



Hayman's diallel analysis of traits related to fruit and seed production in *Citrullus mucosospermus*

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ABSTRACT

Objectives: Information on the type of gene action governing the expression of traits related to fruit and seed production of *Citrullus mucosospermus* (Fursa) are a prerequisite for starting an effective breeding program in Côte d'Ivoire and developing productive varieties.

Methodology and Results: For such purpose, a 4 x 4 full diallel cross was made among four *C. mucosospermus* parents in order to produce 12 hybrids, which, along with their parents, were phenotypically assessed in triplicate in a randomized complete block design. Analysis of variance showed that *C. mucosospermus* genotypes differed significantly for all traits: number of fruits per plant (NFr), mass of fruit (MFr), fruit diameter (DFr), fruit volume (VFr), mass of 100 seeds (M100), seed length (SL) and seed width (SW). The genetic component of variation revealed that non-additive gene effects were more pronounced in the inheritance of MFr, DFr and VFr, while additive gene effects were predominant in SL inheritance. No symmetry in the distribution of favourable and unfavourable alleles for the increase of all investigated traits was observed. The traits under study exhibited high broad and narrow sense heritability. The graphical analysis showed the over-dominance type of gene action in the control of MFr, DFr and VFr, while SL was under the genetic control of partial dominance.

Conclusions and application of findings: The high heritability of the studied traits and the type of gene actions involved in the expression of these traits allow us to deduce the improvement strategy of *C. mucosospermus* crops. Thus, the involvement of over-dominance type of gene action in the control of MFr, DFr and VFr suggests the exploitation of heterosis in specific parental cross combinations for improving these traits. The isolation of superior genotypes by sib selection is good strategy for improving the character SL.

Key words: *Citrullus mucosospermus*, Diallel analysis, Plant breeding, Gene effect, Heritability.

INTRODUCTION

Citrullus mucosospermus (Fursa) is a species belonging to the *Citrullus* genus of *Cucurbitaceae* family and is native to sub-Saharan western Africa, where it was domesticated (Luan *et al.*, 2019). It cultivated for its oleaginous seeds, which are rich in carbohydrates, proteins and lipids (N'Goran *et al.*, 2015; Guédé *et al.*, 2017). Furthermore, oil extracted from *C. mucosospermus* seeds is used in cosmetology and pharmaceutical industries (Manika *et al.*, 2015). In Côte d'Ivoire, however, despite its nutritional and economic importance, yields of traditional cultivars were low (Goré *et al.*, 2011), with a seed yield which may vary from 208 to 370 kg per ha depending on the cultivar (Adjoumani *et al.*, 2012). Thus, it is very necessary to breed high yield cultivars of *C. mucosospermus* in terms of nutritional and economic importance. However, there is still little information about the inheritance of the main quantitative traits of this crop. Knowledge of the genetic control of a trait is of paramount importance in choosing an efficient breeding program. In fact, it permits the determination of the best procedure to be used as well as the most efficient breeding method to conduct on the segregating populations (Cardoso *et al.*, 2015). To achieve knowledge of the genetic control of a trait, several mating schemes are available, including diallel crosses. According to Gami *et*

al. (2020), diallel cross analysis is the fastest method to understand the genetic nature of quantitatively inherited traits and ascertain the prepotency of parents. Several methods have been proposed for analyzing data from diallel crosses (Hayman, 1954a, b; Griffing, 1956; Gardner & Eberhart, 1966). Cardoso *et al.* (2015) suggests that Hayman's diallel analysis provides information on genetic values of parents and the limits of selection of traits under study. Several diallel analysis studies using Griffing's (1956) methodology were done in *C. mucosospermus* (Brou *et al.*, 2018; 2019a; 2020), but it has not been with Hayman's methodology, which is efficient in detecting gene actions such as additive, dominance and epistatic gene effects. However, the use of this method requires some restrictions, namely: absence of epistasis, absence of maternal effect, absence of multiple allelism, genes distributed independent among the parents, diploid segregation and homozygous parents. The satisfaction of these restrictions can be rarely achieved in practice. Most of them, however, can be checked during statistical analyses, when the results are consistent with the additive-dominant model (Barro *et al.*, 2017). The aim of this study was to assess the genetic control of some traits related to fruit and seeds production in *C. mucosospermus* using Hayman's method.

