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DEVELOPMENT OF DOUBLE-CROSS HYBRIDS AS NEW SOURCES OF FAVOURABLE ALLELES IN FUTURE OKRA BREEDING

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ABSTRACT

In present study on okra, the level of heterosis over mid- and better-parents, along with the type of gene action for yield, quality, and resistance to Bhindi Yellow Vein Mosaic Virus (BYVMV) disease were assessed by crossing six single-cross (SC) commercial hybrids in a 2 × 4, line × tester mating design. Two promising SC hybrids, 'Radhika' and 'SVOK-1408', could be recommended for BYVMV disease at hot spot regions. Most traits exhibited non-additive gene action, indicating heterosis breeding as an excellent approach to improve traits. Two genitors among SC hybrids, 'Radhika' and 'Anushri', were identified based on GCA effects and mean performance. These could be utilized for subsequent breeding. In double-cross (DC) hybrids, the percent disease index of BYVMV had the strongest desirable heterotic effect. This was followed by pod yield plant^{-1}, total dietary fibre content of pod, pod length, pod weight, number of pods plant^{-1}, and pod diameter. Commercial utilization of DC hybrids "Radhika × Bindu" and "SVOK-1408 × Anushri" ~~should~~ could be beneficial following multilocational screening in tropics and subtropics. High-yielding DC hybrids, resistant to BYVMV disease, could be utilized in segregating generations, and potential breeding strategies have been addressed to find multiparent advanced generation intercross (MAGIC) populations.

Keywords: Breeding strategy, heterosis, MAGIC population, single cross hybrid

INTRODUCTION

Okra [*Abelmoschus esculentus* (L.) Moench] has gained significance within the realm of vegetables and commands a significant share of 60% among fresh vegetables in global export market (Villacis *et al.*, 2024). Alongside its culinary appeal, okra is renowned for its medicinal properties, which have earned it the well-deserved title of the "Perfect Villager's Vegetable" in developing nations. Despite its excellent nutritional value, market acceptance, and wide range of genetic variability, the average productivity of okra in India (12 t ha^{-1}) lags far behind other high okra-producing countries (Nigeria, Guyana, Mali, Sudan, etc.). In the Indo-Gangetic plains, the primary threat to the cultivation of okra is the high prevalence of virus disease bhindi yellow vein mosaic Virus (BYVMV) (Seth *et al*., 2017). Depending on the stage of infection, it can cause yield loss up to 94% (Venkataravanappa *et al*., 2013). BYVMV infects the crop at every growth stage. To date, no cultivated okra varieties/hybrids have developed a reliable source of resistance to viral infections. However, several wild okra species, including *Abelmoschus crinitus*, *A. angulosus* var. *grandiflorus*, and *A. manihot*, possess dependable and stable sources for resistance to this virus (Seth *et al*., 2017). Crossability between cultivated and wild species is challenging due to polyploidy in nature. The lack of pre-breeding lines with resistance to BYVMV disease necessitates further study to develop new, high-yielding varieties that exhibit reliable BYVMV resistance while maintaining suitable fruit quality.

Okra is a strong candidate for heterosis because of its high fruit setting percentage, good seed density fruit^{-1}, and relative ease of emasculation. Various researchers have extensively studied heterosis for yield, quality traits, and their components in okra (Hadiya *et al.*, 2018; Yadav *et al.*, 2018; Katiyar *et al.*, 2020; Chaudhary *et al.*, 2023). In okra, line × tester analysis is a useful method for identifying suitable genitors, estimating parent performance in crosses, and measuring heterosis in crop plants (Kempthorne, 1957). Double-cross (DC) okra hybrids with economic potential can be created by allowing recombination of genetic variability through line × tester crossings. These hybrids develop better experimental genotypes than commercial F_1s. Utilizing F_1's as parents can be advantageous in producing high-yielding, high-quality DC hybrids with resistance to BYVMV disease. Besides providing a potential segregating generation, the DC hybrids that will be derived from multiple parents can be further used for advanced breeding programmes such as multiparent advanced generation intercross (MAGIC) (Dominguez *et al*., 2025). It is possible to produce significant variation and raise the likelihood of generating segregants with a large gene pool and genetic base by involving several cross-combinations of four or more genitors (Roy *et al*., 2023).

Isolation of transgressive segregants is predicted if DC hybrids perform better and satisfy all breeding objectives. The base population of self-pollinating crops can be improved by crossing a large number of parents (Samineni *et al.*, 2021). There has been a lot of interest in utilising multi-parent experimental populations to study quantitative features and develop new recombinants for the improvement of plants (Huang *et al.*, 2015). Although MAGIC populations can be difficult to manage and need a lot of resources, they have developed into useful resources for next-generation mapping. For their low population structure, high genetic diversity, and recombination, these populations are exceedingly productive. The majority of research on heterosis manifestation and combining ability was on SC F_1's with either pure lines or inbred parents. Utilizing SC F_1's as a parent, the present study aimed to evaluate their potential to produce superior and high-yielding BYVMV disease-resistant DC hybrids to frame advanced breeding strategies for the genetic improvement of important horticultural traits in okra. This was done in order to create elite inbred recombinant okra lines.

