrial value is the appropriate selection of parents to be intercrossed in order to form the base population. Parental selection should be carried out based on two main parameters: variability and performance per se. Thus, genetic diversity in a parent group must be evaluated to identify the crosses with a higher heterosis effect so that in segregating generations, there is a greater possibility of the recovery of superior genotypes. Diallel cross is the leading strategy among the methods based on biometric models for the evaluation of parents’ diversity (Cruz, Regazzi, & Carneiro, 2014). Through these crosses, it is possible to know the genetic control of the characteristics, which helps in carrying out and selecting segregating populations (Ramalho, Santos, & Pinto, 2008).

Diallel cross also allows the breeder to discern information regarding the behavior of the parents between each other, known as general combining ability (GCA), which is attributed to the genes with additive effects, and their hybrid combinations, known as specific combining ability (SCA), which is attributed to non-additive effects (Cruz et al., 2014). In addition to these two parameters, other relevant information includes the nature of the reciprocal effect, which indicates that the genotype exhibits different behavior when used as the male parent or as the female parent in a hybrid combination. This effect is divided into the maternal effect, when genes come from the nucleus of the parent used as the mother, and the extrachromosomal effect, when genes are derived from the mitochondria and the chloroplasts (Ramalho et al., 2008).

There are several methods for diallel analysis, of which the designs I, II and III developed by Griffing (1956) stand out. However, when applied to a reduced number of crosses, composed of only a few parents, the estimators of the functions of the effects of combining ability become subject to great residual variation. On the other hand, crosses involving a large number of parents may be impractical due to high labor demands and a lack of sufficient financial resources. To overcome such problems, Resende (2002) suggested the use of mixed models for diallel analysis, especially when diallel crosses are genetically or statistically unbalanced. The mixed model technique has been widely used in plant breeding to evaluate diallel cross in Eucalyptus spp. (Rocha, Pires, Rocha, Xavier, & Cruz, 2007), beans (Baldissera et al., 2012), and papaya (Ramos et al., 2014; Vivas et al., 2014). However, so far, there are no reports on the employment of this methodology for parents’ selection in Jatropha.

Thus, in this study, diallel crosses in an unbalanced scheme were carried out in Jatropha to (i) evaluate the additive and non-additive genetic components, (ii) select parents through the general combining ability (GCA), (iii) estimate the specific combining ability (SCA) used in the crosses, and (iv) verify the existence of the maternal effect and inbreeding depression.

Material and methods

The experiment was carried out in the experimental area of Embrapa Cerrado in the city of Planaltina, Distrito Federal, Brazil (lat. 15°35’30”S, long. 47°42’30”W, at 1,007 m asl.), between 2010 and 2015. The climate of this area is tropical, with dry winters and rainy summers (Aw), according to the Köppen classification. The average annual temperature is 21°C, with a relative humidity of 68% and an average rainfall of 1,100 mm year⁻¹. Management practices were based on Dias et al. (2007), adapted to the results of research on Jatropha in Brazil and in the world (Bahadur, Sujatha, & Carels, 2013; Carels, Sujatha, & Bahadur, 2013; Resende, Londhe, & Neves, 2013).

Crosses were carried out in a complete diallel scheme, unbalanced for the number of crosses, totaling four selfings and nine hybridizations (Table 1). A randomized block design with five replications and three plants per plot, spaced 4 x 2 m between rows, was used. Four accessions selected from the germplasm bank were used, with the following characteristics: low height (CNPAE-107), high grain yield (CNPAE-190), absence of toxicity in the grains (CNPAE-170), and resistance to powdery mildew (CNPAE-259). After the completion of the crosses, the seeds were germinated in plastic tubes of 500 mL filled with commercial substrate. After two months, the seedlings were transplanted to a pit measuring 40 x 40 x 40 cm that was filled with soil, 5 L of bovine manure and 500 g of superphosphate. In the first year of cultivation, three topdressings with 80 g plant⁻¹ of fertilizer 20-00-20 were performed.

Table 1. Scheme of diallel crosses carried out in the experiment.

| Male/Female | 107 | 170 | 190 | 259 |
|-------------|-----|-----|-----|-----|
| 107         | 107x107 | --- | 107x190 | 107x259 |
| 170         | 170x107 | 170x170 | 170x190 | 170x259 |
| 190         | 190x107 | --- | 190x190 | 190x259 |
| 259         | 259x107 | --- | 259x190 | 259x259 |

Two measurements were carried out for stem diameter (SD, mm); three measurements for number of branches (NB) and mass of one hundred grains (MHG); and four measurements for plant height (PH, m), canopy projection on the row (CPR, m), canopy projection between rows (CPB, m), and grain yield (GY, g plant⁻¹). SD was measured in the first year; NB was evaluated in the first, second and third years; MHG was measured in the second, third and
fourth years; PH, CPR, and CPB were measured in the first, second and third years; and GY was evaluated in the second, third, fourth, and fifth years.

