ARTICLE

Obtaining okra hybrids through partial diallel analysis

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Abstract: *The exploration of heterosis can be an efficient alternative to increase okra yield. The partial diallel strategy optimizes resources by guiding crosses based on genetic diversity between various genotypes. This study aimed to identify potential hybrid combinations through diallel analysis in comparison with commercial cultivars. The hybrids were evaluated by means of a partial diallel scheme based on the genetic divergence of the genotypes. Fourteen hybrids and their reciprocals were evaluated in the winter and summer conditions of Jaboticabal – SP for yield, number of fruits and precocity. No line showed significant general combining ability. The reciprocal effect was not significant for the evaluated characteristics. Four hybrid combinations showed significant and positive specific combining ability for number of fruits, which were considered promising hybrids. In the winter, the experimental hybrids 1 x 8 and 3 x 8 showed superior performance compared to the commercial hybrids. No significant differences were observed in the summer.*

Keywords: *Abelmoschus esculentus L. Moench, heterosis, combining ability*

INTRODUCTION

Okra is widely cultivated for its immature fruits that are consumed in different types of preparations. The consumption of okra tended to increase as it has been elevated to be a functional food with important nutraceutical characteristics (Durazzo et al. 2019). Okra cropping is considered secondary in several countries, with no major investments by the private sector. In addition, most okra production occurs in Asian and African countries, which are socioeconomically vulnerable. This implies two important aspects: okra is important for food security in producing countries, and few investments are made to develop modern cultivars and/or more efficient cultural management techniques (Tadele and Assefa 2012).

In Brazil, there is no reliable socioeconomic data on okra agribusiness, however, in the state of São Paulo (IEA 2019), okra yield has not increased compared to other vegetable crops. This can be attributed mainly to the use of open pollinated cultivars and the occurrence of high root-knot nematodes (Silva et al. 2019). For more than 45 years, the same cultivar 'Santa Cruz 47' has been planted in Brazil, as it is rustic, productive and widely accepted by consumers. Therefore, there is room for introducing more productive cultivars (Chowdhury and Kumar 2019).

The okra is sensitive to low temperatures and with reduced temperatures in mild winter regions, such as the state of São Paulo, okra prices increase

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considerably due to low supply of the product in the market. Although more diseases can occur due to high humidity and precipitation in summer, yield is high due to the adaptation of the species to tropical conditions. Therefore, to strategically producing okra in winter, development of cold tolerant cultivars is necessary (Reddy et al. 2013).

There is a possibility to increase yield through heterosis. Hybrid seeds, in general, are more expensive than seeds obtained by open pollination, however, the advantages, such as greater production, uniformity, and disease resistance, justifies the investment (Maciel et al. 2018). For the Brazilian market, it would be strategic to develop productive hybrids using the 'Santa Cruz 47' genetic background due to its wide acceptance. Therefore, evaluating crosses of this cultivar or similar lines can positively influence the success of a possible new genotype.

The partial diallel strategy optimizes human and financial resources in breeding programs, where crosses are performed between genetically distinct genotypes, increasing the probability of identifying potential combinations. In diallel analysis, estimates of general and specific combining abilities are obtained, which are considerably useful in the selection of lines and hybrid combinations. Moreover, for some characteristics that have a maternal effect, studying the reciprocal effect is paramount (Barata et al. 2019). This study aims to identify promising hybrids by estimating the general and specific combining abilities, and to compare the experimental hybrids with commercial cultivars.

MATERIAL AND METHODS

Location

The experiments were performed in two growing seasons, winter (from April to July 2018) and summer (from October 2018 to February 2019), at the School of Agricultural and Veterinary Sciences of the São Paulo State University "Júlio de Mesquita Filho", Jaboticabal Campus (lat 21° 15' 22'' S, long 48° 18' 58'' W, alt 595 m asl). The daily maximum, mean, and minimum temperature for the two growing seasons are presented in Figure S1. The climate of the region is Cwa according to Köppen classification, which is subtropical with dry winter and rainy summer. The soil of the experimental area is classified as Red Latosol. The harvest period of the two experiments was standardized as two months.