MATERIALS AND METHODS

Planting materials

The study was conducted at the Bidhan Chandra Krishi Viswavidyalaya Research Farm in Kalyani, West Bengal (India) which is located at a mean sea level of 9.75 m and situated at latitudes 23.50° N and longitudes 89° E. Six single-cross (SC) hybrids that are sold commercially: 'Radhika' [Advanta India, Hyderabad], 'SVOK-1408' [Seminis (Monsanto Holdings Pvt. Ltd.), Telangana], 'Singham' [Nunhems India Pvt. Ltd., Telangana], 'Anushri' [Known-You-Seed (India) Pune, Maharashtra], 'Bindu' [Nuziveedu Seeds Ltd, Telangana], 'OH-517' [Syngenta India, Pune, Maharashtra] constituted the initial planting materials. The selection of these hybrids was based on their potential for high yield, tolerance to BYVMV disease, good pod quality and increased acceptance among okra growers in Eastern India and other tropical regions, which are thought to be the hot-spots of BYVMV disease (Jamir *et al.,* 2020).

Field experiments

Pre-soaked as well as thiram-treated (3 g kg^{-1}) seeds of 6 SC hybrids were sown in well-prepared crossing blocks (3.0 × 3.0 m) at plant spacing of 60 cm × 30 cm during spring-summer season 2022. Cow dung manure at 5 t ha^{-1} and 120 N: 60 P: 60 K kg ha^{-1} was applied. One-third of N, full P, and full K were added as basal dose, while the remaining two-third N was applied 30 days after seed sowing and during flowering stage (Chattopadhyay *et al.*, 2007). A Line × Tester mating design involving 'Radhika' and 'SVOK-1408' as lines, and 'Singham', 'Anushri', 'Bindu' and 'OH-517' as testers was employed to generate eight DC hybrids. Lines were selected based on their comparatively higher yield and better BYVMV disease tolerance, and the testers were selected based on superior pod qualities (smooth, less pubescent and pointed tip). Hybridization of SC hybrids was done as per methods described by Seth *et al*. (2017). The 35-day-old mature pods were harvested for seed collection. After being dried, hybrid seeds were kept in desiccators to be sown the following season. The trial was conducted in a randomized complete block design with three replications involving eight DC hybrids and six SC hybrids during the 1st week of August, 2022, to assess and compare the performance of SC and DC hybrids. Each genotype was allocated a plot with dimensions of 3.0 m in length and width. For each DC and SC hybrid, 50 plants $plot^{-1}$ were maintained with plant spacing of 60 cm x 30 cm. For raising good crops, a standard set of practices was used (Chattopadhyay *et al.*, 2007).

Observations recorded

Plant height (cm), days to 1st flowering, number of branches $plant^{-1}$, days to 50% flowering, internodal length (cm), pod length (cm), pod diameter (cm), number of seeds pod^{-1}, number of pods $plant^{-1}$, pod weight (g) and pod yield $plant^{-1}$ (g) were measured on 15 randomly chosen plants from every plot in each replication. Pods were harvested manually on every alternate day at the marketable maturity stage (7 days after anthesis). Total dietary fibre (mg g^{-1}) content of pods was estimated as per the method of Xavier *et al*. (2019).

Disease symptoms and the extent of BYVMV were recorded from 30 days after sowing (DAS) to 90 DAS for every plant of each genotype across each plot. The percent disease index (PDI) was calculated as a percentage of all the plants in a replication using a disease severity scale (0-4) for every single plant through visual examination (Das *et al.*, 2013). PDI was determined as per McKinney and Davis (1925). The resistant/susceptible response of genotypes by PDI was assessed by using a 4-step scale (Bi-hao *et al.*, 2009), with PDI ≤ 10 indicating resistance (R), 10 > PDI ≤ 20 indicating moderate resistance (MR), 21 > PDI ≤ 40 indicating moderate susceptibility (MS), and PDI > 40 indicating high susceptibility (HS). The area under disease progress-curve (AUDPC) was used to calculate the relative spread of BYVMV disease among parents (SC hybrids) and offspring (DC hybrids) (Campbell and Madden, 1990).

Statistical analysis

The mean value of the characters from each genotype in each replication was used for statistical analysis (Gomez and Gomez, 1984). The Line × Tester analysis (Kempthorne, 1957) was useful for evaluating different kinds of gene effects as it gave information on the general and specific combining ability of parents and crosses, respectively. Heterosis was calculated using hybrid's mean values. The extent of heterosis for all SC and DC hybrids was assessed over mid- and better-parents following Hayes *et al.* (1965). The gca effects for both female and male parents and sca effects for each cross-combination were calculated by following ways:

a) gca effect of ith line (g_i) = FH_i – MC (i.e. deviation of line-mean from all hybrid-mean);

b) gca effect of jth tester (g_i) = MM_j – MC (i.e. deviation of tester-mean from all hybrid-mean);

c) sca effect of ijth cross (S_{ij}) = $MH_{ij} – MC – g_i – g_j$ …… ($i \neq j$) (i.e. deviation of each cross-mean from all-hybrid-mean adjusted for corresponding gca effects of parents

d) Standard error of effects: In order to test the significance of gca/sca effects or that of the difference of any two gca/sca effects, the SE and SEd were calculated by following ways:

(i) SE (g_i) = $[(f – 1)\ eMS/mfr]^{5}$ (for lines)

(ii) SE (g_j) = $[(m – 1)\ eMS/\ mfr]^{5}$ (for testers)

(iii) SE (S_{ij}) = $[(f - 1)(m - 1)\ eMS/\ mfr]^{5}$ (for crosses)
(iv) SEd ($g_i - g_k$) = $(2eMS/fr)^{5}$ (between gca effects of two lines)
(v) SEd ($g_j - g_i$) = $(2eMS/fr)^{5}$ (between gca effects of two testers)
(vi) SE ($S_{ij} - S_{jk}$) = $[2eMS\ (m+1)/mr]^{5}$ (SEd for any two sca effects of hybrids with common mother).
(vii) SEd (S_{ij} - Sk_j) = $[(2eMS\ (f+1)/fr]^{5}$ (SEd for any two sca effects of hybrids with common male parents).

The additive and non-additive genetic variances were estimated from the combining ability components as follows:

$\sigma^2 a$ (additive) = $2\sigma^2 g$

where, $$\sigma_g^2 = \frac{1}{n-1}\sum g_1 = \frac{Mg-M'e}{(n+2)}$$

$\sigma^2 na$ (non-additive) = $\sigma^2 s$

where, $$\sigma^2 s = \frac{2}{n(n-1)}\sum_i \sum_i S_{ij} = Ms - M'e$$

and $M'e = \sigma^2 e$

Phenotype variance = $\sigma^2 p$

$\sigma^2 p = 2\sigma^2 g + \sigma^2 s + \sigma^2 e = \sigma^2 a + \sigma^2 na + \sigma^2 e$

Statistical analyses for combining ability and heterosis were done using the analytical software Indostat version 8.6.

RESULTS AND DISCUSSION

The analysis of variance of SC and DC hybrids using RCBD showed significant differences in the majority of traits examined, except the branches plant^{-1}, pod weight, and number of seeds pod^{-1} (Table 1). These radically different SC hybrids offer hope for the development of promising DC hybrids. The top three characters with highest variation were pod yield plant^{-1}, total dietary fibre, and plant height (mean sum of squares for hybrids), indicating a broad range of variation in these specific variables.

Table 1: ANOVA for 14 quantitative characters of double-cross okra hybrids

Source of variation	Mean sum of squares		
	Replication	Genotypes	Error
Degrees of freedom	2	13	26
Plant height (cm)	100.92	90.07*	33.64
No. of branches plant^{-1}	1.35	0.40	0.56
Internodal length (cm)	0.64	1.73**	0.59
Days to 1st flowering	1.35	6.54**	1.89
Days to 50 % flowering	2.00	8.90**	1.51
Pod length (cm)	0.21	4.58**	0.12
Pod diameter (cm)	0.20	0.64**	0.14
No. of pods plant^{-1}	0.73	6.29**	1.04
Pod weight (g)	0.26	0.94	0.21
No. of seeds pod^{-1}	2.88	45.40	23.26
Pod yield plant^{-1} (g)	12.65	1533.35**	219.58
Days to 1st appearance of YVMV disease	8.64	22.03**	4.05
PDI at 90 DAS (%)	0.44	3.10**	0.19
Total dietary fibre in pod (mg g^{-1})	3.96	242.94**	0.83

*,** Significant at 0.05 and 0.01 level of probability, respectively.

Performance of SC hybrids

The mean values of 14 characters measured in 6 SC hybrids grown in the Gangetic plains of West Bengal are given in Table 2. Plant height showed significant variation. SC hybrids took different time to produce 1st flower in 50% of the population. Radhika exhibited early flowering followed by SVOK-1408 and OH-517. On the other hand, Bindu showed late flowering. Pod length and diameter did not significantly vary among the SC hybrids. The SC hybrids showed no significant variations in average weight of pods and number of seeds pod^{-1}. There was significant heterogeneity in pod yield plant^{-1}. The

Table 2: Mean performance of 6 single cross hybrids as parents for different quantitative characters in okra

Single cross hybrid	PH[a]	NBPP	IL	DFF	D50F	PL	PD	NPPP	PW	NSPP	PYPP	DFA-YVMV	PDI-90 DAS	TDF
Raadhika	135.00	3.33	8.03	35.33	39.67	10.67	1.57	14.67	10.90	47.00	159.83	41.67	8.84	71.38
SVOK 1408	125.33	2.67	7.96	36.33	41.67	11.01	1.57	13.67	10.80	45.67	147.47	40.00	9.25	68.60
Singham	138.66	2.33	9.50	37.00	42.00	10.54	1.51	12.33	10.83	40.67	133.53	39.33	12.54	61.37
Anushri	131.33	3.00	8.03	37.00	42.00	10.84	1.54	12.33	10.56	43.00	130.40	37.33	12.84	56.12
Bindu	126.67	2.33	7.53	38.33	43.33	10.57	1.52	11.67	10.80	44.33	126.27	38.67	12.52	55.91
OH 517	134.67	3.33	7.56	37.66	41.67	10.87	1.54	12.67	10.36	39.67	131.37	38.33	11.63	60.64
Mean	131.94	2.83	8.10	36.94	41.72	10.75	1.54	12.89	10.71	43.39	138.15	39.22	11.27	62.34
$C.D_{0.05}$	8.50	NS	1.18	1.63	1.72	NS	NS	1.13	NS	NS	14.84	NS	0.42	1.24
CV (%)	4.23	15.38	9.61	2.90	2.71	2.82	6.80	5.74	2.94	9.45	7.07	5.04	2.46	1.31

