Diallel analysis in *Citrullus mucosospermus* (Fursa) for fruit traits

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For the estimation of genetic parameters (such as heterosis effect, potency ratio, combining ability and reciprocal effects) of five fruit traits, in order to suggest breeding strategies in *Citrullus mucosospermus* (Fursa), a field trial was carried out at Kononfla city in Western Côte d'Ivoire using 4x4 full diallel. All 12 F₁ hybrids and their parents were planted in a randomized complete block design with three replications. A positive heterosis effect relative to mid-parental values was observed to hybrids having one parent *Bebu* for characters' fruit weight, fruit diameter and fruit volume. Variances due to general (GCA) and specific (SCA) combining abilities were significant (P˂0.001) for all studied traits, indicating the involvement of both additive and non-additive gene actions in the inheritance of these traits. Non-additive gene effects were predominant for all studied traits. *Bebu* was the best general combiner for all traits except fruit number which the best combiners were three morphotypes of *Wss*. For NF, Wss1×Wss2 and Wss2×Wss3 recorded the highest positive SCA values. Crosses involving *Bebu* as one parent, presented the best SCA values for other traits.

Key words: *Bebu*, *Wlêwlê* small seeds, heterosis, potency ratio, combining ability.

INTRODUCTION

In Côte d'Ivoire, the term “pistachio” is used to designate the oleaginous cucurbit species including *Citrullus mucosospermus* (Fursa) (Zoro Bi et al., 2003). This species belongs to *Citrullus* genus of *cucurbitaceae* family and is native to West Africa where it was domesticated (Chomicki and Renner, 2015). *C. mucosospermus* or egusi watermelon is specially cultivated for its oleaginous seeds which have nutritive, therapeutic, social and economic values (Adetutu et al., 2015; Kumawat et al., 2017). For example, dried slightly toasted and ground seeds are used as soup thickener. The "egusi" seeds are reported to be rich in nutrient such as carbohydrates (10.45 to 26.30%), proteins (21.78 to 30.42%) and lipids (41.78 to 56.08%) (Marie et al., 2015). Further, the seeds are good sources of amino acids, vitamins (B1 and B2) (Abrefa et al., 2002) and minerals...
like sulfur, calcium, manganese, potassium and zinc (Acar et al., 2012; Manika et al., 2015; Marie et al., 2015). Edible oil extracted from *C. mucosospermus* seeds can also be used in cosmetology and pharmaceutical industries (Manika et al., 2015; Erhirhie and Ekene, 2013).

Despite their economic, cultural, therapeutic and nutritive importance, along with their good adaptation to extremely divergent agro-ecosystems, *C. mucosospermus* cultivation is neglected. This crop is underutilized (also called orphan crops) and lacks attention from research and development. Consequently, there is lack of data about genetics and breeding of this important crop in many African countries particularly, in Côte d’Ivoire (Adjourmani et al., 2016a, b). In addition, lack of high yielding traditional cultivars (Koffi et al., 2009) along with a lack of local high yielding hybrids constitute one of the major problems of *C. mucosospermus* cultivation in Côte d’Ivoire. The productivity of this crop should be increased by improving the genetic architecture through hybridization between different elite cultivars or through selection of high yielding cultivars. Estimation of heterosis, polen ratio, gene actions, combining ability and reciprocal effects of yield and its components should be greatly emphasized for the improvement of this crop. One of the several biometrical techniques available to plant breeders to achieve above-mentioned information in the crop species is diallel analysis (Seyyed-Nazari et al., 2016). Diallel crosses reportedly provided early information on the genetic behavior of these attributes in the first generation (Farshadfar et al., 2011, 2014). That is why they have been widely used in plant breeding programs to obtain information on the behavior of a group of parents per se and their hybrid combinations (Queiroz et al., 2017). They represent the best strategy for determining the general (GCA) and specific (SCA) combining abilities which help to identify the best parents and hybrid combinations and provide sufficient genetic data about character inheritances (Farshadfar et al., 2011, 2014; Iqbal et al., 2015; Farshadfar and Amiri, 2015; Chukwu et al., 2016; Golabadi et al., 2017). In fact, the significance of the GCA reflects additive gene actions while the significance of SCA reflects the non-additive genetic effects which indicates relevant non-allelic interactions (Hossein et al., 2014; Fasahat et al., 2016; Seyyed-Nazari et al., 2016; Golabadi et al., 2017; Queiroz et al., 2017; Santos et al., 2017). If both GCA and SCA values are not significant, epistatic gene effects may play a remarkable role in determining these characters (Farshadfar and Amiri, 2015; Fasahat et al., 2016). However, no data concerning combining ability of *C. mucosospermus* local cultivars are available in the literature. The study of reciprocal effect as well as extra chromosomal inheritance or maternal effects is important in breeding programs which allows the determination of parents to be used as donors or recipients of pollen (Bahari et al., 2012).