Parents and partial diallel crosses

Nine genotypes were separated into two groups based on genetic divergence (Silva et al. 2021). The seven genotypes of the first group (CNPH-19, CNPH-24, CNPH-11, CNPH-09, CNPH-05, CNPH-02, and CNPH-35, namely genitors 1 to 7) were crossed with the two genotypes of the second group (Santa Cruz 47 and CNPH-42, namely genitor 8 and 9, respectively) and vice versa, resulting in 14 hybrids and 14 reciprocal hybrids.

The hybrid seeds were obtained as described by Dhankhar et al. (2009), as follows: one day before pollination, the female lines were emasculated and protected using a paper bag; the following morning, the female lines were manually pollinated with pollen from the male line; the pollinated flowers were identified and protected again for at least three days; finally, ripe fruits were harvested, and seeds were removed manually. After reaching 7% humidity, the seeds were then packed in paper bags and stored in a cold chamber at a temperature of 10 °C.

Experimental design and protocol

A randomized block design was adopted, with three replications. The evaluated treatments were the hybrids and their reciprocals. In addition, four commercial cultivars were evaluated as controls. Seedlings with two fully developed non-cotyledon leaves were transplanted to the open field, spaced one meter between planting rows and 0.25 m between plants. The plots consisted of four planting rows with six plants. The four central plants of the two central rows were considered as a useful plot.

The plants were cultivated according to the okra crop recommendations (Passos et al. 2014). The flowering day of each plant was noted to estimate the genotypes precocity. The fruits were harvested at maximum length before becoming fibrous, on alternate days, with subsequent counting and weighing on an analytical balance. The number of fruits and yield were extrapolated to ha^{-1} and $t\ ha^{-1}$, respectively.

Data analysis

The diallel analysis was carried out according to method III proposed by Griffing (1956) and adapted for partial diallel (Cruz et al. 2012, Abreu et al. 2018). The treatment effect (14 hybrids and 14 reciprocals), considered as fixed, was partitioned into general (GCA) and specific (SCA) combining capabilities. The effect of the environment was considered to be random. The reciprocal effects were also estimated. The values of GCA, SCA, reciprocal effect, and the components of variance associated with these effects were predicted using REML/BLUP (residual maximum likelihood - best linear unbiased predictor) using the Proc IML routine of SAS version 9.2 (SAS Institute 2008). We tested whether the estimates of GCA, SCA, and reciprocal effect were statistically equal to zero according to the t test described by Efron et al. (2001) and Efron and Tibshirani (2007). Furthermore, contrasts of interest between experimental hybrids and the cultivar 'Santa Cruz 47' and commercial hybrids were estimated.

RESULTS AND DISCUSSION

Diallelic analysis

The variance components of the general combining ability ($\hat{g}$) ranged from 0.002 for precocity to 0.1 for number of fruits, and those of specific combining ability ($\hat{s}$) from 0.009 for fruit production to 50.4 for number of fruits (Table 1). Estimates of GCA close to zero indicate that the allelic frequency of the parental line does not differ from the group average (Abreu et al. 2018), thus, these lines do not contribute to the hybrid average beyond what is expected. Moreover, the magnitude of the GCA provides information about the concentration of genes with an additive effect (Cruz et al. 2012), thus, higher the GCA, higher is the lines contribution to the trait.

The variance of the interaction between GCA and the environments was high for the characteristic number of fruits, especially for genotypes in group 2. In general, the variance of the interaction between the genotypes of group 2 was greater than that of group 1, for all the characteristics, indicating greater genetic variability in this set of lines. High values of $\hat{\sigma}^2_s$, as observed for number of fruits, indicate that the lines of the two groups have favorable contrasting alleles in locus with non-additive effects (Table 1) (Cruz et al. 2012).

