African Crop Science Journal, Vol. 26, No. 2, pp. 245 - 258
ISSN 1021-9730/2018 $4.00

DOI: http://dx.doi.org/10.4314/acsj.v26i2.7

HERITABILITY AND NUMBER OF GENES CONTROLLING SEED YIELD IN BOTTLE GOURD

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(*Received 18 August, 2017; accepted 10 May, 2018*)

ABSTRACT

Bottle gourd [*Lagenaria siceraria* (Molina) Standley] is an important tropical specie characterised by a wide diversity and a low yield, mainly due to no selection for improved varieties. Selection for a particular trait depends on the relative importance of genetic and nongenetic factors influencing the expression of phenotypic differences among crop population. The objective of this study was to examine the genetics basis of seed yield and yield components, by crossing oleaginous type and calabash-type of bottle gourd [*Lagenaria siceraria* (Molina) Standley]. The parental lines (P1 and P2), with the respective hybrids F1 and F2 generations, were grown in two contrasted locations in terms of pedoclimatic conditions. Results showed no significant difference between the two locations for studies traits (P=0.06). For seed yield per plant, 100-seed weight per fruit, and number of seeds per fruit, a positive hypothetical heterosis was observed when calabash type was a maternal parent. Negative real heterosis was observed in all studied traits. For all traits, the genetic variance was higher than the environmental variance in the most of the crosses, implying greatest genes action in the expression of studies traits. Heritability was medium for fruit weight (mean, 42.12%) and seed number per fruit (mean, 47.36%). But for 100-seed weight (mean, 61.00%) and seed yield per plant (mean, 53.28%) high heritability were observed. The minimum number of genes that controlled the expression of 100-seed weight (0.58), seed yield per plant (1.58) and number of seeds per plant (0.98) was low (close to 1). These observations suggest that distinct genotypes for interest characters would be fixed by using a small number of selfing generations (F3 to F4) in West African bottle gourd.

Key Words: Heritability, heterosis; *Lagenaria siceraria,* number of genes, seed yield

RESUME

La gourde oléagineuse est une espèce tropicale caractérisée par une grande diversité agromorphologique et un faible rendement qui s'explique par l'absence de sélection pour les variétés améliorées. La sélection d'un caractère d'intérêt dépend de l'importance relative des facteurs génétiques et non génétiques qui influencent l'expression des différences phénotypiques observées dans la population étudié. L'objectif de cette étude est d'examiner les bases génétiques et le nombre de gènes contrôlant le rendement en graines et ses composantes en croisant quatre accessions de *Lagenaria siceraria* (Molina) Standley : deux du type calebasse (NI-CM001 et NI-CSM001) et deux du type oléagineux (NI-232 et NI-135). Pour se fait, les lignées parentales (P1 et P2) et les générations hybrides (F1 et F2) ont été cultivés sur deux sites contrastés (nord et sud de la Côte d'Ivoire). Les résultats de l'analyse multivarié de la variance (MANOVA) n'ont montré aucune différence significative entre les deux sites pour l'ensemble des caractères étudiés (F = 2,29; P = 0,06). L'hétérosis théorique (parent moyen) était positive lorsque le type de calebasse servait de parent maternel pour le poids de 100 graines par fruit, le rendement des graines par plante et le nombre de graines par fruit, alors que l'hétérosis réelle (meilleur parent) était négative pour ces caractères. L'héritabilité était moyenne pour le poids des fruits (42,12%) et le nombre de graines par fruit (47,36%). Cependant, une forte héritabilité a été observée pour le poids de 100 graines (61,00%) et le rendement en graines par plante (53,28%). Un faible nombre gènes a été observé dans l'expression de la masse de 100 graines (0,58), le rendement en graines par plante (1,58) et le nombre de graines par plante (0,98). Ces résultats suggèrent que dans les programmes futurs d'amélioration de *L. siceraria*, la sélection des génotypes les plus performants pour les composantes du rendement pourrait se faire dès les générations d'autofécondation F3 ou F4.

Mots Clés: Hétérosis; héritabilité, *Lagenaria siceraria*, nombre de gènes, rendement en graines

INTRODUCTION

Cucurbitaceae family is one of the economically most significant families, supplying edible, nutritious fruits and seeds to humanity (Bisognin, 2002). This family contains several other species, including *Lagenaria siceraria* that have the highest capacity of seed production among Cucurbitaceae (Achigan-Dako *et al.*, 2006). This specie is well adapted to various cropping systems, characterised by minimal inputs (Taffouo *et al.*, 2008). It has been reported that *L. siceraria* is the most abundant of cucurbits on the West African market, and consists of two main groups according to fruit size and seed thickness: Oleaginous type and calabash type (Zoro Bi *et al.*, 2006).