The objectives of this work were to study through a complete diallel cross analysis, (i) the level of heterosis over the mid- and better parent, (ii) the type of gene actions, (iii) GCA and SCA effects of parents and crosses respectively and (iv) reciprocal effects in order to suggest breeding strategies for *C. mucosospermus*.

**MATERIALS AND METHODS**

**Experimental site**

The study was carried out in West-Center of Côte d’Ivoire precisely at Kononfa city located in Sinfra department which is in the Marahoue District. Kononfa is located at latitude 6° 37’ 18” N, longitudes 5° 54’ 37” W and altitude 243 m above sea level. Average temperature is between 25 and 30 °C and rainfall varies from 1500 to 2000 mm per annual. Soil type in the area is of ferrallitic form.

**Plant material**

Plant material comprised four accessions of *C. mucosospermus* which were collected from four regions (North, Center, West-Center and East) of Côte d’Ivoire (Table 1). The choice of the four genotypes is based on a wide range of morphological diversity in the fruit and seed characteristics that prominently distinguish one line from another.

**Experimental design, inbred line and F1 hybrid creations**

The purity of four parent accessions (*Bebu, Wss1, Wss2* and *Wss3*) was achieved previously after four generations of self-pollination before crosses in order to obtain different F1 families. Then, seeds of four parental lines were sowed during the period from January to April 2016 for crossing. At anthesis, hybridization was made among the four inbred lines according to a full diallel mating design to produce 12 F1 hybrids along with their four inbred lines. Field evaluation of the parents and their 12 F1’s hybrids was conducted from May to August 2016 in a randomized complete block design with three replications. The experimental field area was 2067 m² (53 m × 39 m) and divided into three blocks. Each block comprised 16 plots with a space of 1 m between plots and the area of one plot was 32 m² (8 m × 4 m). Only one F1 family or parental inbred line was sowed on 3 rows distant each other from 2 m within a plot. A total of 3 seeds of each family were planted per hole with an intrarow spacing of 2 m. Two weeks after sowing, seedlings were separated and the most vigorous were chosen per hole. The experimental field was regularly weeded during the vegetative growth stage.

**Fruit traits measurements**

Data collection was made on 10 plants sampled at random in each plot giving a total of 30 plants per genotype. Three fruits per plant were randomly selected in parental and F1 generations to evaluate five agronomic traits that are:

- **Fruit maturity period:** determined by counting days between sowing and the fruit harvest characterized by total plant drying.
- **Fruit number per plant:** determined by counting total fruits per plant,
Table 1. Description of parental C. mucosospermus accessions used for full diallel cross.

<table>
<thead>
<tr>
<th>Accession names</th>
<th>Origin of collect</th>
<th>Code of accessions</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bebu</td>
<td>Korhogo (North)</td>
<td>B</td>
<td>Big fruit with big seeds</td>
</tr>
<tr>
<td>Wlêwlê small seeds 1</td>
<td>Béoumi (Center)</td>
<td>Wss1</td>
<td>Small white fruit with small seeds</td>
</tr>
<tr>
<td>Wlêwlê small seeds 2</td>
<td>Gohitaifa (West-Center)</td>
<td>Wss2</td>
<td>Small green fruit with small seeds</td>
</tr>
<tr>
<td>Wlêwlê small seeds 3</td>
<td>Tanda (East)</td>
<td>Wss3</td>
<td>Medium green fruit with small seeds</td>
</tr>
</tbody>
</table>

**Fruit weight per plant:** Each fruit was weighed with an electronic balance (Kein HD5K5; sensitivity 5 g). Fruit weight per plant corresponds to average of 3 fruits weight per plant.

**Fruit diameter per plant:** Diometric lateral opposite board after fruit median section was measured with digital caliper (Stainless Hardened). Fruit diameter per plant corresponds to average of 3 fruits diameter per plant.

**Fruit volume per plant:** Fruit of *C. mucosospermus* cultivars are supposed spherical and their volume are evaluated like spherical volume as follow: \( V_Fr = 4/3\pi r^3 \), where \( r = DFr/2 \).

**Statistical analyses and genetic parameter estimates**

The data was subjected to statistical analyses using R version 3.3.1 (R Development Core Team 2011) Software. Analysis of variance (ANOVA) and the post ANOVA test (Turkey test) was performed according to Turkey’ HSD at 0.05 level of probability to test differences among treatment means. Heterosis percentage according to the mid-parent (MPH) and better parents (BPH), for the different studied characters were calculated using the formula proposed by Mather and Jinks (1971) as follows:

\[
MPH = \frac{(F_1 - MP) \times 100}{MP}
\]

\[
BPH = \frac{(F_1 - BP) \times 100}{BP}
\]

where \( F_1 \) = mean value of the particular hybrid, \( MP = (P_1 + P_2)/2 \) = mean value of the two parents for that hybrid, and \( BP = \) better parent mean value for that hybrid.