[a]PH = Plant height (cm); NBPP = No. of branches plant^{-1}; IL = Internodal length (cm); DFF = Days to 1st flowering; D50F = Days to 50% flowering; PL = Pod length (cm); PD = Pod diameter (cm); NPPP = No. of pods plant^{-1}; PW = Pod weight (g); NSPP = No. of seeds pod^{-1}; PYPP = Pod yield plant^{-1} (g); DFA-BYVMV = Days to first appearance of BYVMV; PDI-90 DAS = PDI at 90 DAS (%); TDF = Total dietary fibre content of pod (mg g^{-1}).

incidence of BYVMV disease was observed late in Radhika as compared to SVOK-1408. Radhika exhibited lowest disease severity as indicated by per cent disease index (PDI), followed by SVOK-1408 (Fig. 1). These two SC hybrids showed promising resistance to the disease (Bi-hao *et al.*, 2009), while the other hybrids showed moderate resistance. The total dietary fibre in pods varied widely. Radhika and SVOK-1408 are the two potential SC hybrids based on their performance in the Gangetic plains of West Bengal. The genetic differences observed among high-yielding and BYVMV-resistant SC hybrids hold potential significance for breeding programs. The variability resulting from the hybridization of contrasting hybrids can be harnessed to obtain desirable recombinants in future.

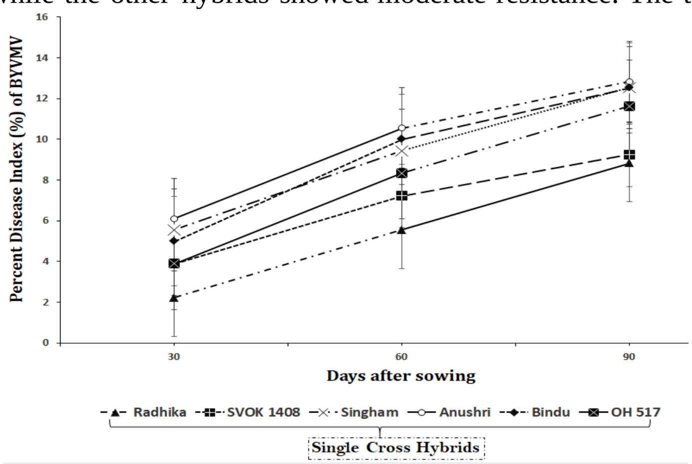

Fig. 1: Screening of single-cross (SC) okra hybrids against BYVMV disease

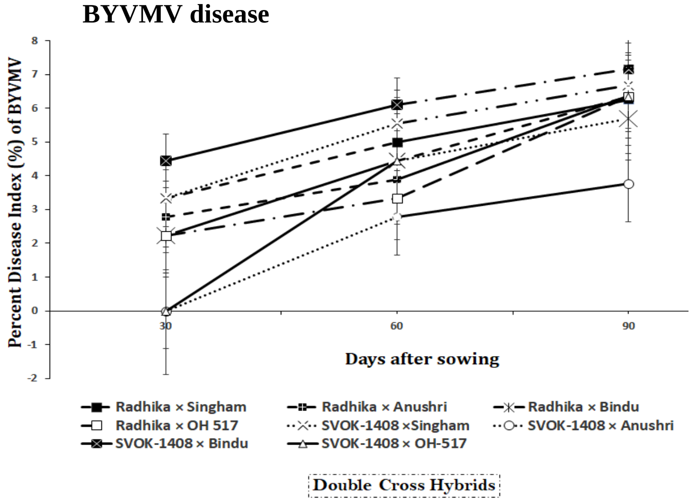

Fig. 2: Screening of double-cross (DC) okra hybrids against BYVMV disease

Performance of DC hybrids

The mean values for 14 different traits observed in 8 DC hybrids, generated through line × tester crosses, are given in Table 3. There were no significant variations in the internodal length and number of branches plant^{-1}. The DC hybrid SVOK-1408 × Anushri exhibited the shortest duration to produce 1st flower. The earliest flowering was observed in SVOK-1408 × Anushri, followed by Radhika × Bindu. There were significant variations in pod length and diameter among DC hybrids. The average pod weight did not show any significant variations among DC hybrids. Among DC hybrids, pod yield plant^{-1} showed wide variation, highest in Radhika x Anushri. The appearance of BYVMV disease was delayed in SVOK-1408 × OH-517. The PDI values varied significantly among different DC hybrids. The lowest disease severity was observed in SVOK-1408 × Anushri, followed by Radhika × Bindu (Fig. 2). All DC hybrids exhibited resistant disease reactions (Bi-hao *et al.*, 2009). Evaluating DC hybrids for variables like yield, pod quality, and disease severity can reveal important information about the biological mechanisms involved, and could produce new alleles for specific breeding efforts.