Oleaginous type is mainly cultivated for seed consumption. Cultivation of this type permits achievement of food security for the family unit and represents a potential source of additional income for the rural women, who are the main producers in West Africa (Zoro Bi *et al.*, 2003). Loukou (2007) showed that seeds contain 45% of oil and 35% of protein. Thus, oil extracted from the seed was used as an alternative to vegetable oil (Loukou *et al.*, 2012); while the defatted cake and the by-products (dried leaves, fermented and non-fermented fruit, seeds shells) also contain appreciable amounts of nutrients and can be used as valuable animal feedstuffs (Achu *et al.,* 2005, Touré *et al.,* 2015). Oleaginous type was characterised by small fruits, containing seeds with fragile coat. Seed yield per plant varied from 12 to 56 g plant^{-1} (Yao *et al.*, 2015). The weight of 1000 seeds ranged between 150 and 200 g (Achigan-Dako *et al.*, 2006).

In sub-African area, the productivity of *L. siceraria* remains very low, mainly due to the absence new improved varieties with high level of seed yield. Recently, Yao *et al.* (2015) were revealed that seed yield components like fruit weight, number of seeds per fruit, and 100-seed weight had positive and relatively strong, direct effects on the enhancement of seed yield per plant of *L. siceraria*. Kushawaha and Ram (1997) and Pandey *et al.* (2004) earlier observed an asymmetrical distribution of dominant genes, with positive or negative effects for number of seeds per fruit and 100-seed weight in bottle gourd. Dubey and Ram (2007) showed that the number of seed per fruit was conditioned by both additive and dominance gene action.

Fehr (1987) indicated that the effectiveness of selection for a trait depends on the relative importance of genetic and nongenetic factors in the expression of phenotypic differences among genotypes in a population. Hence, knowing the nature and the number of alleles involved in the expression of interest traits would provide a genetic basis for ongoing breeding efforts.

In bottle gourd, the genetic basis of various phenotypes observed is not well known. Consequently, the wide range of genetic variability and the great potentiality of *L. siceraria* are lowly exploited, despite its socio-economic importance (Zoro Bi *et al.,* 2006). Precise information on the inheritance of seed yield and its components traits and the production of new traits combinations should provide broader genetic variations and success in bottle gourd breeding. In other words, the exploitation of the wide genetic variability from both calabash type and oleaginous type in breeding works could help to generate plants with high seed production. Indeed, the use of contrasted lines in breeding programmes could contribute to create high yield varieties (Aquaah, 2007). On the other hand, plant selection for high yield can be effective only if the variables under selection have high heritability values (Akbar *et al.*, 2008).

Heritability of a character describes the extent to which it is transmitted from one generation to the next one. Thus, knowledge of the heritability of a trait guides a plant breeder to predict behavior of succeeding generations, and helps to predict the response to selection. High heritability estimates offer a most suitable condition for selection (Akbar *et al.*, 2008).

Heterosis refers to the increased yield and overall performance (vigour, growth rate, reproductive success, etc.) of F1 hybrids derived from the cross of two inbred lines. Higher levels of heterosis are more likely when the parents carry a high frequency of dominant alleles or when over dominance gene action is present. Therefore, heterosis can identify the selective parents, that can be used in breeding and exploiting the potential parents of higher yields in bottle gourd (Pandey *et al.*, 2004).

The objective of this study was to examine the manifestation of heterosis, degrees of dominance, heritability and the number of genes involved in the expression of seed yield and yield components.

MATERIALS AND METHODS

Study site. Experiments were conducted under field conditions during 2012 and 2013 in two localities of Côte d'Ivoire, namely Dikodougou at Northern and in Abidjan at Southern end of the country. The two locations were used to evaluate environment effect on the expression of the traits of interest.

The first cropping was carried out in Dikodougou in June to December 2012. Dikodougou is located at latitudes 9°03' and 9°59 North and longitudes 5°46' and 5°18' west. This locality is characterised by two main seasons: the dry season, generally from November to March (six months) and the rainy season from April to October (six months). Mean annual temperature was 25.8 °C. The mean annual precipitation was 1473 mm. In rainy season, precipitation oscillates between 800 and 1700 mm, with a maximum between July and September. The soil is ferralitic type. Dikodougou area is occupied by a vast granite complex that also includes shale locations (Stessens, 2002).