Estimates of variance components were obtained using the method of restricted maximum likelihood (REML), while breeding values were estimated by using the best linear unbiased prediction (BLUP). These procedures are associated with a linear mixed model, which contains, in addition to the general mean, the random effects of treatments and of plots and environmental fixed effect. Estimates of genetic values were obtained using the Selegen-REML/BLUP software, considering the following mixed model (Resende, 2007):

\[ y = Xr + Zm + Wf + Tc + Qs + Sp + e \]

in which: \( y \) is the data vector; \( r \) is the vector of the effects of the repeated measurement combinations (fixed), added to the general mean; \( m \) is the vector of the parent effects of the male population (random); \( f \) is the vector of the parent effects of the female population (random); \( c \) is the vector of the effects of the specific combining ability of the parents of the male population with the parents of the female population (random); \( s \) is the vector of individual permanent effects (random); \( p \) is the vector of plot effects (random); \( e \) is the vector of error or residue (random); \( X, Z, W, T, Q, \) and \( S \) represent the incidence matrices for these effects.

Variance components for each trait were estimated according to Resende (2007).

**Results and discussion**

The likelihood ratio test showed that the coefficient of determination of the effects of male parents (\( c_{a,m}^2 \)) was significant for the traits PH, CPB and CPR, while the coefficient of determination of the effects of females parents was significant for the traits SD, CPB, and CPR (Table 2). The estimates of genetic variance between males (\( \sigma_{gm}^2 \)) and females (\( \sigma_{gl}^2 \)) were used to obtain the additive genetic variance (\( \sigma_a^2 \)), while the estimates of the variance of dominance effects (\( \sigma_d^2 \)) were expressed from the variance of the interaction between female and male parents (\( \sigma_{dm}^2 \)). It was possible to verify that the estimates of \( \sigma_d^2f \) were higher in relation to \( \sigma_d^2 \) for SD, CPB, and CPR (Table 2). In the identification and selection of superior genotypes, \( \sigma_a^2 \) is characterized as one of the fundamental tools to quantify the breeding potential of the studied population, allowing the direct selection strategy to be used, aiming to increase the frequency of favorable alleles (Cruz et al., 2014). Similar results were observed by Santana, Carvalho, Blank, and Silva-Mann (2013), who found a higher prevalence of \( \sigma_a^2 \) in the SD expression in diallel crosses with Jatropha. These results suggest that the improvement of these characteristics can be accomplished by applying simple techniques of selection and that the strategy to be used is intra population recurrent selection, highlighting the additive genetic effects.

On the other hand, dominance effects were prevalent in the genetic control of PH, MHG, NB, and GY (Table 2), suggesting that there are differences in the genetic compositions of the parents used. Estimates observed for PH and GY were reflected in the coefficient of determination of the effects of specific combining ability (\( c_{a,m}^2 \)) obtained for these characteristics, which presented intermediate values according to the classification of Resende et al. (2013). Biabani, Rafii, Saleh, Shabanimofrad, and Latif (2012) and Santana et al. (2013) observed higher \( \sigma_a^2 \) for PH, compared to \( \sigma_a^2 \) in diallel crosses with Jatropha. These results suggest that to improve the population in terms of these characteristics, methods must be adopted that prioritize the capitalization of heterosis (genetic dominance and divergence), and the breeding strategy should be recurrent inter-population selection to improve the best hybrids.

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The coefficient of determination of permanent effects (\( c_{perm}^2 \)) presented a low magnitude (Table 2) and was significant only for SD, indicating that environmental variation from one year to another is important for this characteristic. Good experimental precision and accuracy in relation to the data analysis were evidenced by the low values of the coefficient of determination of the plot effects (\( c_{plot}^2 \)), which were practically zero and did not present as significant, indicating the absence of environmental heterogeneity to be corrected between plots within blocks. Similar results were observed by Laviola et
al. (2012), who found low estimates of $c_{perm}^2$ and $c_{perm}^{2}_{parc}$ evaluated for the same characteristics in 110 Jatropha genotypes for two years.