MATERIALS AND METHODS

Plant material: Plant material comprised four inbred lines of *C. mucosospermus* from Côte d'Ivoire and 12 F1 descents from 4×4 full diallel crosses of these inbred lines. The four inbred lines were composed: *Bebu* (P1), *Wlêwlê small seeds 1* (P2), *Wlêwlê small seeds 2* (P3) and *Wlêwlê small seeds 3* (P4). The inbred lines were obtained from purification following four generations of self-pollination of four accessions of *C. mucosospermus*. The choice of these inbred lines was based on a wide range of phenotypes in fruit and seed

characteristics that prominently distinguish one line from another (Brou *et al.*, 2019b).

Site description: The experiment was carried out at Kononfla in the west-center of Côte d'Ivoire, precisely between latitude 6° 37' 18" N - longitudes 5° 54' 37" W and at an altitude 243 m above sea level. Kononfla has a bimodal rainfall distribution, with a long rainy season from March to June and a short rainy season from September to November. The rainy seasons at the target site are separated by a short dry period (July – August) and a long dry

season (December–February). Annual rainfall varies from 1500 to 2000 mm and the annual mean temperature is 23°C.

Experimental design: The experimental field size was 2 067 m² (53 m × 39 m). The experimental design was a randomized complete block design with three repetitions. Each block consisted of 16 subplots, each with an area of 32 m² (8 m × 4 m). Subplots were separated by a 1 m buffer zone. Each parental line or each F1 descent was sowed on 3 rows with a spacing of 2 m × 2 m within a subplot. Two weeks after sowing, the most vigorous seedling has been retained per seedling point. Weed control was regularly performed, manually with a hoe, during the vegetative growth stage.

Data collection: Fruits were harvested after 4 months. Data were collected on 10 plants randomly selected per subplot, giving a total of 30 plants per genotype. Measurements were carried out on seven quantitative characters: number of fruits per plant (NFr), mass of fruit (MFr), fruit diameter (DFr), fruit volume (VFr), mass of 100 seeds (M100), seed length (SL) and seed width (SW). The traits related to fruits and seeds were evaluated on three mature fruits randomly selected from each of the 30 plants by parental or F1 genotypes, except the number of fruits where all the fruits of one plant were counted.

Data analysis: All data were subjected to analysis of variance. Following this,

RESULTS

Analysis of variance: Analysis of variance showed significant variation among 16 genotypes (parents and hybrids) for all investigated traits. The experimental

restrictions on the use of Hayman's method (1954 b) were evaluated by sufficiency tests of the additive-dominant model, based on heterogeneity of $W_r - V_r$ and the regression coefficient of W_r on V_r (Nishimura & Hamamura, 1993). Only character fits the additive-dominant model in other words, presenting no significance in the three tests was used for diallel analysis according to Hayman's method (1954 b). The software GENES (Cruz, 2013) was used for all analysis. The graphical analysis was done according to Hayman (1954b) as described by Shukla *et al.* (2019). When the regression line passes through the origin, it indicates complete dominance ($D = H1$). When it passes above the origin, cutting the W_r -axis, it suggests the existence of partial dominance ($D > H1$). When it passes above the origin, cutting the W_r -axis and touching the limiting parabola, it suggests the absence of dominance. However, when it passes below the origin, cutting the V_r -axis, it denotes the presence of over dominance. The position of parental points on the regression line indicates the dominance order of the parents. The parents with more dominant genes are located near to the origin, while those with more recessive genes are far from the origin. The parents with equal frequencies of dominant and recessive genes occupy an intermediate position.

coefficient of variation comprised between 3.11 and 12.86 %, indicating an experimental accuracy and validating the conclusion to be inferred (Table 1).