The second cropping study was carried out in Abidjan from June to December 2013. The experimental site was located at the University of Nangui Abrogoua research farm. Abidjan is located between 5°17'N and 5°31'N and 3°45'W and 4°22'W. Abidjan is characterised by four growing seasons; two dry seasons and two rainy seasons. The first dry season, from December to March (4 months), is followed by the first rainy season, which goes from April to July (4 months). The second dry season is from August to September (2 months), followed by the second rainy season from October to November. The rainfall is abundant (annual mean > 2,000 mm), with the maximum in July. The mean temperature is 28 °C. Due to sea breeze, the two dry seasons of Abidjan were soft (Avit and Pedia, 1999; Yao *et al.*, 2015).The soils of Abidjan districts are also ferralitic type (Yao-Kouamé and Allou, 2008).

In both study areas, the experiment was conducted during the rainy season and sowing done the first day of a significant fall of rain.

Plant material. The plant material consisted of four accessions, representing two types of *Lagenaria siceraria* collected at University Nangui Abrogoua (Abidjan, Côte d'Ivoire) germplasm. These included oleaginous type and calabash type. Each type consisted of two accessions; NI-135 and NI-232 for oleaginous type representing Parent P1; while NI-CM001 and NI-CSM001 were calabash type representing parent P2.

Cultural practices. Two experimental set ups were conducted to obtain F1, F2 hybrids under field conditions. The first field test conducted at Dikodougou permitted generation of F1 ($F1_{P1}$ and $F1_{P2}$) seeds. The $F1_{P1}$ was a result of direct crosses between oleaginous type and calabash type, where oleaginous type was the maternal parent (NI-232 × NI-CM001 and NI-135 × NI-CSM001). For reciprocal crosses $F1_{P2}$, the calabash type was the maternal parent (NICM001 × NI-232 and NI-CSM001 × NI-135. Thus, two families, resulting from direct and reciprocal of crosses, were studied; namely NI-232 ×× NI-CM001 and NI-135 ×× NI-CSM001.

The study at the Research Station of Nangui Abrogoua University generated F_2 ($F2_{P1}$ and $F2_{P2}$) seeds. During this test, parental lines (P1 and P2), $F1_{P1}$ and $F1_{P2}$ seeds were sown on the same parcel. From $F1_{P1}$ and $F1_{P2}$ plants, self-pollination was performed to produce respectively $F2_{P1}$ and $F2_{P2}$ plants.

For the hybrids seeds obtained, the whole generation (P1, P2, $F1_{P1}$, $F1_{P2}$, $F2_{P1}$ and $F2_{P2}$) from the two cross families (NI-232 ×× NI-CM001 and NI-135 ×× NI-CSM001) were sown from June to December 2012 and 2013, respectively in Dikodougou and Abidjan.

Seeds from all six generations (P1, P2, $F1_{P1}$, $F1_{P2}$, $F2_{P1}$ and $F2_{P2}$) of each cross family were sown in independent rows. The number of rows for each field was two for each parental line (P1 and P2), two for each F1 generation ($F1_{P1}$ and $F1_{P2}$,) and ten for each F2 generation ($F2_{P1}$ and $F2_{P2}$). Two to three seeds of each generation were sown per hole. Distance between and within rows was 2 m, and distance between experimental plots was kept at 2 m.

Ten days after sowing, seedlings were separated and only one plant was left per hole. In each location, individual number per generation was 20 plants for P1, 20 for P2, 20 for $F1_{P1}$, 20 for $F1_{P2}$, 120 for $F2_{P1}$ and 120 for $F2_{P2}$. Regular weeding of the fields was done during the plant vegetative cycle.

Data collection and analysis. Four parameters were considered in this study; fruit weight per plant (FW); 100-seed weight (100-SW); seed yield per plant (SY) and number of seeds per fruit (NS). Measurements were done according to Yao *et al.* (2015) and Koffi *et al.* (2009).

The collected data were processed using multivariate analysis of variance (MANOVA) for testing environment and generation-environment effect.

Analysis of variance (ANOVA 1) was performed with STATISTICA 7.1 (StatSoft, 2005) to investigate the difference between individual's generations. When significant difference was observed for each parameter, multiple comparisons using the Least Significant Difference (LSD) were carried out to determine the generation that differed signicatly from the other generations (Dagnelie, 1998). All LSD tests were performed at $\alpha = 0.05$ significance level.