The t-test was manifested to determine whether \( F_1 \) hybrid means were statistically different from mid parent and better parent means. Potence ratio was calculated according to Smith (1952) to determine the degree of dominance as follows:

\[
P = \frac{(F_1 - MP)}{0.5 \times (P_2 - P_1)}
\]

where \( P \) = relative potence of gene set, \( F_1 = \) first generation mean, \( P_1 = \) the mean of lower parent, \( P_2 = \) the mean of higher parent, and \( MP = \) mid-parents value = \( (P_1 + P_2)/2 \). Complete dominance was indicated when \( P = \pm 1 \), while partial dominance is indicated when “P” value varies between -1 and +1 except the value zero, which indicates absence of dominance. Over-dominance was considered when potence ratio exceeds 1. The positive and negative signs indicate the direction of dominance of either parent.

The analysis of variance of GCA, SCA and reciprocal effects and their respective effect estimates were carried out according to Griffing’s (1956) model 1 method 1. The statistical model for the mean value of a cross \((i \times j)\) in Griffing’s analysis is:

\[
Y_{ij} = m + g_i + g_j + s_{ij} + r_{ij} + 1/b\sum e_{ijkl}
\]

where \( Y_{ij} = \) mean of \((i\times j)\) genotype over replications \( k (k = 1, 2, \ldots, b)\), \( m = \) general population mean, \( g_i = \) general combining ability effects of \( i^\text{th} \) and \( j^\text{th} \) parent, respectively, \( s_{ij} = \) specific combining ability effect for the cross involving \((i\times j)\) and \( r_{ij} = \) reciprocal effect involving the reciprocal crosses between the \( i^\text{th} \) and \( j^\text{th} \) parents and \( 1/b\sum e_{ijkl} = \) mean error effect.

The significance of the estimates of variance due to GCA, SCA and reciprocal effects was tested using F-values at threshold probabilities of 1 and 5%, while significance of estimates of GCA, SCA and reciprocal effects was tested using their respective standard errors. The estimates of genetic components were obtained based on the expectations of the mean squares, Zeinanloo et al. (2009):

Component due to GCA; \( \sigma^2 \text{GCA} = (\text{MS}_{\text{GCA}} - \text{MSError})/6n \)

Component due to SCA; \( \sigma^2 \text{SCA} = \text{MS}_{\text{SCA}} - \text{MSError} \)

where \( \text{MS}_{\text{GCA}} = \) variance due to GCA, \( \text{MS}_{\text{SCA}} = \) variance due to SCA, \( \text{MSError} = \) mean error, and \( n = \) number of replications.

**RESULTS**

**Agronomic performances of \( F_1 \) hybrids and their inbred lines**

Table 2 shows the mean values of four *C. mucosospermus* inbred lines and their \( F_1 \) hybrids for fruit characters. Mean values of parental lines showed that the cultivar Bebu (B) and accessions of cultivar Wlêwlê small seeds (Wss) have very contrasted characters (Figure 1). Bebu’s fruit reached a short maturity period thus it was precocious and possessed big fruits with a low fruit numbers per plant. In opposition, accessions of Wss had small fruits with higher fruit numbers and it was late because it possessed a long fruit maturity period. However, among Wss accessions, Wss3 presented big fruit with a long period of their maturity while Wss1 and Wss2 differed only by fruit color.

Results about \( F_1 \) hybrids illustrate that most of them produced average values that tend to be either than their respective mid-parental values or exceed the better-parental values. Thus, for characters’ fruit weight (FW), fruit diameter (FD) and fruit volume (FV), crosses involving cultivar Bebu as one of parents, obtained mean values which were equal or superior to the better-parental values while for the same traits, other crosses recorded average values more or less equal to their respective mid-parental values. The same crosses (without Bebu as one parent) obtained mean equal to their parental mean values for fruit number (NF) and fruit maturity period.
Table 2. Means ± standard deviation of four inbred lines and their F₁ hybrids for the studied fruit traits.