No GCA estimate was significant (Table 2). The genitor 4 (CNPH-09) presented negative estimates for all characteristics in both environments, indicating that this line when crossed with others in the group tends to decrease the average fruit production, number of fruits, and precocity. The highest GCA values for fresh fruit production and number of fruits, in the two growing seasons, were observed in the genitor 1 (CNPH-19), suggesting that this line tends to increase the average of the yield components, although it did not present a significant estimate. The GCA estimates of each line assist breeders in the selection of parents for hybrid crosses, as they make it possible to infer the frequency of favorable alleles of a given trait of interest, by estimating the average behavior of the lines as a parent in the crosses involved (Abreu et al. 2018). If the aim of the breeding program is to obtain segregating populations in which potentially superior lines are selected, then genetically divergent parents with high GCA are chosen. In the present study, little success is expected if this pathway is considered, since no line stood out significantly in terms of GCA estimates.

The performance of hybrid combinations is studied using SCA, which. can indicate whether the characteristic is controlled by non-additive genes. Significant differences were observed only for number of fruits, totaling eight significant

Table 1. Estimates of the variance components of the general combining ability ($\widehat{\hat{\sigma}^2_g}$), specific combining ability ($\hat{\sigma}^2_s$), and their interaction with the environments for fresh fruit yield (t ha^{-1}), number of fruits, and precocity (days for flowering) in okra hybrids

Parameters	Yield	Number of fruits	Precocity
$\hat{\sigma}^2_{g1}$	0.005	0.100	0.002
$\hat{\sigma}^2_{g2}$	0.008	0.100	0.010
$\hat{\sigma}^2_{s}$	0.009	50.400	0.020
$\hat{\sigma}^2_{g1\,x\,e}$	2.100	154.400	0.500
$\hat{\sigma}^2_{g2\,x\,e}$	9.900	1930.500	14.500
$\hat{\sigma}^2_{s\,x\,e}$	0.010	0.300	0.400
$\hat{\sigma}^2_{e}$	11.300	1017.200	38.100

Table 2. Estimates of the effects of general combining ability ($\hat{g}$) for fresh fruit yield (t ha^{-1}), number of fruits, and precocity (days for flowering) in okra hybrids

Seasons	Genitor	Yield	Number of fruits	Precocity
Winter	1	0.0036	0.0045	0.0006
	2	0.0022	0.0020	-0.0001
	3	0.0001	-0.0003	-0.0012
	4	-0.0018	-0.0015	-0.0006
	5	-0.0026	-0.0039	0.0008
	6	-0.0002	0.0017	0.0004
	7	-0.0006	-0.0021	0.0002
	8	-0.0031	-0.0043	-0.0008
	9	0.0023	0.0039	0.0006
Summer	1	0.0031	0.0026	-0.0016
	2	0.0011	0.0008	0.0018
	3	-0.0019	-0.0017	-0.0008
	4	-0.0002	-0.0007	-0.0008
	5	-0.0020	-0.0023	-0.0026
	6	-0.0011	-0.0009	0.0035
	7	-0.0005	0.0011	0.0000
	8	0.0004	0.0002	0.0003
	9	0.0010	0.0009	0.0003

No significant effect was detected by the t test.

Table 3. Estimates of the effects of the specific combining ($\hat{s}$) for fresh fruit yield (t ha^{-1}), number of fruits, and precocity (days for flowering) in okra hybrids

Hybrids	Yield	Number of fruits	Precocity
1x8	0.008	4.50**	-0.004
2x8	-0.003	-1.70	0.008
3x8	0.005	3.13*	-0.006
4x8	-0.007	-3.16*	0.000
5x8	0.004	0.23	-0.009
6x8	-0.001	-0.60	-0.002
7x8	-0.010	-6.21**	0.010
1x9	0.003	0.47	0.005
2x9	0.009	3.80*	-0.005
3x9	-0.006	-3.99**	-0.003
4x9	0.003	1.57	-0.005
5x9	-0.011	-4.60**	0.010
6x9	0.000	1.80	0.011
7x9	0.008	4.77**	-0.008

* and ** Significant at 5% and 1% probability, respectively, by the t test.

hybrid combinations (Table 3). Although significant results have not been observed for fresh fruit yield, it can be inferred that crosses that allowed a greater number of fruits, would also provide greater yield. Number of fruits is one of the main yield components and can be even more important when the fruits are destined for bulk trade (Medagam et al. 2012). Only half of the eight significant crossings had positive estimates (1x8, 3x8, 2x9, and 7x9). The other significant hybrid arrangements (4x8, 7x8, 3x9, and 5x9) tended to decrease the average number of fruits.