Means, heterosis effect in F1-hypothetical and real and depression (Omarov, 1975), degree of dominance (hp1 and hp2) in F1 and in F2, respectively (Romero and Frey, 1973), degree of transgression (Tn) in F2 (Voskresenskaya and Shpota, 1967), phenotypic, environment and genetic variance (Warner, 1952) and (Allard, 1960), heritability (Burton and De Vane, 1953) and number of genes (Lande, 1981) were assessed using the following formulae:

Real heterosis: $((F1-HP)/HP*100$ .... Equation 1

Hypothetical heterosis: $(F1-MP)/MP*100$ .... Equation 2

MP: mid-parent value $(P1+P2)/2$; and HP: best parent value

Depression (%): $(F1-F2)/F1*100$ .... Equation 3

Degrees of dominance:

in F1 $hp1 = (F1\text{-}MP)/D$ .... Equation 4

in F2 $hp2 = (F2\text{-}MP)/D$ .... Equation 5

With $D = (HP\text{-}MP)$ .... Equation 6

Degree Tn (%) of transgression in F2" (%)

$$= \frac{Пг * 100}{Пр} - 100$$ .... Equation 7

Where:

"*Пs*" is the maximum value of the trait (average from the three best plants) in F2 hybrids; and

"*Пр*" is the maximum value of the trait (average from the three best plants) in better parent.

"Frequency Tf (%) of transgression in F2"

$$= \frac{A}{Б} * 100$$ .... Equation 8

"A" is number of hybrids plants exceeded the best parent for the investigated trait in F2; and

"Б" is number of hybrids plants for the investigated trait in F2.

Heritability in broad sense and heritability in narrow sense expressions were calculated as follows:

Broad-sense heritability

$$H^2 = \frac{\sigma^2(P) - \sigma^2(E)}{\sigma^2(P)}$$ .... Equation 9

Where:

σ^2 (P), σ^2 (E), σ^2(G), are phenotypic (P), environmental (E), genotypic (G) respectively

Number of genes:

$$N = \frac{[\mu(P1) - \mu(P2)]^2}{8x[\sigma^2(F2) - \underline{\sigma^2(P1)+\sigma^2(P2)+2\sigma^2(F1)}]} \atop 4$$

.... Equation 10

Where:

μ(P1) , μ(P1) are the mean value of the character for Parent 1, Parent 2, respectively σ^2(P1), σ^2(P2), σ^2(F1), σ^2(F2) are the variance estimated from generations parent 1, parent 2, hybrids F1, hybrids F2, respectively.

RESULTS

The trends of multivariate analysis (MANOVA) related to the effects of study environment (P=0.06) and individuals' generation × environment interactions (P = 0.21) were not significant. But significant effect was found for generations (P < 0,001). Thus, data were pooled over sites and only the means are presented (Table 1).

Generation means. The mean values of fruit and yield components per plant for the four crosses senses are presented in Table 1.

Fruit weight per plant differed significantly among the six generations, in both crosses families (P < 0.001). The highest value for this trait was obtained with parental line P2 3111.11±728.33 and 5075.00±1283.48 in crosses NI-232 ×× NI-CM001 and NI-135 ×× NI-CSM001, respectively. In the F1 generation, fruit weight varied according to cross senses. The highest values of fruit weight were observed in $F1_{P2}$, where calabash type (P2) was the maternal parent, with 2,262.71±3,53.42 and 2,979.55±488.73 g, respectively; for cross families NI-232 ×× NI-CM001 and NI-135 ×× NI-CSM001.

F2 generation also varied significantly according to the cross direction (Table 1). The

TABLE 1. Mean value of parental lines (P1 and P2) and the offspring's F1 ($F1_{P1}$ and $F1_{P2}$) and F2 ($F2_{P1}$ and $F2_{P2}$) for seed yield, 100 seed weight, fruit weight and seed number in bottle gourd *L. siceraria* for two crosses family in a study in Côte d'Ivoire