Table 1. Analysis of variances of traits under study of *Citrullus mucosospermus* parents and hybrids derived from 4×4 diallel cross

Source of variation	df	Mean squares						
		NFr	MFr	DFr	VFr	M100	SL	SW
Blocks	2	0.997	1048.069	0.0175	856.345	0.103	0.023	0.099
Genotypes	15	5.492**	101393.635**	2.243**	102833.519**	29.764**	8.883**	6.772**
Error	30	0.381	5325.944	0.128	5191.290	0.148	0.078	0.072
CV (%)		11.172	9.039	3.110	8.774	5.189	2.367	4.504

** Significant at $p < 0.001$

NFr = Number of fruits; **MFr** = mass of fruit; **DFr** = diameter of fruit; **VFr** = volume of fruit; **M100** = mass of 100 seeds; **SL** = seed length; **SW** = seed width.

Test of assumption for the additive-dominance model: Table 2 shows the results of the sufficiency tests of the additive-dominance model. For characters **MFr**, **DFr**, **VFr** and **SL**, the heterogeneity of $W_r - V_r$ was

not significant. For the same characters, the regression coefficients of W_r on V_r were not different from 0 and from 1. For the other characters, there was a significance in at least one of the tests.

Table 2: Scaling test for adequacy of additive-dominance model for traits under study in *C. mucosospermus*.

Traits	ANOVA ($W_r - V_r$)	Regression $W_r = \frac{1}{4}(D - H_1) + bV_r$		
		$b \pm Se$	$t(H:b=1)$	$t(H:b'=0)$
NFr	0.050ns	0.785 ± 0.084	-2.567 *	2.205 *
MFr	100049073.474ns	0.905 ± 0.245	-0.386ns	0.122ns
DFr	0.016ns	0.966 ± 0.182	-0.187ns	0.002ns
VFr	42831561.025ns	0.952 ± 0.195	-0.246ns	0.044ns
P100	0.139ns	1.059 ± 0.032	2.209*	-2.301*
SL	0.009ns	0.995 ± 0.063	-0.084 ns	0.020 ns
SW	0.175*	1.256 ± 0.134	1.896 ns	-2.273*

* Significant at $p < 0.05$

NFr = Number of fruits; **MFr** = mass of fruit; **DFr** = diameter of fruit; **VFr** = volume of fruit; **M100** = mass of 100 seeds; **SL** = seed length; **SW** = seed width; V_r = the variance of the rth array; W_r = the covariance between the parents and the offspring on the rth array.

Estimates of genetic variation components: Table 3 showed the estimates of genetic components such as component of variation due to additive effects (**D**), component of variation due to dominance effects (**H1**), proportion of dominance due to positive and negative effect of genes (**H2**) and F1 deviation from the average parent (h^2) with their standard deviations. For characters **MFr**, **DFr** and **VFr**, the magnitudes of components **H1** and **H2** were higher than those of component **D**, indicating the predominance of non-additive gene effects in the control of these characters. The additive gene effects (**D**) was

higher than the dominant gene effects for **SL**, suggesting additive gene effects act in the control of this trait. The estimates of mean degree of dominance, $(H1/D)^{1/2}$, were greater than 1 for all characters, except **SL** which showed a $(H1/D)^{1/2}$ value lower than 1. The results of this genetic parameter allow us to infer the presence of over-dominance in the control of **MFr**, **DFr** and **VFr**, and partial dominance in **SL**. The values of the parameter $H2/4H1$ vary from 0.198 to 0.206 and were found to be less than the expected value 0.25 for all studied traits, implying inequality between the number of dominant and recessive

alleles (H2/4H1) in the parents. For the traits related to fruit (MFr, DFr and VFr), the value of ratio K_D/K_R was lower than 1, indicating that the parents contained a high recessive gene prevalence. However, the estimate of K_D/K_R of SL was higher than 1, suggesting an excess of dominant genes in parent genotypes. Estimates of $h^2/H2$ allowed us to infer that there was at least one group of dominant genes in determination of all traits under study. All investigated characters showed high broad and narrow sense heritability. The estimates of broad sense heritability ranged from 0.719 to 0.978 and those of narrow sense heritability comprised between 0.954 and 0.992. The correlation between the average value of the parents (Y_r) and average frequency of