Table 3: Mean performance of 8 double-cross hybrids for different quantitative characters in okra

Double cross hybrid	PH[a]	NBPP	IL	DFF	D50F	PL	PD	NPPP	PW	NSPP	PYPP	DFA-YVMV	PDI- 90 DAS	TDF
Raadhika × Singham	127.33	3.00	6.60	35.33	39.00	12.77	1.48	15.33	11.57	50.33	177.36	41.33	6.25	77.07
Raadhika × Anushri	139.67	2.67	7.27	35.67	39.33	12.78	1.49	15.33	11.73	53.67	179.91	42.33	6.36	75.58
Raadhika × Bindu	140.33	2.33	6.63	33.67	38.00	13.62	1.61	16.00	12.13	48.00	194.13	45.67	5.68	82.52
Raadhika × OH 517	123.33	2.67	6.90	35.67	39.33	12.71	1.57	14.67	11.60	45.67	170.13	41.67	6.33	77.68
SVOK-1408 ×Singham	128.67	2.33	7.47	36.33	40.00	12.94	1.49	14.67	11.47	43.67	168.18	46.33	6.67	75.62
SVOK-1408 × Anushri	132.33	2.33	6.90	32.67	37.33	13.95	1.52	16.33	11.33	49.00	185.11	44.33	3.77	81.39
SVOK-1408 × Bindu	127.33	2.67	7.03	35.33	39.00	12.77	1.57	14.67	14.67	50.33	171.11	40.33	7.15	75.35
SVOK-1408 × OH-517	132.33	3.00	7.07	35.67	39.67	12.39	1.54	14.33	14.33	47.33	172.96	39.67	6.34	74.74
Mean	130.72	2.55	7.00	34.89	38.89	13.06	1.55	15.11	12.59	47.33	176.94	43.00	5.99	77.88
$CD_{0.05}$	6.25	NS	NS	1.83	1.43	0.42	0.04	1.33	NS	4.86	2.54	1.96	0.53	0.76
CV (%)	3.21	21.60	6.75	3.52	2.48	2.20	1.58	5.95	3.68	6.77	7.94	3.10	5.86	0.66

[a]PH = Plant height (cm); NBPP = No. of branches plant^{-1}; IL = Internodal length (cm); DFF = Days to first flowering; D50F = Days to 50% flowering; PL = Pod length (cm); PD = Pod diameter (cm); NPPP = No. of pods plant^{-1}; PW = Pod weight (g); NSPP = No. of seeds pod^{-1}; PYPP = Pod yield plant^{-1} (g); DFA-BYVMV = Days to first appearance of YVMV; PDI-90 DAS = PDI at 90 DAS (%); TDF = Total dietary fibre content of pod (mg g^{-1}).

Comparing SC vs DC hybrids

DC hybrids consistently outperformed SC hybrids for the majority of traits (Table 4). The utilization of double cross hybrids significantly improved various horticultural traits in okra, such as pod weight, diameter, and length, number of seeds pod^{-1}, pod yield plant^{-1}, total dietary fibre content, and resistance to BYVMV disease. However, these methods did not yield significant improvements in intermodal length, plant height, and the number of branches plant^{-1}. In addition, pod yield plant^{-1} and total dietary fibre content in pods showed wide variation. DC hybrids outperformed SC hybrids in terms of disease severity, pod yield, and quality.

Table 4: Mean performance of 6 single-cross (SC) and 8 double-cross (DC) hybrids for different quantitative characters in okra

Characters	Single cross Hybrids	Double cross hybrids	% increase (+) or decrease (−) of traits
Plant height (cm)	131.94	130.72	−0.92
No. of branches plant^{-1}	2.83	2.55	−9.89
Internodal length (cm)	8.10	7.00	−13.58
Days to 1st flowering	36.94	34.89	−5.55
Days to 50 % flowering	41.72	38.89	−6.78
Pod length (cm)	10.75	13.06	+21.49
Pod diameter (cm)	1.54	1.55	+0.65
No. of pods plant^{-1}	12.89	15.11	+17.22
Pod weight (g)	10.71	12.59	+17.55
No. of seeds pod^{-1}	43.39	47.33	+9.08
Pod yield plant^{-1} (g)	138.15	176.94	+28.07
Days to 1st appearance of YVMV disease	39.22	43.00	+9.64
PDI at 90 DAS (%)	11.27	5.99	−46.85
Total dietary fibre content of pod (mg g^{-1})	62.34	77.88	+24.92

The range of AUDPC at 90 DAS varied greatly between SC and DC hybrids (Fig. 3). The AUDPC values were higher in moderately resistant group (> 482.77) and lower in resistant group (≤ 420). Utilising AUDPC values has an advantage over using a single severity evaluation since it reveals disease progression over the entire developmental phase (Seth *et al*., 2017). Campbell and Maddan (1990) claimed that AUDPC uses multiple evaluation rather than transformation, is simple to calculate and yields a more accurate phenotypic evaluation. The genotype becomes more sensitive as its AUDPC increases. In this study, AUDPC was used to assess the condition's cumulative progression. The findings showed a modest cumulative disease progression in the resistant genotype, with notable distinctions between the resistant and moderately resistant groups.