Hybrids	Generation (mean ±SD)						Statistics	
	P1	$F1_{P1}$	$F1_{P2}$	$F2_{P1}$	$F2_{P2}$	P2	F	P-value
Fruit weigth (g)								
NI-232××NI-CM001	1223.22±432.8c	1100.00±234.52c	2262.71±353.42b	1250.00±484.89c	2137.98±1232.584b	3111.11±728.33a	21.956	<0.001
NI-135××NI-CSM001	1482.05±414.13d	1808.64±621.43cd	2979.55±488.73b	1666.11±916.85d	1961.36±978.50c	5075.00±1283.48a	46.14	<0.001
100 seed weight								
NI-232××NI-CM001	19.41±7.34b	25.08±2.76a	26.29±4.84 a	21.27±7.78ab	25.80±7.53a	26.86±4.11a	9.21	<0.001
NI-135××NI-CSM001	17.48±3.49d	26.24±4.96bc	26.26±5.49bc	22.03±6.26c	24.45±10.11b	33.18±3.64a	11.70	<0.001
Seed yield								
NI-232××NI-CM001	28.85±10.83c	47.73±17.05bc	63.19±14.37b	31.44±20.86c	52.34±29.88b	88.33a	25.11	<0.001
NI-135××NI-CSM001	32.80±16.06d	61.32±23.76b	85.78±30.74a	42.40±29.24 cd	46.02±30.43bc	104.77±18.53a	21.41	<0.001
Seed number								
NI-232××NI-CM001	143.78±37.53d	193.83±80.53bcd	256.71±63.63ab	138.79±71.22d	196.08±84.90c	300.83±76.05a	21.54	<0.001
NI-135××NI-CSM001	181.73±57.30b	231.09±63.26b	315.14±104.61a	185.90±106.38b	184.44±103.93b	313.88±24.85a	9.27	<0.001

P1 = oleaginous type (NI-232; NI-135), P2 = calabash-type (NI-CM001; NI-CSM001), $F1_{P1,}$ $F2_{P1}$: F1 and F2 where oleaginous type was the maternal parent. $F1_{P2,}$ $F2_{P2}$: where calabash type was maternal parent, SD = standard deviation. Values followed by the same letter are not significantly different at P= 0.05 (LSD's test) mean value of fruit weight for $F2_{P1}$ was low and close to parent P1 in both crosses. But in $F2_{P2}$, fruit weight values were intermediate of those of the parental lines. In the cross NI-232 ×× NI-CM001, $F2_{P2}$ was close to $F1_{P2}$; while in cross NI135 ×× NI-CSM001, $F2_{P2}$ was lower than $F1_{P2}$ (1961.36±978.50 g vs. 2979.55±488.73 g).

There was a complete difference between the studies generations (P < 0.001) in both crosses in terms of 100-seed weight (Table 1). In the F1, there was no significant difference between $F1_{P1}$ and $F1_{P2}$ had been observed (Table 1). In generation F2, 100-seed weight varied according cross direction ($F2_{P1}$ and $F2_{P2}$). In the cross NI-232 ×× NI-CM001, 100 seed weight of $F2_{P2}$ was higher (25.80±7.53 g) than the mean value of $F2_{P1}$ (21.27±7.78 g). A similar observation was made in the cross NI135 ×× NI-CSM001 for $F2_{P2}$ (24.45±10.11 g) and $F2_{P1}$ (22.03±6.26).

Seed yield from each plant differed significantly among the six generations in the both crosses (Table 1). Calabash plants yielded more seeds than plants of other families, with approximately 88.33 and 104.77 g for NI-232 ×× NI-CM001 and NI-135 ×× NI-CSM001 (Table 1), respectively in the crosses. Hybrids F1 were intermediate between the two parental lines. However, the highest value (63.19±14.37 g and 85.78±30.74 g) was observed when calabash type was the maternal parent. In both crosses families, all hybrids (F1 and F2) yielded higher seeds than parent P1 (oleaginous type), with except in the cross NI-232 ×× NI-CM001. In this cross, seed yield of $F2_{P1}$ was close to the parent P1 mean. In generation F2, seed yield per plant was lower than those observed in F1 at both crosses families (Table 1).

Seeds per fruit varied significantly (P < 0.001) between generations in the both crosses families (Table 1). The fruits of the calabash produced more seeds than the oilseed type. Seeds per fruit in hybrid F1 were higher than the parent P1. In the both crosses, the highest value of F1 was obtained when calabash type was the maternal parent (256.71±63.63 and 315.14±104.61). In the generations F2, seeds per fruit were lower than the value observed in the generation F1. They were not significant difference between F2 and the parent P1.

In most traits under study, the highest mean in F1 and F2 generations were observed when the calabash-type was a maternal parent (Table 1).

Heterosis, dominance and transgression. Among traits, the hybrids displayed negative real heterosis (best parent heterosis), with exception of the number of seeds that was expressed as a positive value (0.4) in the crosses of NI-CSM001 × NI-135 (Table 2).

Negative hypothetical heterosis (mid-parent heterosis) was observed for fruit weight in all hybrids, except in the cross NI-CM001 × NI-232 (4.41%). According to the cross direction, the highest value of depression was observed in the reciprocal crosses, where the calabash-type was the maternal parent (0.73 vs. -13.64% and 34.17 vs. 7.88%).