The best hybrid combination has the highest SCA, with at least one of the parents with high GCA (Griffing 1956). However, not always two lines with high GCA will result in the best hybrids (Cruz and Vencovsky 1989, Liu et al. 2021). Furthermore, it is possible that parents with low GCA result in hybrids with high SCA, which can be attributed to the genetic distance between the lines (Reddy et al. 2013). This phenomenon can be explained by the associated gene effects, since components of dominance, overdominance, or epistasis are added to the favorable additive contributions of each parent (Mayo 1980).

When the lines involved in the crossing are not in contrast to the alleles that control the trait in loci with a dominance effect, low SCA values are obtained (Cruz et al. 2012), which is not desirable in a breeding program.

The SCA information enable the selection of the most promising hybrid combinations for the characteristics of interest, however it is necessary to investigate whether a particular line should be used as female or male parent, justifying the study of the reciprocal effect (Cruz et al. 2012). There was no significant reciprocal effect, suggesting that it is not imperative which line should be female or male in obtaining the hybrids (Table 4). When the inheritance of a given trait is controlled by cytoplasmic genes, the phenotype of the offspring is the same as that of the maternal parent (Hallauer et al. 2010). On the other hand, when it is the nuclear genes that control the trait, there are no significant differences between the hybrid and its reciprocal, as observed in this study (Table 5).

Agronomic analysis

There was a relation between the genotypes and growing seasons for the characteristics of number of fruits and fresh fruit yield (Table 6). Significant differences between the growing seasons were seen for all characteristics. As expected, higher yield and number of fruits were observed in summer cropping, probably because the climatic conditions are more favorable for the crop, which is adapted to tropical and subtropical conditions.

Contrasts of interest were estimated between the hybrids that showed significant and positive SCA for number of fruits against the okra 'Santa Cruz 47' (leading open-pollinated Brazilian cultivar) and against commercial hybrids (V-8, Esmeralda, and Speedy), in both the growing seasons (Table 7).

The hybrids 1x8 and 3x8 performed better than the commercial hybrids in winter conditions, with a yield of 6.61 and 4.57 t ha^{-1}, in two months of harvest, respectively (Table 7). The hybrid 1x8 also showed superiority for the number of fruits trait, compared to commercial hybrids. The ideal temperature for okra cropping is around 25-30 °C, but development occurs normally between 18-35 °C (Bhatt and Rao 2009). The temperature was lower than what was required by the okra crop on some days or some part of the days in winter cropping (Figure S1), which may explain the lower yield.

The fresh fruit yield observed in winter was, as expected, considerably lower than in summer, the ideal growing season. The okra is known to be sensitive to low temperatures. However, these hybrids seem to have potential for cultivation in the off-season and must be evaluated in production systems to be better defined, i.e., sowing date, spacing, and cultural practices suitable for milder temperature conditions. Moreover, okra is sensitive to stress due to water deficiency, especially in the vegetative, flowering, and initial fruit development phases, which can affect the photosynthetically active area, biomass, and yield (Chaturvedi et al. 2019). Thus, when evaluated in winter, a period in which the rainfall is considerably low, the use of irrigation and water management must be considered.

Developing hybrids with satisfactory performance in winter conditions can be beneficial, as the best market prices are achieved, increasing the profitability of the grower. As it is easier to produce okra in the hottest part of the year, the

Table 4. Estimates of the variance components of general combining ability ($\hat{g}$), specific combining ability ($\hat{s}$), reciprocal effect ($\hat{r}$) and the interactions with the environments for fresh fruit yield (t ha^{-1}), number of fruits, and precocity (days for flowering) in okra hybrids

Parameters	Yield	Number of fruits	Precocity
$\hat{\sigma}^2_{g1}$	0.004	0.060	0.001
$\hat{\sigma}^2_{g2}$	0.010	0.140	0.005
$\hat{\sigma}^2_{s}$	0.010	50.280	0.010
$\hat{\sigma}^2_{r}$	0.010	0.090	0.010
$\hat{\sigma}^2_{g1\,x\,a}$	2.060	154.420	0.520
$\hat{\sigma}^2_{g2\,x\,a}$	9.880	1930.480	14.470
$\hat{\sigma}^2_{s\,x\,a}$	0.010	0.250	0.340
$\hat{\sigma}^2_{r\,x\,a}$	0.010	0.200	0.030
$\hat{\sigma}^2_{e}$	11.300	1017.100	38.100

No significant effect was detected by the t test.