dominant and recessive genes ($W_r + V_r$) explains the proportion of genes showing the positive and negative effects, and can allow estimation of the direction of dominance. A negative correlation means that most dominant alleles work to increase the mean value of the trait and a positive correlation shows that most recessive alleles work to increase the mean value of the trait. Thus, for the mass, diameter and volume of fruits, the high negative correlations observed show that most dominant alleles work to increase the mean value of these characters. Recessive alleles work to increase mean value of seed length since it recorded a positive value of the correlation (Table 3).

Table 3. Estimations of genetic and non-genetic parameters of traits under study of *Citrullus mucosospermus* parents and hybrids derived from 4× 4 diallel cross

Variance components	Parameter values			
	MFr	DFr	VFr	SL
D	21714.949±4882.504	0.634±0.077	28456.387±3819.448	7.937±0.045
F	-28480.007±12543.380	-0.678±0.173	-31304.876±9812.339	0.744±0.109
H1	51325.805±14192.895	0.810±0.221	38516.763±11102.708	0.226±0.122
H2	40585.546±13101.133	0.667±0.205	31688.894±10248.654	0.219±0.114
h ²	38645.184±8886.292	0.740±0.138	34005.532±6951.500	-0.014±0.256
E	1775.315±690.492	0.043±0.032	1730.430±1708.109	0.026±0.055
D – H1	-29610.856±12778.736	-0.175± 0.02	-10060.376±9996.451	7.671±0.109
(H1/D) ^{1/2}	1.537	1.130	1.163	0.183
(H2/4H1)	0.198	0.206	0.206	0.206
K_D/K_R	0.402	0.358	0.358	1.688
h ² /H2	0.952	1.110	1.073	-0.066
h_R^2	0.719	0.776	0.775	0.978
h_A^2	0.958	0.954	0.960	0.992
r($Y_r, W_r + V_r$)	-0.904	-0.913	-0.896	0.287

NFr = Number of fruits; **MFr** = mass of fruit; **DFr** = diameter of fruit; **VFr** = volume of fruit; **M100** = mass of 100 seeds; **SL** = seed length; **SW** = seed width; **D** = component of variation due to additive effects ; **H1** = component of variation due to dominance effects ; **H2** = proportion of dominance due to positive and negative effect of genes; **h²** = F1 deviation from the average parent; **E** = environment effect ; **(H1/D)^{1/2}** = mean degree of dominance over all loci; **H2/4H1** = average frequency of negative versus positive alleles showing dominance in the parents; **Kd/Kr** = the ratio of the total number of dominant to recessive alleles in the parents; **h2/H2** = number of effective factors which exhibited dominance; **h_A²** = Heritability in narrow-sense; **h_R²** = Heritability in broad sense.

Graphical analysis: For three traits related to fruit (MFr, DFr and VFr), the regression line passes below the axis origin, intercepting the W_r -axis in the negative region, indicating the

presence of over-dominance in these traits. In the character SL, the regression line cuts W_r -axis above the origin, in the positive region, suggesting partial dominance. These results

confirm those obtained by the average degree of dominance $(H1/D)^{1/2}$. The dispersion of parents around the regression line showed that P4 (*Wlêwlê small seeds 3*) is located further from the origin for the traits MFr, DFr, VFr and SL, indicating this parent contains the largest concentration of recessive alleles. P1 (*Bebu*) is

near to the origins for MFr, DFr and VFr, and P2 (*Wlêwlê small seeds 1*) for SL, suggesting these parents have mostly dominant alleles for these characters respectively. P3 (*Wlêwlê small seeds 2*) was intermediary, indicating that recessive and dominant genes are equally distributed in this parent (Figure 1).