Positive dominance was estimated in all crosses, with exception of NI-CM001 × NI-232. Epistatic gene action (hp2 > hp1) was found in NI-232 × NI-CM001 for fruit weight per plant (Table 2). But for the other hybrids, a negative dominance was observed (hp1).

A negative degree of transgression was also observed in all crosses for this trait. The frequency of transgression was 0 for three hybrids for fruit weight, except NI-232 × NI-CM001 (11.36%).

For 100 seed weight, a positive hypothetical heterosis was observed for all hybrids (Table 2). To the contrary, a negative real heterosis was observed for all hybrids; with the highest value when calabash type was the female parent. Positive depression in F2 was observed with the highest value when oleaginous type was the maternal parent. A positive dominance was found in all crosses, with exception of NI-232 × NI-CM001. This cross was characterised by a negative dominance and negative degree of transgression (-5.47%). The greatest degree of transgression was in NI-CM001 × NI-232

TABLE 2. Heterosis, depression and degree of dominance for seed yield and its relative components of the investigated crosses in Côte d'Ivoire

Hybrids	Heterosis F1 (%)		Depression F2 (%)	Degrees of dominance		Degree of transgression Tn (%)	Frequency of transgression Tf (%)
	Hypothetical	Real		in F1 hp1	in F2 hp2		
Fruit weight							
NI-232 × NI-CM001	-0.49	-0.57	-13.64	-0.57[2]	-0.49	-30.56	11.36
NI-CM001 × NI-232	4.41	-27.27	0.73	0.05	0.04	-29.29	0
NI-135 × NI-CSM001	-44.83	-64.36	7.88	-0.41	-0.45	-36.63	0
NI-CSM001 × NI-135	-9.12	-41.29	34.17	-0.08	-0.37	-35.48	0
100 seed weight							
NI-232 × NI-CM001	8.41	-6.61	15.21	-0.18	-0.46	-5.47	0.00
NI-CM001 × NI-232	13.65	-2.10	1.89	0.08	-0.10	27.62	10.70
NI-135 × NI-CSM001	3.61	-20.90	16.07	0.06	-0.21	3.13	2.00
NI-CSM001 × NI-135	3.69	-20.84	6.89	0.06	-0.06	28.16	2.73
Seed yield per plant							
NI-232 × NI-CM001	-18.53	-45.96	34.13	-0.18	-0.46	-19.69	0.00
NI-CM001 × NI 232	7.85	-28.46	17.16	0.08	-0.10	27.98	4.81
NI-135 × NI-CSM001	-10.85	-41.47	30.85	-0.10	-0.37	-2.63	1.00
NI-CSM001 × NI-135	24.71	-18.12	46.35	0.24	-0.32	-0.33	0.91
Seed number							
NI-232 × NI-CM001	-12.81	-35.57	28.40	-0.18	-0.53	-24.81	0.00
NI-CM001 × NI-232	15.47	-14.67	23.62	0.22	-0.17	-0.84	0.53
NI-135 × NI-CSM001	-6.74	-26.37	19.56	-0.13	-0.47	35.24	9.00
NI-CSM001 × NI-135	27.17	0.40	41.47	0.51	-0.48	36.38	8.18

Calabash-type NI-CM001 and NI-CSM001; oleaginous type: NI-232 and NI-135

(27.62%) and NI-CSM001 × NI-135 (28.16%). The frequency of transgression was positive and varied from 0 to 10.70.

For seed yield, a negative real heterosis (-45.96 to -18.12%) was observed for all cross directions (Table 2). When oleaginous was the female parent (NI-232 × NI-CM001 and NI-135 × NI-CSM001), the hypothetical heterosis was also negative (-18.53 to -10.85%) But, a positive hypothetical heterosis (7.85 to 24.71) was found in the reciprocals crosses NI-CM001 × NI-232 and NI-CSM001 × NI-135, where calabash-type was used like maternal parent. High depression was found in all hybrids (17.6 to 46.35%). However, in the hybrids NI-232 × NI-CM001 and NI-135 × NI-CSM001, seed yields were inherited by a negative dominance with -0.18 and -0.10%, respectively. The greatest positive degree and frequency of transgression was observed in NI-CM001 × NI-232 with 27.98 and 4.81%, respectively.

For number of seeds per fruit, without the cross NI-CSM001 × NI-135, negative real heterosis was observed in all crosses (Table 2). The highest positive hypothetical heterosis and positive dominance were observed in NI-CM001 × NI-232 and NI-CSM001 × NI-135, where calabash type was the maternal parent. High positive depression exists in all hybrids (19.56 to 41.47%). The greatest positive degree and frequency of transgression were observed in the crosses between NI-CSM001 and NI-135.