Table 5. Estimates of the reciprocal effect obtained through the model III (Griffing 1956) and differences between the estimates for fresh fruit yield (t ha^{-1}), number of fruits, and precocity (days for flowering) in okra hybrids

			Reciprocal effect			Differences		
Cross	**Hib.**	**Rec.**	**Yield**	**Number of fruits**	**Precocity**	**Yield**	**Number of fruits**	**Precocity**
1x8	1	1	0.003	0.007	0.002	0.002	0.005	0.002
8x1	1	2	0.001	0.002	0.004			
2x8	2	1	0.000	0.001	-0.003	0.002	0.006	0.003
8x2	2	2	-0.002	-0.004	0.000			
3x8	3	1	0.002	0.002	-0.003	0.003	0.003	0.001
8x3	3	2	0.000	-0.001	-0.003			
4x8	4	1	-0.003	-0.007	0.004	0.005	0.007	0.004
8x4	4	2	0.002	0.000	0.001			
5x8	5	1	0.002	0.001	-0.004	0.002	0.003	0.003
8x5	5	2	0.000	-0.002	-0.001			
6x8	6	1	0.000	0.002	-0.002	0.005	0.011	0.008
8x6	6	2	-0.005	-0.009	0.006			
7x8	7	1	0.000	0.004	0.004	0.002	0.000	0.008
8x7	7	2	0.003	0.004	-0.003			
1x9	8	1	0.002	0.001	-0.004	0.005	0.006	0.005
9x1	8	2	-0.003	-0.005	0.001			
2x9	9	1	0.002	0.004	-0.001	0.005	0.006	0.001
9x2	9	2	-0.002	-0.001	0.000			
3x9	10	1	0.000	-0.002	-0.002	0.000	0.002	0.003
9x3	10	2	0.000	0.000	0.001			
4x9	11	1	-0.003	-0.004	0.001	0.003	0.005	0.001
9x4	11	2	0.000	0.001	0.003			
5x9	12	1	0.003	0.005	0.001	0.007	0.011	0.001
9x5	12	2	-0.004	-0.005	0.000			
6x9	13	1	0.002	0.001	-0.001	0.003	0.001	0.000
9x6	13	2	-0.001	0.000	-0.001			
7x9	14	1	0.000	-0.001	0.002	0.003	0.005	0.003
9x7	14	2	0.002	0.005	-0.001			

No significant effect was detected by the t test.

Table 6. Summary of the joint analysis of variance of the okra experiments conducted in the winter and summer, for fresh fruit yield (t ha^{-1}), number of fruits, and precocity (days for flowering)

Source of variation	**df**	Mean square		
		Yield	**Number of fruits**	**Precocity**
Block/Growing Seasons	4	72.57	5125.31	159.98
Genotypes (G)	31	11.68	1666.50	39.84
Growing Seasons (S)	1	3179.08**	483656.94**	2566.69**
G x S	31	16.47*	2393.77**	46.83
Residue	124	10.01	1014.03	37.04
Mean winter		3.43	41.97	51.37
Mean summer		11.57	142.35	44.06
CV winter		28.73	30.58	8.04
CV summer		14.96	13.91	2.08
MSr+/MSr-		2.06	2.15	18.96

Observed values with statistics based on the data transformed to $(x+1)^{0.5}$. * and ** Significant at 5 and 1% probability, respectively.