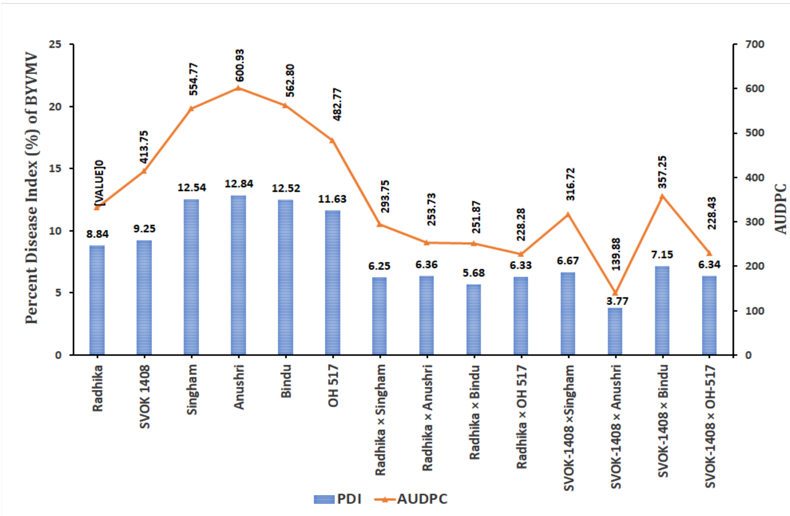

Fig. 3: Disease incidence (%) and AUDPC of okra genotypes against BYVMV disease

Gene action for different characters

Under the line × tester analysis, the main requirements for quick genetic assaying of the test genotypes are the general and specific combining ability (Table 5). These statistics seem to be exploratory in nature because it is unable to assess the significance of the variation for gca and sca derived from the line × tester design. Except for internodal length and pod weight, the gca and sca variances revealed a significant range of variation for each character. Since okra is a self-pollinating crop, the dominance variance (α^2H) and additive variance (α^2D) could be computed from the gca and sca variances at F = 1. The prediction states that $\alpha^2D = 2\ \alpha^2gca$ and $\alpha^2H = \alpha^2gca$. These estimates of additive and non-additive variance components provide a broad insight into the genetic influence of the traits. By using the predictability ratio, as suggested by Baker (1978), the relative importance of additive and non-additive genetic effects on the characteristics can be evaluated. While a ratio below 0.5 reveals a non-additive gene effect, a predictability ratio near unity (above 0.8) demonstrates a predominant additive gene effect on a particular characteristic.

Table 5: Estimates of component of variance for different quantitative characters in okra

Component of genetic variance	PH[a]	NBPP	IL	DFF	D50F	PL	PD	NPPP	PW	NSPP	PYPP	DFA-YVMV	PDI-90 DAS	TDF
α^2 GCA	4.05	0.05	0.03	0.02	0.03	0.03	0.04	0.02	0.005	0.17	1.13	0.20	0.14	1.26
α^2 D (2 α^2 GCA)	8.10	0.10	0.06	0.04	0.06	0.06	0.08	0.04	0.010	0.34	2.26	0.40	0.28	2.52
α^2 H (α^2 SCA)	35.54	0.06	0.06	5.97	0.51	1.29	1.32	0.13	0.02	2.41	8.13	8.89	1.44	14.35
Predictability ratio $\alpha^2 D/(\alpha^2 H+\alpha^2 D)$	0.19	0.62	0.53	0.03	0.15	0.16	0.05	0.28	0.33	0.12	0.39	0.04	0.17	0.15

[a]PH = Plant height (cm); NBPP = No. of branches plant^{-1}; IL = Internodal length (cm); DFF = Days to 1st flowering; D50F = Days to 50% flowering; PL = Pod length (cm); PD = Pod diameter (cm); NPPP = No. of pods plant^{-1}; PW = Pod weight (g); NSPP = No. of seeds pod^{-1}; PYPP = Pod yield plant^{-1} (g); DFA-BYVMV = Days to 1st appearance of BYVMV; PDI-90 DAS = PDI at 90 DAS (%); TDF = Total dietary fibre content of pod (mg g^{-1})

With the exception of the number of branches plant^{-1}and intermodal length, which were regulated by both additive and non-additive gene effects, the predictability ratio showed that non-additive gene action predominated in controlling all of the characters under study (Table 5). The majority of traits are controlled by non-additive gene action, which highlights the function of cross-pollination in moulding these traits over evolution and shows how dependent they are on heterozygous loci. Breeding for heterosis would be a good way to enhance these qualities. The results are consistent with Seth *et al.* (2016) regardless of the parental lines and biometrical techniques followed For characters like internodal length and the number of branches plant^{-1}, a population improvement strategy that uses mass selection with simultaneous random mating or diallel selective mating (Redden and Jensen, 1974) or restricted recurrent selection through intermating desirable segregates and then selecting (Shende *et al.*, 2012) could harness both additive and non-additive gene actions. These outcomes are consistent with the report by Jindal *et al*. (2009) in terms of the number of branches plant^{-1}.