Heritability and numbers of genes. For fruit weight, genotypic variance was larger than environmental variance in direct cross NI-232 × NI-CM001, and the reciprocal cross NI-CM001 × NI-232 (Table 3). But in the cross between NI-135 and NI-CSM001, the genotypic variance was lower than environmental variance in direct and reciprocal cross. Heritability values varied according to crosses directions. When calabash-type NI-CSM001 or NI-CM001, was the maternal parent, the heritability was high (22.93 and 93.53%). The number of genes varies from 0.13 to 15.83, with a mean of 7.13.

For 100-seed weight, the genotypic variance was larger than the environmental variance in all crosses, with exception of NI-CM001 × NI-232 (Table 3). Heritability of this trait was high in all cross direction (48.18 to 79.03%). The number of genes was between 0.18 and 1.51, with a mean of 0.58.

For seed yield, the mean value of the genotypic variance was higher than the environmental variance in the crosses between NI-232 and NI-CM001 (Table 3). But in crosses between NI-135 and NI-CSM001, the genotypic variance was lower than the environmental variance. The minimum number of genes for this trait was low (from 0.62 to 2.14). Heritability was high, with a mean 53.28%. The highest values were observed in the crosses between NI-232 and NI-CM001 (50.42 to 80.56%).

For number of seeds per plant, environmental variance was higher than the genotypic variance in all cross direction with exception to NI-135 × NI-CSM001 (σ^2 (E) = 2976.31 vs. σ^2 (G) = 8339.93) (Table 3). The heritability of this trait varied from 28.45 to 73.70% with mean value 47.36%. The minimum number of genes also varied from 0.26 to 2.14.

DISCUSSION

Generation means. The mean value of fruit weight, the 100-seed weight, seeds yield and the number of seeds per plant recorded for F1 genotypes varied according to the cross sense. They were higher than the values of parent P1 but lower than the best parent P2. Therefore, the highest mean value in F1 and F2 generations was observed when the calabash-type (P2) was a maternal parent. These results could suggest a maternal inheritance in the expression of quantitative traits in the offspring. According to Acquaah (2007), genes carried in the maternal cytoplasm may influence the hybrid phenotype. Thus, the choice of parents

TABLE 3. Variance, heritability and number of genes estimate for the bottle gourd tested for seeds yield components in Côte d'Ivoire

Hybrids	Variances			Genetics parameters	
	σ^2(E)	σ^2(P)	σ^2(G)	Heritability (%)	Number of genes
Fruit weight					
NI-232 × NI-CM001	206962.43	235114.94	28152.51	11.97	15.83
NI-CM001 × NI-232	241916.61	3736504.73	3494588.12	93.53	0.13
NI-135 × NI-CSM001	647793.80	840620.69	192826.89	22.94	8.37
NI-CSM001 × NI-135	574134.71	957461.43	383326.72	40.04	4.21
Means	417701.89	1442425.45	1024723.56	42.12	7.13
100 seeds yield					
NI-232 × NI-CM001	21.52	60.59	39.07	64.49	0.18
NI-CM001 × NI-232	29.41	56.75	27.34	48.18	0.25
NI-135 × NI-CSM001	18.67	39.13	20.46	52.29	1.51
NI-CSM001 × NI-135	21.43	102.21	80.78	79.03	0.38
Means	22.76	64.67	41.91	61.00	0.58
Seed yield					
NI-232 × NI-CM001	215.68	434.99	219.31	50.42	2.02
NI-CM001 × NI-232	173.55	892.55	719.00	80.56	0.62
NI-135 × NI-CSM001	432.62	854.98	422.36	49.40	1.53
NI-CSM001 × NI-135	622.86	925.95	303.09	32.73	2.14
Means	361.18	777.12	415.94	53.28	1.58
Seed number					
NI-232 × NI-CM001	3629.66	5072.73	1443.07	28.45	2.14
NI-CM001 × NI-232	3822.06	7207.58	3385.52	46.97	0.91
NI-135 × NI-CSM001	2976.31	11316.24	8339.93	73.70	0.26
NI-CSM001 × NI-135	6446.92	10802.47	4355.55	40.32	0.50
Means	4218.74	8599.76	4381.02	47.36	0.95

σ^2 (E) = Environment variance. σ^2 (P) = Phenotypic variance. σ^2 (G) = Genotypic variance

is considered an important aspect in *L. siceraria* breeding programme aimed at improving yield and its components (Dubey and Ram, 2007).