### Table 2. Estimates of components of variance (individual REMEL) for the characteristics of plant height (PH m), stem diameter (SD mm), number of one hundred grains (MHG, g), number of branches (NB), canopy projection between rows (CPB, m), canopy projection on the row (CPR, m), and grain yield (GY, kg ha$^{-1}$) evaluated in 13 Jatropha diallel crosses.

| Parameters | PH | SD | MHG | NB | CPB | CPR | GY |
|------------|----|----|-----|----|-----|-----|----|
| $c_{g}^2$  | 0.014 | 4.424 | 14.096 | 2.147 | 0.038 | 0.018 | 159.352 |
| $s_{g}^2$  | 0.099 | 22.097 | 0.043 | 0.010 | 0.103 | 0.065 | 9,412.826 |
| $s_{a}^2$  | 0.046 | 54.788 | 28.278 | 4.314 | 0.282 | 0.166 | 19,144.356 |
| $s_{g}^2$  | 0.043 | 4.611 | 10.835 | 2.705 | 0.025 | 0.014 | 22,596.119 |
| $s_{a}^2$  | 0.172 | 18.444 | 43.340 | 10.820 | 0.100 | 0.056 | 90,384.476 |
| $c_{g}^{2}_{parc}$ | 0.009 | 18.098 | 4.145 | 0.162 | 0.021 | 0.024 | 375.889 |
| $s_{g}^{2}_{parc}$ | 0.004 | 0.182 | 29.576 | 1.058 | 0.002 | 0.002 | 3,457.197 |
| $c_{g}^2_g$ | 0.027 | 3.980 | 554.430 | 17.965 | 0.049 | 0.039 | 85,288.984 |
| $s_{g}^2_g$ | 0.106 | 54.266 | 613.124 | 24.047 | 0.238 | 0.163 | 121,290.366 |
| $c_{a}^2$  | 0.130 | 0.082 | 0.023 | 0.089 | 0.162 | 0.163 | 0.001 |
| $c_{a}^2$  | 0.086 | 0.423 | 0.000 | 0.000 | 0.431 | 0.400 | 0.078 |
| $c_{a}^2$  | 0.406 | 0.585 | 0.101 | 0.113 | 0.107 | 0.085 | 0.368 |
| $c_{a}^2$  | 0.089 | 0.344 | 0.007 | 0.007 | 0.078 | 0.148 | 0.003 |
| $c_{g}^2_{dom}$ | 0.037 | 0.003 | 0.048 | 0.044 | 0.007 | 0.13 | 0.029 |
| $s_{g}^2_{dom}$ | 0.748 | 0.927 | 0.096 | 0.253 | 0.793 | 0.759 | 0.297 |
| $c_{g}^2_{gg}$ | 0.518 | 0.326 | 0.092 | 0.357 | 0.647 | 0.451 | 0.005 |
| $s_{g}^2_{gg}$ | 0.342 | 0.000 | 0.000 | 0.002 | 0.000 | 0.002 | 0.01 |
| $c_{g}^2_{parc}$ | 0.450 | 0.046 | 0.179 | 0.117 | 0.629 | 0.158 | 0.745 |
| $s_{g}^2_{parc}$ | 0.340 | 0.071 | 0.450 | 0.426 | 0.341 | 0.745 | 0.903 |

* and * Not significant and significant at 5% probability, respectively, according to the likelihood ratio test; $\sigma_{gm}^2$: Genetic variance between males; $\sigma_{gf}^2$: Genetic variance between females; $\sigma_{g}^2$: Additive genetic variance; $\sigma_{d}^2$: Variance of dominance effects; $\sigma_{perm}^2$: Variance of permanent effects; $\sigma_{g}^2_{parc}$: Variance between plots; $\sigma_{a}^2$: Residual variance; $\sigma_{g}^2_{dom}$: Individual phenotypic variance; $c_{g}^2$: Coefficient of determination of the effects of male parents; $c_{g}^2_{gg}$: Coefficient of determination of the effects of females parents; $c_{g}^2_{parc}$: Coefficient of determination of the effects of specific combining ability; $c_{g}^{2}_{perm}$: Coefficient of determination of permanent effects; $c_{g}^{2}_{dom}$: Coefficient of determination of the plot effect; $f_{gg}$: Individual repeatability; $h_{gg}^2$: Narrow-sense individual heritability of females; $h_{g}^2$: Narrow-sense individual heritability; $h_{g}^2_{dom}$: Individual heritability of dominance effects; $h_{g}^2_{dom}$: Broad-sense individual heritability; $f_{gg}$: It was not possible to estimate the value due to the small number of parents.

Individual repeatability ($f_{gg}$) allows for evaluating the time necessary so that the selection of the genetically superior individuals can be carried out with greater accuracy. The interpretation of the measurements over time is essential to characterize the productive performance of perennial crops, such as Jatropha, which are characterized by their long reproductive cycle and differential expression of the characteristics over time (Cruz et al., 2014). In this research, high $f_{gg}$ are reported (> 0.60), according to the classification of Resende (2002), for PH, SD, CPB, and CPR (Table 2), indicating that the progenies maintain relative superiority over the years (at least two measurements for SD). Results for these characteristics at similar magnitudes were also observed by Laviola et al. (2012), who evaluated 110 Jatropha genotypes for two years. However, low estimates (< 0.30) were obtained for MHG, NB and GY, which suggests the need for a large number of measurements to achieve a satisfactory determination value. Similarly, Laviola et al. (2013) found four measurement estimates for $f_{gg}$ of 0.37 for GY.