Table 7. Contrasts of interest between promising hybrids and commercial okra cultivars, in two growing seasons (winter and summer) for fresh fruit yield (t ha^{-1}), number of fruits, and precocity (days for flowering)

Contrasts	Yield		Number of fruits		Precocity	
	Winter	Summer	Winter	Summer	Winter	Summer
1x8	6.61 a	12.18	76.33 a	155.33	54.00	44.33
Hybrids	1.40 b	14.15	22.56 b	188.44	48.00	43.00
F-Test	7.34**	0.35	4.82*	0.49	1.96	0.12
P-value	0.0077	0.5559	0.0299	0.4847	0.1642	0.7350
1x8	6.61	12.18	76.33	155.33	54.00	44.33
'Santa Cruz 47'	3.12	7.51	41.67	98.00	57.00	43.00
F-Test	1.37	2.05	0.75	1.51	0.39	0.08
P-value	0.2433	0.1546	0.3878	0.2213	0.5316	0.7822
3x8	4.57 a	11.00	51.33	143.00	47.00	44.33
Hybrids	1.40 b	14.15	22.55	188.44	48.00	43.00
F-Test	4.23*	1.02	2.23	0.99	0.09	0.12
P-value	0.0418	0.3145	0.1381	0.3223	0.7703	0.7350
3x8	4.57	11.00	51.33	143.00	47.00 a	44.33
'Santa Cruz 47'	3.12	7.51	41.67	98.00	57.00 b	43.00
F-Test	0.41	1.19	0.09	0.98	4.03*	0.08
P-value	0.5240	0.2778	0.7708	0.3240	0.0467	0.7822
2x9	4.17	14.32	47.33	164.67	46.00	44.33
Hybrids	1.40	14.15	22.55	188.44	48.00	43.00
F-Test	3.30	0.00	1.51	0.27	0.20	0.12
P-value	0.0718	0.9712	0.2220	0.6025	0.6550	0.7350
2x9	4.17	14.32	47.33	164.67	46.00 a	44.33
'Santa Cruz 47'	3.12	7.51	41.67	98	57.00 b	43.00
F-Test	0.09	3.55	0.01	1.89	4.56*	0.08
P-value	0.7590	0.0618	0.9400	0.1715	0.0347	0.7822
7x9	4.26	13.42	49.33	162.67	48.00	43.00
Hybrids	1.40	14.16	22.56	188.44	48.00	43.00
F-Test	2.58	0.06	1.37	0.28	0.00	0.00
P-value	0.1105	0.8068	0.2447	0.5992	0.9778	1.0000
7x9	4.26	13.42	49.33	162.67	48.00	43.00
'Santa Cruz 47'	3.12	7.51	41.67	98.00	57.00	43.00
F-Test	0.07	2.94	0.00	1.88	3.21	0.00
P-value	0.7861	0.889	0.9780	0.1727	0.0755	1.0000

* and ** Significant at 5% and 1% probability, respectively.

supply increases considerably, decreasing the price paid to the grower. Similarly, there is little supply of okra in winter due to climatic conditions, increasing the price. In addition, it should be considered that okra consumers are culturally inclined to buy frequently, if the price is attractive. In the literature, there are no reports of suitable cultivars for this cropping condition. Thus, the two experimental hybrids, 1x8 and 3x8, may possibly fill this gap.

The hybrids 3x8 and 2x9 were significantly earlier than the standard open-pollinated 'Santa Cruz 47' (Table 7). In general, all genotypes flowered later in the winter, but 'Santa Cruz 47' was more influenced by the temperature difference. Some authors argue that earlier genotypes tend to generate economic returns more quickly to the grower, with longer harvest duration and greater number of fruits per plant, which is a trait of interest in okra breeding programs (Medagam et al. 2012, Mattedi et al. 2015).

The reciprocal effect was not significant for fruit yield, number of fruits, and precocity. Four hybrid combinations showed positive and significant SCA for number of fruits, being potential genotypes. Among these, the hybrids 1x8 and 3x8 showed superior performance compared to commercial hybrids in winter conditions. There were no significant differences between experimental and commercial hybrids in the summer. All genotypes flowered later in the winter, however, the open-pollinated 'Santa Cruz 47' was more influenced than the experimental and commercial hybrids.

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