Heterosis, dominance and transgression. For fruit weight per plant, 100-seed weight, seed yield plant and number of seeds per fruit, negative real led heterosis (best parent heterosis) in all cross (Table 2). This indicates that all hybrids F1 are lower performing than the best parent (calabash type). These results were in agreement with those of Singh *et al.* (2012) indicating negative "best parent heterosis" (BPH) for number of seeds per fruit and 100 seed weight in *L. siceraria.*

Negative hypothetical heterosis and negative dominance were observed in the crosses where the oleaginous type was used as the maternal parent (Table 3). But in the crosses where calabash type was a maternal parent, a positive hypothetical heterosis and positive dominance were observed. This positive hypothetical heterosis value suggests that hybrids $F1_{P2}$ are higher performing than the mid parent. These results indicates maternal effect and mid-parent heterosis for studies traits. Thus, the cross sense could influence the expression of heterosis and the degree of dominance in cucurbits and others crops.

Similar results have been reported on *Pisum sativum* (Fabaceae) by Kosev (2014) and in *Citrullus lanatus* (Cucurbitaceae) by Adjoumani *et al.* (2016). The authors indicated that phenotypic similarity between and hybrids (maternal effect) may be more caused by genes inherited from mother than the environment effect. On the other hand, our observation was in accordance with the finding of Dubey and Ram (2007), suggesting a positive and dominance gene effects for number of the seed per plant and the 100-seed weight in bottle gourd.

In all crosses, the degrees of dominance (hp) values were lower than 1 (Table 3). These findings indicate lack of heterosis and incomplete inheritance for the studies traits, including fruit weight per plant. These results were in disagreement with the observations of Quamruzzaman *et al.* (2009), who worked on the expression of heterosis in bottle gourd and suggested over dominance inheritance of fruit weight in *L. siceraria*.

The frequency of transgression was low (between 0 and 11.36) (Table 2), indicating that few F2 hybrids were presented higher performance than the better parent in F2 generation for all traits. This result could be explained by the action of the gene transgression, which causes some individuals in a segregating population from a cross to express the trait of interest outside the boundaries of the parents (Acquaah, 2007). These results suggest that selection of the best hybrids for studies traits would be more effective in later generations F3 or F4. In the entire study traits, a high depression was observed in F2 hybrids. Indeed, *L. siceraria* is allogamus specie that prefers cross pollination (Morimoto *et al.*, 2002). Hence, the self-pollination of F1 to generate F2 could decrease the expression in quantitative traits. These results confirmed that *L. siceraria*, like several other cucurbits does not react positively to inbreeding for quantitative traits (Robinson and Whitaker, 1974).

Variances, heritability and numbers of genes. For fruit weight, a high heritability in broad sense was observed in the cross where calabash-type was the maternal parent (Table 3). The high value of heritability indicates that a higher genetic effect was predominant compared to environment one. These results indicate that inheritance of fruit weight is not only due to direct effects of nucleus genes, but also to maternal effect caused by cytoplasmic factors and their interactions (Sabouri *et al.,* 2013). A large number of genes (7.13) observed for fruit weight in *L. siceraria* is in accordance with the finding of Gusmini and Wehner (2007), who showed that many genes controlled fruit weight in watermelon.

For 100-seed weight and seed yield per plant, a high heritability (Table 3) indicated a great genetic effect and a low environment effect on the expression of these traits. Number of genes for the three seed traits was low (0, 91 to 2.02). According to the findings of Shivali *et al.* (2013) traits controlled by a small number of genes show high heritability in early generations.

CONCLUSION

This study showed a maternal inheritance in the expression of heterosis and the degree of dominance in seed yield and its components. Thus, to improve seed yield and its components in *L. siceraria*, breeders could use calabash type like female parent.

This work also has shown that, all studies characters are controlled by a relative small number of genes (0.58 to 7.13), with moderate to high heritability. Therefore, the distinct genotypes with interest traits like seed yield and number of seeds per fruit would be fixed by using a small number of selfing generations (F3-F4). To achieve this, it may be easier to introgress desire quantitative and qualitative traits into breeding lines of desired seeds yield by a recurrent cross with the oleaginous type as male parent and calabash type as maternal parent.

ACKNOWLEDGEMENT

This research was financed by the « Direction Générale de la Coopération au Développement » (DGCD, Brussels, Belgium) and supervised by the « Commission Universitaire pour le Développement » (CUD, Brussels, Belgium).

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