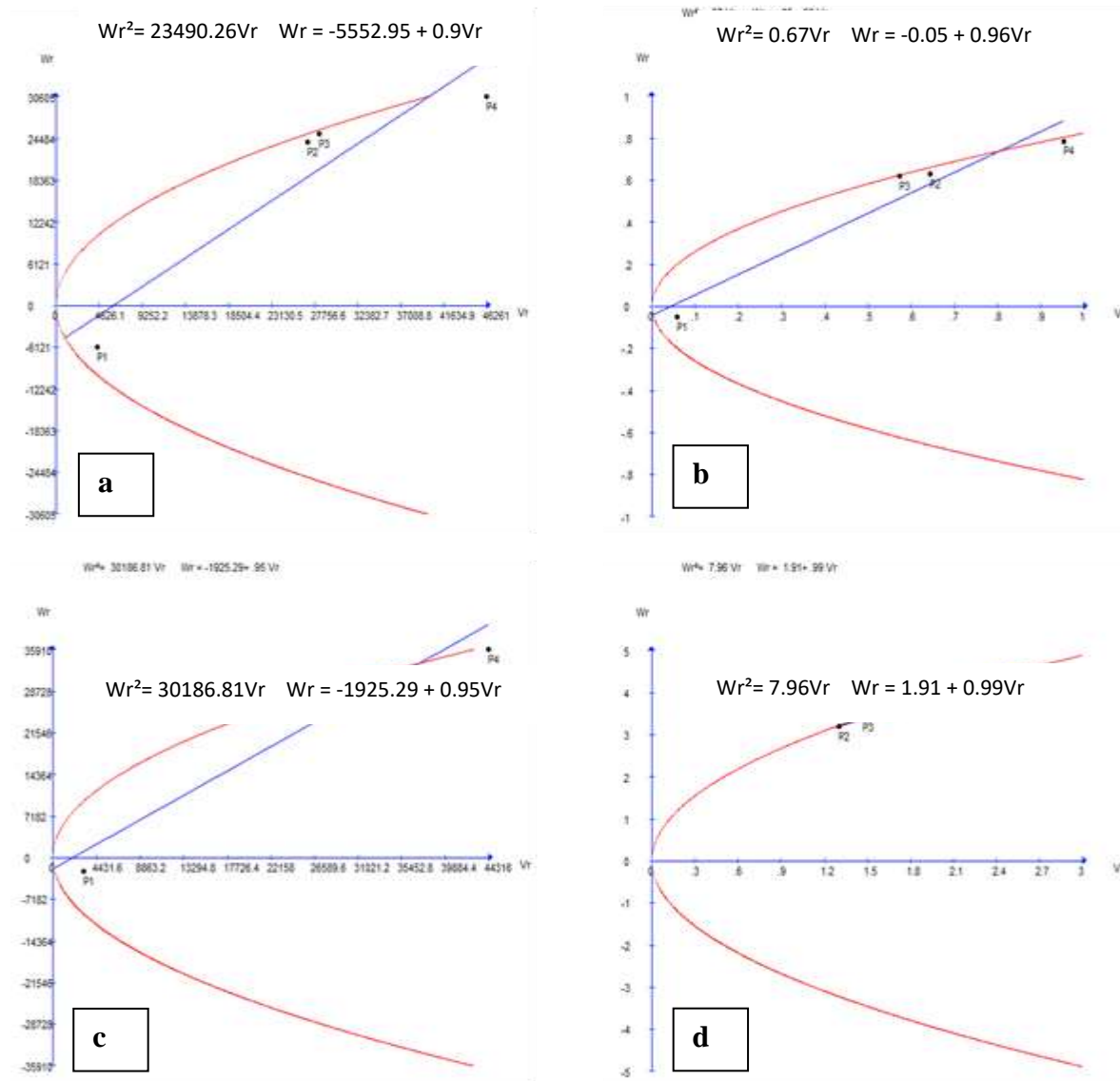


Figure 1. Vr - Wr graph for all investigated traits in a 4× 4 diallel cross of *C. mucosospermus* **a** = Mass of fruit; **b** = diameter of fruit; **c** = volume of fruit; **d** = seed length; **P1** = *Bebu*; **P2** = *Wlêwlê small seeds 1*; **P3** = *Wlêwlê small seeds 2*; **P4** = *Wlêwlê small seeds 3*. The red line is the parabola with equation $Wr^2 = aVr$ and blue line in the graph is a regression line of Wr on Vr .