Effects of combining ability

The gca effects for 14 quantitative traits of parental testers and lines employed in the study (Table 6) revealed that for every characteristic, taken into consideration, the gca effects varied. No parent consistently demonstrated a good combining ability for all the characters. The gca effect in the desired direction was highest in Anushri out of the six parental SC hybrids for four traits: pod yield plant^{-1}, pod length, total dietary fibre content, and the percent disease index (PDI) of BYVMV at 90 days after sowing (DAS). With regard to the pod yield plant^{-1} and the PDI of BYVMV at 90 DAS, Radhika

Table 6: Estimates of general combining ability (gi) effects in 6 SC hybrids as parents over 8 DC hybrids

Characters	Raadhika	SVOK−1408	Singham	Anushri	Bindu	OH−517	SE(gi) of lines	SE(gi) of testers
Plant height (cm)	1.25 (135)[a]	−1.25 (125.33)	−3.42 (138.67)	4.59 (131.33)	2.42 (126.67)	−3.59 (134.67)	2.37	3.35
No. of branches plant^{-1}	0.04 (3.33)	−0.04 (2.67)	0.04 (2.33)	−0.12 (3.00)	−0.13 (2.33)	0.21 (3.33)	0.31	0.43
Internodal length (cm)	−0.13 (8.03)	0.13 (7.97)	0.05 (9.5)	0.10 (8.03)	−0.15 (7.53)	0.00 (7.57)	0.31	0.45
Days to 1st flowering	0.04 (35.33)	−0.04 (36.33)	0.79 (37)	−0.88 (37.00)	−0.54 (38.33)	0.63 (3767)	0.56	0.79
Days to 50% flowering	−0.04 (39.67)	0.04 (41.67)	0.54 (42)	−0.62 (42.00)	−0.46 (43.33)	0.54 (41.67)	0.5	0.71
Pod length (cm)	−0.02 (10.67)	0.02 (11.00)	−0.14 (10.54)	0.37* (10.85)	0.21 (10.57)	−0.44** (10.87)	0.14	0.2
Pod diameter (cm)	0.05 (1.57)	−0.05 (1.57)	−0.69** (1.51)	−0.67** (1.55)	0.98** (1.52)	−0.62** (1.55)	0.16	0.28
No. of pods plant^{-1}	0.17 (14.67)	−0.17 (13.67)	−0.17 (12.33)	0.67 (12.33)	0.17 (11.67)	−0.67 (12.67)	0.41	0.59
Pod weight (g)	0.06 (10.90)	−0.06 (10.8)	−0.18 (10.83)	−0.16 (10.57)	0.20 (10.8)	0.14 (10.37)	0.19	0.26
No. of seeds pod^{-1}	0.92 (47.00)	−0.92 (45.67)	−1.5 (40.67)	2.83 (43.00)	0.67 (44.33)	−2.00 (39.67)	1.97	2.78
Pod yield plant^{-1} (g)	3.94** (159.83)	−3.94* (147.47)	-4.34** (133.53)	5.16** (130.40)	5.06** (126.27)	-5.88** (131.37)	1.05	1.56
Days to 1st appearance of YVMV disease	0.04 (41.67)	−0.04 (40)	1.12 (39.33)	0.62 (37.33)	0.29 (38.67)	−2.04* (38.33)	0.82	1.16
PDI at 90 DAS (%)	-0.90** (8.84)	0.90** (9.25)	0.39* (12.5)	−1.00** (12.8)	0.35* (12.5)	0.27 (11.6)	0.16	0.23
Total dietary fibre in pod (mg g^{-1})	0.72* (71.38)	−0.72* (68.6)	-1.15** (61.37)	0.99* (56.12)	1.44** (55.91)	-1.29** (60.64)	0.37	0.53

*,** Significant at 0.05 and 0.01 level of probability, respectively.

[a] Figures in parentheses in bracket indicate *per se* performance.

demonstrated notable GCA effects in the intended direction. Additionally, Bindu demonstrated a GCA effect on pod yield plant^{-1}. Radhika recorded the highest individual pod yield plant^{-1}, followed by Anushri (Table 6). Anushri exhibited the lowest severity of BYVMV disease, followed by Radhika. Thus, the two SC hybrids, Radhika and Anushri, showed promising combining abilities in terms of their GCA effects. Future breeding projects can use these two combiners to create high-yielding DC hybrids with desired BYVMV disease tolerance.

The sca effect was estimated for 14 traits in 8 crosses. Pod yield plant^{-1}, total dietary fibre content, and the percentage PDI of BYVMV at 90 DAS all demonstrated notable sca effects in the preferred direction in 2 DC hybrids (Table 6). Radhika × Bindu was the DC hybrid that showed significant sca effects in the preferred direction for pod length, total dietary fibre content, BYVMV disease tolerance, and pod yield plant^{-1}. Additionally, the double cross SVOK-1408 × Anushri showed substantial sca effects in the intended direction for pod length, total dietary fibre content, days to first manifestation of BYVMV disease, PDI of BYVMV at 90 DAS and pod yield plant^{-1}. Radhika × Bindu and SVOK-1408 × Anushri were identified to be good specific combiners for a number of horticultural traits based on their individual performance and sca effects.