<table>
<thead>
<tr>
<th>Genotypes</th>
<th>FMp (das)</th>
<th>NF</th>
<th>FW (g)</th>
<th>FD (mm)</th>
<th>FV (mm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>83.77 ± 1.7&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2.93 ± 0.87&lt;sup&gt;e&lt;/sup&gt;</td>
<td>910.44 ± 242.52&lt;sup&gt;d&lt;/sup&gt;</td>
<td>122.63 ± 10.55&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>986683.4 ± 246596.14&lt;sup&gt;bcd&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss1</td>
<td>98.33 ± 4.01&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.23 ± 1.81&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>574.89 ± 101.33&lt;sup&gt;h&lt;/sup&gt;</td>
<td>104.34±5.89&lt;sup&gt;f&lt;/sup&gt;</td>
<td>600495.5 ± 102484.35&lt;sup&gt;ef&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss2</td>
<td>98.50 ± 4.18&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.27 ± 1.95&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>615.89 ± 138.77&lt;sup&gt;gh&lt;/sup&gt;</td>
<td>106.25±8.23&lt;sup&gt;f&lt;/sup&gt;</td>
<td>639101.7 ± 145291.80&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss3</td>
<td>102.50 ± 5.04&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>6.50 ± 1.89&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>728.55 ± 150.83&lt;sup&gt;g&lt;/sup&gt;</td>
<td>109.67±7.54&lt;sup&gt;de&lt;/sup&gt;</td>
<td>700236.2 ± 142036.46&lt;sup&gt;e&lt;/sup&gt;</td>
</tr>
<tr>
<td>B × Wss1</td>
<td>91.27 ± 3.67&lt;sup&gt;c&lt;/sup&gt;</td>
<td>4.13 ± 1.04&lt;sup&gt;de&lt;/sup&gt;</td>
<td>929.56 ± 218.97&lt;sup&gt;d&lt;/sup&gt;</td>
<td>120.86±9.26&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>940260.3 ± 207389.74&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss1 × B</td>
<td>91.47 ± 4.07&lt;sup&gt;c&lt;/sup&gt;</td>
<td>4.27 ± 1.39&lt;sup&gt;de&lt;/sup&gt;</td>
<td>991.56 ± 182.60&lt;sup&gt;c&lt;/sup&gt;</td>
<td>122.30±6.67&lt;sup&gt;c&lt;/sup&gt;</td>
<td>966365.7 ± 159288.65&lt;sup&gt;cd&lt;/sup&gt;</td>
</tr>
<tr>
<td>B × Wss2</td>
<td>90.63±4.29&lt;sup&gt;c&lt;/sup&gt;</td>
<td>4.10 ± 1.09&lt;sup&gt;de&lt;/sup&gt;</td>
<td>1092.11 ± 212.21&lt;sup&gt;a&lt;/sup&gt;</td>
<td>127.35±7.96&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1094127±206775.62&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss2 × B</td>
<td>90.83 ± 4.60&lt;sup&gt;c&lt;/sup&gt;</td>
<td>4.63 ± 1.67&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1050.78 ± 174.81&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>126.09±5.86&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1056282.3 ± 147136.80&lt;sup&gt;ab&lt;/sup&gt;</td>
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<tr>
<td>B × Wss3</td>
<td>93.53 ± 5.53&lt;sup&gt;c&lt;/sup&gt;</td>
<td>4.60 ± 1.40&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1006.44 ± 150.92&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>124.99±6.73&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1031283.1 ± 166786.40&lt;sup&gt;abc&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss3 × B</td>
<td>93.87 ± 5.92&lt;sup&gt;c&lt;/sup&gt;</td>
<td>4.83 ± 1.62&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>1010.44 ± 155.77&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>125.67±8.08&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>1056181.8 ± 177508.46&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss1 × Wss2</td>
<td>99.67 ± 3.92&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>6.60 ± 1.99&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>654.78 ± 131.07&lt;sup&gt;fg&lt;/sup&gt;</td>
<td>107.88±6.96&lt;sup&gt;def&lt;/sup&gt;</td>
<td>665518.7 ± 125721.43&lt;sup&gt;ef&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss2 × Wss1</td>
<td>99.83 ± 4.45&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>7.30 ± 2.26&lt;sup&gt;e&lt;/sup&gt;</td>
<td>648.33 ± 171.41&lt;sup&gt;fg&lt;/sup&gt;</td>
<td>106.33±9.43&lt;sup&gt;def&lt;/sup&gt;</td>
<td>644139.2 ± 186207.46&lt;sup&gt;ef&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss1 × Wss3</td>
<td>102.00 ± 5.96&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>5.07 ± 2.43&lt;sup&gt;bcd&lt;/sup&gt;</td>
<td>679.44 ± 145.33&lt;sup&gt;f&lt;/sup&gt;</td>
<td>110.30±7.90&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>713433.5 ± 155849.68&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss3 × Wss1</td>
<td>101.33 ± 6.29&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>6.83 ± 2.05&lt;sup&gt;e&lt;/sup&gt;</td>
<td>690.26 ± 161.50&lt;sup&gt;ef&lt;/sup&gt;</td>
<td>110.10±7.44&lt;sup&gt;de&lt;/sup&gt;</td>
<td>708472.0 ± 148178.12&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss2 × Wss3</td>
<td>102.83 ± 6.39&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.87 ± 1.89&lt;sup&gt;a&lt;/sup&gt;</td>
<td>679.78 ± 148.47&lt;sup&gt;f&lt;/sup&gt;</td>
<td>110.27±7.37&lt;sup&gt;d&lt;/sup&gt;</td>
<td>711439.2 ± 148236.90&lt;sup&gt;e&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wss3 × Wss2</td>
<td>103.00 ± 5.19&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.27 ± 2.35&lt;sup&gt;a&lt;/sup&gt;</td>
<td>643.83 ± 113.28&lt;sup&gt;fg&lt;/sup&gt;</td>
<td>106.63±6.76&lt;sup&gt;def&lt;/sup&gt;</td>
<td>642380.3 ± 124939.76&lt;sup&gt;ef&lt;/sup&gt;</td>
</tr>
<tr>
<td>F</td>
<td>42.5</td>
<td>17.128</td>
<td>108.04</td>
<td>111.7</td>
<td>113.64</td>
</tr>
<tr>
<td>P</td>
<td>&lt; 2.2 10^-16</td>
<td>&lt; 2.2 10^-16</td>
<td>&lt; 2.2 10^-16</td>
<td>&lt; 2.2 10^-16</td>
<td>&lt; 2.2 10^-16</td>
</tr>
</tbody>
</table>