DISCUSSION

The results showed the presence of genetic variation among the investigated genotypes, indicating genetic effects on the investigated traits and thus, the possibility of selection for favourable phenotypes. Indeed, the existence of genetic variability is fundamental for the development of any plant breeding program. Also, the selection efficiency and heterosis expression are largely dependent upon the degree of genetic variability present in the plant population (Farshadfar *et al.*, 2014). Otherwise, these results indicate that genetic parameter estimates can be performed on all the observed characters. Testing the suitability of the additive-dominance model is the first step in Hayman's Diallel analysis. The validity of hypothesis of additive-dominance model allows inference of the absence of non-allelic interactions (Nishimura & Hamamura, 1993). In our experimental study, three sufficiency tests of the additive-dominance model were not significant for the characters MFr, DFr, VFr and SL, indicating the absences of epistasis. These characters were in agreement with the additive-dominant model. In other words, these characters are in accordance with the restrictions of Hayman's method and thus allows further analysis. For the other characters, three sufficiency tests of the additive-dominance model revealed the presence of non-allelic interactions. These characters, therefore do not satisfy this method's conditions and consequently must be excluded from subsequent analysis. Knowledge about nature of gene action is essential in increasing the efficiency of selection (Kumar *et al.*, 2017). Non-additive gene effects were observed in the inheritance of MFr, DFr and VFr. Farshadfar *et al.* (2014) recommend hybrid production and heterosis breeding for the improvement of the traits controlled by non-additive gene effects. The

predominance of additive gene effects in the expression of SL suggests that simple selection in early generations would be adequate for the improvement of seed length, as was reported by Kumar *et al.* (2017). The estimates of the average degree of dominance indicated the presence of over-dominance in MFr, DFr and VFr. Adjoumani *et al.* (2016) also reported over-dominance in the same characters. The expression of over-dominance results in hybrids that are more vigorous than their parent or, in other words, the presence of heterosis. Angui *et al.* (2020) showed heterosis effects on fruit weight in *C. mucosospermus*. The heterosis effect in hybrids for a given trait indicates their potential for producing superior cultivars through the selection of transgressive segregants in segregating populations (Wannows *et al.*, 2015). The concept of heritability provides a unitive statement of the relative importance of heredity and environment in determining trait expression. This helps in planning an efficient breeding programme. In this study, all investigated traits recorded high broad and narrow sense heritability, confirming that the inheritance of all traits has a major genetic component. The high broad sense heritability values indicated that sustainable improvement can be achieved using standard selection procedures. The high narrow sense heritabilities are the consequence of additive variance, much higher than those of the environment. The high heritability of the investigated traits indicates that they are controlled by genes with additive, fixable effects (Heydari *et al.*, 2012; Kamer *et al.*, 2015) and / or could result from large genetic differences between parents, as reported by Ogbonna & Obi (2010). Furthermore, highly heritable traits can be stabilized through early selection in segregating populations (Adeniji *et al.*, 2007; Heydari *et al.*, 2012).

CONCLUSION AND APPLICATION OF RESULTS

In this study we can retain that the predominance of non-additive gene effects in the inheritance of MFr, DFr and VFr, while additive gene effects were predominant in SL inheritance. No symmetry in the distribution of favourable and unfavourable alleles for the increase of all investigated traits was observed. High broad and narrow sense heritability were observed for all studied traits. The over dominance type of gene action in the control of MFr, DFr and VFr and partial dominance in SL

permit us to infer that isolation of superior genotypes by sib selection and exploitation of heterosis in specific parental cross combinations are good strategies for improving *C. mucosospermus* crops. Concretely, for the improvement of characters MFr, DFr and VFr, the exploitation of heterosis would be the best method and for the improvement of character SL, isolation of superior genotypes by sib selection would be the best.

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