Narrow-sense individual heritability ($h_{gg}^2$) quantifies the relative contribution of additive genes in the expression of the characteristics (Cruz et al., 2014). $h_{gg}^2$ estimates can be considered intermediate for SD, NB, CPB and CPR; low for MHG; and high for GY, according to the classification proposed by Resende (2002). Values at magnitudes similar to those in this work were reported by Laviola, Rosado, Bhering, Kobayashi, and Resende (2010) for SD, NB, and GY, measured at 12 months in 110 Jatropha accessions. These authors observed $h_{gg}^2$ estimates for CPB and CPR lower than those obtained in this research. Spinelli, Dias, Rocha, and Resende (2015) also found lower $h_{gg}^2$ estimates for these characteristics in 16 Jatropha half-sib families in the second, third, and fourth years after planting.

In general, the values obtained, especially for GY, show the possibility of selecting highly productive individual plants since $\sigma_{g}^2$ is associated with the mean effect of gene substitution obtained by recombination of selected plants. This can be confirmed by the broad-sense individual heritability estimate ($h_{gb}^2$) for GY, which represents the upper limit that $h_{gg}^2$ can reach after repeated selfings.

Plant height (PH) is an important characteristic in choosing the most appropriate spatial arrangement for planting, as Jatropha can exceed 5 m in height (Dias et al., 2007). Thus, breeding efforts can be focused on selecting plants with lower height for easier harvesting. In this sense, the cross 190x190 stands out as promising to reduce PH, in addition to presenting the highest specific combining ability (SCA) for grain yield (GY) (Table 3).

These results are similar to those reported by Teodoro, Costa, Rocha, and Laviola (2016), who observed a negative effect of PH on GY. These authors found that the main characteristics that have direct effects on GY are the stem diameter (SD), the mass of one hundred grains (MHG), and the canopy projection between rows (CPB). Thus, another cross that may be promising is 170x190, which had high estimates of SCA for SD and MHG and an intermediate estimate for GY.
The effects related to SCA advocates the presence of non-additive interactions resulting from genetic complementation between the parents, allowing the improvement of genetic gain from the exploitation of heterosis (Ramalho et al., 2008). Although for SD, a high prevalence of $\sigma_{a^2}$ compared to $\sigma_{d^2}$ was observed, the combination between 190x259 provided the highest increase for this characteristic. This fact demonstrates that the effect of the non-additive gene should not be considered in the expression of the characteristic. However, with the exception of the combination 170x170, which had an SCA lower than most crosses, the other crosses derived from selfing showed intermediate estimates (107x107 and 259x259), and the cross 190x190 presented the highest estimate for SCA compared to GY (Table 3), suggesting the absence of inbreeding depression.

Table 4 contains the predicted genetic effects (individual BLUP) of general combining ability. When increased SD is preferred, the cross between genotype 190 (male parent) and 259 (female parent), due to the greater GCA of these parents, should be used in order to obtain the highest genotypic mean for this characteristic (Table 5). For MHG, the most promising combination, based both on the GCA effects (Table 4) and on the predicted genotypic values (Table 5), occurred between genotype 170 (male parent) and 259 (female parent). For GY, the best combination was between 190 (male parent with high grain yield) and 107 (female parent with low height), a fact confirmed by the highest genotypic mean obtained with this cross (Table 5).

Low magnitude differences for SCA were observed between the crosses 107x190, 107x259, and 190x259 and their reciprocals for PH, NB, CPB, and CPR (Table 3), indicating that the inheritance of these characteristics is controlled by nuclear genes (Ramalho et al., 2008). However, for SD, MHG, and GY, a pronounced difference of considerable magnitude in the crosses 107x190, 107x259, and 190x259 and their reciprocals was observed, suggesting that these characteristics are influenced by the cytoplasmic effect and by nuclear genes of maternal genotype. Thus, it is important to identify which genotype is more promising when used as the female parent (pollen receptor) or male parent (pollen donor) for these characteristics.

Table 5. Mean genetic values (individual BLUP) of 13 Jatropha diallel crosses for the characteristics of plant height (PH m), stem diameter (SD mm), mass of one hundred grains (MHG, g), number of branches (NB), canopy projection between rows (CPB, m), and grain yield (GY, kg ha⁻¹).
Based on the estimates of overall combining ability, parents 107 and 190 are promising for reducing the size and increasing the grain yield.

There was no inbreeding depression for stem diameter, mass of one hundred grains and grain yield, and the most favorable crosses for increasing grain yield were 190x107 and 190x190.

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