Means within a column followed by the same letter are not significantly different (P = 0.05). B = Cultivar Bebu; Wss1 = *Wlêwlê small seeds* 1; Wss2 = *Wlêwlê small seeds* 2; Wss3 = *Wlêwlê small seeds* 3; FMp = Fruit maturity period; NF = Number of fruits per plant; FW = Fruit weight; FD = Fruit diameter; FV = Fruit volume; das= days after sowing.

Figure 1: Fruits of four parental lines showing their differences. **Wss1**: *Wlêwlê small seeds* 1; **Wss2**: *Wlêwlê small seeds* 2; **Wss3**: *Wlêwlê small seeds* 3; **B**: cultivar Bebu.

(FMp), while for the same traits, crosses which used *Bebu* as one parent, recorded average values noticeably equal to their respective mid-parental values.

**Heterosis and potency ratio estimations in F₁ hybrids for five fruit traits**

Estimates of heterosis (%) of F₁ hybrids over mid and better parents along with potency ratio values for some fruit traits are presented in Table 3.

**Fruit maturity period**

Percentages of heterosis of F₁ hybrids according to mid-parent were not significant and were positive for majority of crosses. Hybrids of all crosses involving *Bebu* as one of the parents, recorded the highest significant values of negative heterosis relative to the best parental values, indicating the precocity of these hybrids in comparison with better parent. Potence ratio values were comprised between -1 and 1 without 0 for all crosses except *Wss1 × Wss2* and *Wss2 × Wss3* which exhibited higher values.
than 1. 

Number of fruits per plant

Estimates of heterosis (%) of F₁ hybrids over mid and better parents were not significant for all hybrids and exhibited a range of heterosis (%) from -20.42 to 16.80% and from -55.48 to 16.49 % over the mid and higher parent, respectively. Crosses using Bebu as one parent recorded potence ratio comprised between -1 and 1 while in the other crosses, potence ratio values were superior to 1. However, Wss1 × Wss3 exhibited the only negative value of potence ratio (-9.75).

Fruit weight

Only hybrids of crosses having Bebu as one parent recorded a significant positive heterosis according to mid-parent (Figure 2). Percentages of heterosis according to the best parent were not significant for all hybrids. In the majority of cases, potence ratio were over 1.

Fruit diameter

All hybrids with one parent Bebu, exhibited significant positive heterosis over mid-parent (Figure 2) except hybrids from B × Wss1 which obtained non-significant value of heterosis according to mid-parent like other hybrids. Concerning heterosis according to the best parent, values recorded were not significant and were positive for all hybrids except hybrids resulting from B × Wss1, Wss1×B and Wss3 × Wss2. The same hybrids have obtained potence ratio values comprised between -1 and 1 while the other hybrids had values superior to 1.

Fruit volume

Crosses involving Bebu as one of the parents, exhibited significant positive heterosis over mid-parent (Figure 2) except cross B×Wss1 which recorded non-significant value of heterosis according to mid-parent as well as other hybrids. For heterosis according to the best parent, values obtained were not significant and were positive for all hybrids except hybrids resulting from B × Wss1, Wss1×B and Wss3 × Wss2. These hybrids had potence ratio values comprised between -1 and 1 while the other hybrids recorded values superior to 1.

General and specific combining abilities for five fruit traits in pistachio cultivars

Analysis of variances for combining ability
revealed that the mean squares (MS) of GCA and SCA were highly significant (p < 0.001) for all studied traits suggesting the presence of both additive and non-additive gene actions in the inheritance of these traits. The magnitude of specific combining ability variance was higher than general combining ability variance for all studied trait indicating that non-additive gene actions play an important role in the expression of these studied traits. The very low values of GCA/SCA ratio for these traits further substantiated this finding. The mean squares of reciprocal, maternal and non-maternal effects were not significant for all characters studied, indicating that these characters were under strict nuclear control (Table 4).

The estimates of general combining ability (GCA) and specific combining ability (SCA) effects for studied traits are presented in Table 5. Concerning GCA effects, results revealed that Bebu have recorded the highest significant positive values of GCA for fruit weight (FW), fruit diameter (FD) and fruit volume (FV). The same inbred line showed the highest significant negative values of GCA for number of fruit (NF) and fruit maturity period (FMp).

A negative value of GCA for FMp indicates earliness in fruit maturity while a positive value translates lateness in the fruit maturity. Thus, Bebu appeared as the best general combiner for FW, FD, FV and FMp while Wlêwlê small seed accessions were the best general combiners for NF since they exhibited highest positive values of GCA for this trait. Results about specific combining ability (SCA) effect showed that B × Wss2 cross had the highest negative estimated value of SCA for FMp indicating that non-
mother effect; NMAT = non-maternal effect; σ²GCA = Component due to GCA mean squares; σ²SCA = Component due to SCA mean squares; GCA/SCA = ratio σ²GCA/ σ²SCA.

Table 4. Analysis of variances for general and specific combining abilities (GCA and SCA), reciprocal, maternal and non-maternal effects and variance components.

<table>
<thead>
<tr>
<th>Sources of variation</th>
<th>Df</th>
<th>FMp</th>
<th>NF</th>
<th>FW</th>
<th>FD</th>
<th>FV</th>
</tr>
</thead>
<tbody>
<tr>
<td>GCA</td>
<td>3</td>
<td>163.03*</td>
<td>7.86*</td>
<td>120318.05**</td>
<td>295.56**</td>
<td>135497.88**</td>
</tr>
<tr>
<td>SCA</td>
<td>6</td>
<td>6105.20**</td>
<td>21.40**</td>
<td>381786.08**</td>
<td>8293.85**</td>
<td>400030.63**</td>
</tr>
<tr>
<td>REC</td>
<td>6</td>
<td>0.06ns</td>
<td>0.34ns</td>
<td>584.90ns</td>
<td>1.68ns</td>
<td>665.37ns</td>
</tr>
<tr>
<td>MAT</td>
<td>3</td>
<td>0.05ns</td>
<td>0.53ns</td>
<td>188.20ns</td>
<td>0.86ns</td>
<td>226.39ns</td>
</tr>
<tr>
<td>NMAT</td>
<td>6</td>
<td>0.07ns</td>
<td>0.16ns</td>
<td>981.61ns</td>
<td>1.25ns</td>
<td>1104.3 ns</td>
</tr>
<tr>
<td>error</td>
<td>30</td>
<td>0.78</td>
<td>0.11</td>
<td>827.23</td>
<td>1.78</td>
<td>809.89</td>
</tr>
<tr>
<td>σ² GCA</td>
<td></td>
<td>9.01</td>
<td>0.43</td>
<td>6638.38</td>
<td>16.32</td>
<td>7482.67</td>
</tr>
<tr>
<td>σ² SCA</td>
<td></td>
<td>6104.42</td>
<td>21.30</td>
<td>380958.86</td>
<td>8292.07</td>
<td>399220.74</td>
</tr>
<tr>
<td>GCA/SCA</td>
<td></td>
<td>0.00</td>
<td>0.02</td>
<td>0.02</td>
<td>0.00</td>
<td>0.02</td>
</tr>
</tbody>
</table>

ns: no significant, * and **: significant at 5% and at 1% respectively. FMp = Fruit maturity period; NF = Number of fruits per plant; FW = Fruit weight; FD = Fruit diameter; FV = Fruit volume. REC = reciprocal effect; MAT = maternal effect; NMAT = non-maternal effect; σ²GCA = Component due to GCA mean squares; σ²SCA = Component due to SCA mean squares; GCA/SCA = ratio σ²GCA/ σ²SCA.

Figure 2. F1 hybrids and their respective parents showing heterosis in crosses involving parental line Bebu as one of parents.

DISCUSSION

A 4 x 4 diallel cross design is used for agronomic performance study in inbred lines and their F1 hybrids through effects of heterosis, potence ratio, general and
specific combining ability and reciprocal effects. Concerning agronomic performances, the results showed that cultivar *Bebur* and accessions of *Wlêwêlê small seeds* (Wss) have very contrasted traits. The results also revealed that accessions of Wss cultivar were distinct one from other, indicating existence of variability between them. Our finding come to substantiate those of Zoro Bi et al. (2006), Adjoumani et al. (2012) and Gbotto et al. (2016).

The comparison of parental agronomic performance with those of their F₁ hybrids revealed that some hybrids presented mean values equal or superior to those of the best parent for some traits, occurring heterosis effects over mid- and the best parent. The significance of heterotic effects showed that non-additive genetic type of gene action affects such traits (Wannows et al., 2015). Indeed, according to Yousfi (2011), hybrids vigor is based on the complementation of parental gametic contribution by favorable dominant genes and therefore, the expression of heterosis effect could be resulted from non-additive gene action. Also, for explaining these hybrid vigor, Moll and Stuber (1974) listed three possible causes of hypothesis, partial to complete dominance, over dominance and epistasis. The results of heterosis in one crop suggested that hybrid vigor is available for the commercial production of this crop and selection of desirable hybrids among the crosses having heterotic and heterobeltiotic effects in other characters is the best way to improve the yield of this crop (Wannows et al., 2015). However, it is worth noting that a positive heterosis effect for FMp translating the lateness is not desirable. On the contrary, a negative heterosis effect for this trait indicates the earliness in the fruit maturity and therefore is desirable. Some hybrids had recorded mean values more or less equal or inferior to mid parental values for some traits justifying the low or very low heterosis effects observed. This fact could be explained by additive gene effects in the inheritance of these traits. In fact, Mather and Jinks (1971) reported that, under additive gene action, the F₁ mean is expected to be midway between the means of their parental combination. According to Jung and Lelly (1985), absence of heterosis or its low value in barley probably reflected a large additive gene action. Potence ratio values were strictly superior to zero in some crosses or were strictly inferior to zero in other crosses. These values of potence ratio reflected various degrees of gene dominance or recessiveness. Thus, in some F₁ crosses, potence ratio values were comprised between 0 and 1 or were superior to 1 for some trait suggesting that these traits were respectively under partial or over dominance gene actions control. On the contrary, traits having potence ratio values comprised between -1 and 0 or inferior to -1, indicated the presence of partial or over recessiveness gene action respectively in the inheritance of these characters. Similar results had been reported by El-Tahawey et al. (2015), Kamer et al. (2015) and Wannows et al. (2015). These various degrees of dominance are in agreement with hypothesis of partial or over dominance proposed by Moll and Stuber (1974) for explaining the hybrid vigor. In fact, hybrids which manifested positive heterosis effect over mid-parent have recorded potence ratio values comprised between 0 and 1 or superior to 1 while hybrids with a negative heterosis effect have obtained values of potence ratio comprised between -1 and 0 or inferior to -1 (Kamer et al., 2015; Wannows et al., 2015).

Results concerning combining ability showed that

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**Table 5. Estimates of GCA and SCA in four inbred lines and their hybrids for five fruit traits.**

<table>
<thead>
<tr>
<th>Genotypes</th>
<th>FMp</th>
<th>NF</th>
<th>FW</th>
<th>FD</th>
<th>FV</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>-6.57**</td>
<td>-1.47**</td>
<td>181.03**</td>
<td>8.97**</td>
<td>192.46**</td>
</tr>
<tr>
<td>Wss1</td>
<td>1.32*</td>
<td>0.31**</td>
<td>-88.73**</td>
<td>-4.31**</td>
<td>-92.38**</td>
</tr>
<tr>
<td>Wss2</td>
<td>1.51**</td>
<td>0.64**</td>
<td>-56.52**</td>
<td>-2.99**</td>
<td>-60.76**</td>
</tr>
<tr>
<td>Wss3</td>
<td>3.74*</td>
<td>0.53**</td>
<td>-35.78**</td>
<td>-1.68**</td>
<td>-39.32**</td>
</tr>
<tr>
<td>SEij</td>
<td>0.27</td>
<td>0.10</td>
<td>8.81</td>
<td>0.41</td>
<td>8.71</td>
</tr>
</tbody>
</table>

| ASC of crosses | B × Wss1 | 0.16ns | -0.16ns | 61.56** | 1.80*  | 30.96ns |
|                | B × Wss3 | 0.07ns | 0.13ns  | 56.50** | 3.02** | 68.32** |
|                | B × Wss2 | -0.67ns| -0.32ns | 140.24**| 5.62** | 121.24**|
|                | Wss1 × Wss2 | 0.46ns | 0.48** | -9.89ns | -0.71ns | -14.31ns |
|                | Wss1 × Wss3 | 0.15ns | -0.41* | 2.67ns  | 1.07ns  | 20.37ns |
|                | Wss2 × Wss3 | 1.21** | 0.37*  | -52.59**| -2.00** | -45.28**|
| SEij          | 0.49    | 0.18   | 16.08  | 0.75   | 15.91  |

ns: no significant *and **: significant at 5% and at 1% respectively. B = Cultivar Bebur; Wss1 = *Wlêwêlê small seeds* 1; Wss2 = *Wlêwêlê small seeds* 2; Wss3 = *Wlêwêlê small seeds* 3; FMp = Fruit maturity period; NF = Number of fruits per plant; FW = Fruit weight; FD = Fruit diameter; FV = Fruit volume. SEij = standard error.
analysis of variances due to general and specific combining ability were highly significant for all studied traits suggesting the presence of both additive and non-additive gene actions in the expression of these traits. No studies were done about general and specific combining ability in C. mucosospermus. However, the works carried out on its sister C. lanatus and on another cucurbitaceae species have also emphasized the importance of both additive and non-additive gene action in the inheritance of many traits (Feyzian et al., 2009; Gvozdanović-Varga et al., 2011; Bahari et al., 2012; El-Tahawy et al., 2015: Golabadi et al., 2015; Ogbu et al., 2016; Santos et al., 2017). The presence of both additive and non-additive gene actions in the expression of these traits suggests the use of reciprocal recurrent selection or Bi-parental mating for improving these traits (Jatocht et al., 2014). The magnitude of specific combining ability variance was higher than general combining ability variance for all studied traits bringing about the lower values of AGC/ASC ratio for all traits indicating that non-additive genetic effects play an important role in the expression of these traits. Similar results had been reported by Hemalatha et al. (2014), Pandey et al. (2014) and Iqbal et al. (2015) who had found lower values of GCA variance compared with SCA variances which caused lower values of ratio AGC/ASC respectively in maize (Zea mays L.), Pigeonpea [Cajanus cajan (L.) Millsp.] and dry beans (Phaseolus vulgaris L.). This result confirms these obtained with potence ration values. The predominance of non-additive gene action in the expression of investigated characters suggests the possibility of the hybrid vigor exploitation (Hasanuzzaman et al., 2012; Pandey et al., 2014, Poodineh and Rad, 2015; Santos et al.; 2017) or the possibility to postpone the selection to later generations for improving genetically these traits (Kiran et al., 2012).

The parental lines comparison in GCA term, showed that cultivar Bebu was the best general combiner for all studied traits except number of fruits per plant which the best general combiner were the three accessions of Wss. These four inbred lines could be used in C. mucosospermus breeding programs. In fact, the highest GCA effects shown by genotypes for a trait indicate that these genotypes contain more genes with additive effects (Nataša et al., 2014) and have high potential for generating superior offspring. This underlies that this trait is heritable (Ogibu et al., 2016). Consequently, these genotypes could be a good parent for this trait in a breeding program designed to improve that trait (Zeinanloo et al., 2009; Nataša et al., 2014). In addition, high significant values of GCA for one trait reveals selection and hybridization methods would result in interesting genetic improvement for this trait thanks to desirable genes accumulation of two parents in the targeted genotype (Golabadi et al., 2015). However, lines with higher GCA effects can be used more effectively in the development of synthetic variety (Hemalatha et al., 2014).

Results concerning SCA effect showed that crosses with high SCA effects involved at least one parent with high general combining ability for all characters. Significant SCA effects for one trait, obtained in crosses which were involving one parent with high GCA effect (high x low), suggested the involvement of additive x dominance gene interaction in expression of this trait (Nataša et al., 2014). According to Banerjee and Kole (2009), the diversity in parental GCA-effects plays an important role for the production of hybrids F_{1} with significant positive SCA effect. Crosses with significant SCA effects could be advanced further for the isolation of transgressive segregants in order to develop good inbred lines (Hemalatha et al., 2014; El-Tahawy et al., 2015).

Conclusion

Overall, parent lines exhibited significant genetic variations for investigated traits in this study. A positive heterosis effect relative to mid-parental values was observed to hybrids having one parent Bebu for characters’ fruit weight, fruit diameter and fruit volume, while a negative heterosis effect relative to the best parental values was recorded to same hybrids for fruit maturity period. Non-additive gene actions involved in the inheritance of all studied traits, suggests the exploitation of heterosis effect or the postponement of selection to later generations for improvement of these traits. Bebu appeared the best general combiner for FMp, FW, FD, and FV while Wss accesses were for NF suggested that these four parents can be incorporated into C. mucosospermus breeding programs. Crosses Wss1×Wss2 and Wss2×Wss3 showed significant SCA effects for NF while crosses using Bebu as one parent presented significant positive values of SCA for FW, FD and FV. B×Wss2 had recorded a negative value of SCA for FMp. All these crosses could be used for developing high yielding genotypes.

CONFLICT OF INTERESTS

The authors have declared no conflict of interests.

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ABBREVIATIONS

GCA, general combining ability; SCA, Specific combining
ability; B, Cultivar Bebu; das, Days after sowing; Wss, Wévélé small seeds; FM, Fruit maturity period; NF, Number of fruit per plant; FW, Fruit weight; FD, Fruit diameter; FV, Fruit volume.

REFERENCES