Along with their individual *per se* (mean) for various qualities, the comparative potential of parents was evaluated with respect to their gca effects as parents of SC hybrids (gi) and sca effects of DC hybrids (sij). The aim was to identify parents and crosses with favourable combining abilities for the traits under consideration. For all of the characters studied, no SC hybrid performed effectively as a general combiner. When crossed with other hybrids, the most often occurring high-producing DC hybrids with significant resistance to BYVMV disease were developed by SC hybrids Radhika and Anushri, making them the most promising combiners. According to Fasahat *et al.* (2016), the parents having high gca impact are more adaptive and have fewer environmental influences. Superior attribute parents often fail to pass on their traits to their children (Sharma *et al.*, 2013); hence, combining ability assessment is more reliable than line performance average. Previous research utilized different parents but comparable environmental conditions found positive, substantial gca impacts on pod yield plant^{-1} as well as significant negative GCA effects on PDI of BYVMV (Seth *et al.*, 2016). Similarly, no DC hybrid proved to be an effective specific combiner for all of the studied characters. Radhika × Bindu and SVOK-1408 × Anushri are two excellent specific combiners that also include one parent being a good general combiner for pod yield plant^{-1} and other important horticultural traits. This suggests that these crosses should be further exploited in segregating generations to find superior lines. Under comparable climatic conditions, prior research has documented strong sca effects among SC hybrids in the preferred direction for all economically important traits of okra, such as pod yield plant^{-1} and severity of BYVMV disease (Seth *et al.*, 2016).

Although the high cost of seed production may prevent the direct commercialisation of the promising DC hybrids found in this study, SVOK-1408 × Anushri and Radhika × Bindu, they can still be used in segregating generations in order to isolate MAGIC populations for future breeding programs focused on developing BYVMV disease-resistant varieties. MAGIC populations have been successfully implemented in chickpea (Samineni *et al.*, 2021) and tomato (Campanelli *et al.*, 2019).

Manifestation of heterosis for various traits

The heterosis over better-parent (heterobeltiosis) manifests in 8 DC hybrids for various quantitative characters (Table 7). For internodal length, plant height, number of branches plant^{-1}, pod diameter, and number of seeds pod^{-1}, none of the DC hybrids showed any noticeable heterosis as compared to the better-parent. Days to 50% flowering and days to first flowering would both benefit from negative estimations regarding heterosis, which show early hybrid maturity. For flowering traits, Radhika × Bindu and SVOK-1408 × Anushri showed highest negative estimates regarding heterosis over better parent. All DC hybrids exhibited significant desired heterobeltiosis for pod length, with maximum in Radhika × Bindu and SVOK-1408 × Anushri. SVOK-1408 × Anushri and SVOK-1408 × OH-517 showed the highest, significant heterobeltiosis for the number of pods plant^{-1} and pod weight, respectively.

Table 7: Estimates of heterobeltiosis, SCA effects, and the type of combinations for different quantitative characters of DC hybrids in okra

Character	Promising heterotic cross combinations in desired direction	Significant heterobeltiosis (%)	Range of heterobeltiosis (%)	SCA effects	Type of cross combinations*
Days to 1st flowering	Raadhika × Bindu	−12.17 **	−12.27 to −1.80%	−0.87(33.67)	L × L
	SVOK−1408 × Anushri	−11.71 **		−1.46(32.67)	L × L
Days to 50 % flowering	Raadhika × Bindu	−12.31 **	−12.31 to −4.76%	−0.46(38.00)	L × L
	SVOK−1408 × Anushri	−11.11 **		−1.04(37.33)	L × L
Pod length (cm)	Raadhika × Bindu	27.61 **	12.60 to 27.61%	0.44*(13.62)	L × L
	SVOK−1408 × Anushri	26.75 **		0.56*(13.95)	L × L
No. of pods plant^{-1}	SVOK−1408 × Anushri	19.51**	0 to 19.51%	0.67(16.33)	L × L
Pod weight (g)	Raadhika × Bindu	11.31 **	4.94 to 11.73%	0.17(12.13)	L × L
	SVOK−1408 × OH−517	11.73 **		0.29(12.07)	L × L
Pod yield plant^{-1} (g)	Raadhika × Bindu	21.25 *	6.40 to 25.54%	8.36*(194.13)	H × H
	SVOK−1408 × Anushri	25.54 **		5.48*(185.11)	L × L
Days to first appearance of YVMV	Raadhika × Bindu	9.60 *	−0.80 to 15.83%	2.62*(45.67)	L × L
	SVOK−1408 × Singham	15.83 **		2.54*(46.33)	L × L
	SVOK−1408 × Anushri	10.83 *		1.04(44.33)	L × L
PDI[a] at 90 DAS[b] (%)	Raadhika × Bindu	−54.62 **	−70.66 to −42.88%	−0.82**(5.68)	H × L
	SVOK−1408 × Anushri	−70.66 **		−1.21**(3.77)	L × H
Total dietary fibre content (mg g^{-1})	Raadhika × Bindu	15.62 **	5.89 to 18.65%	2.87 **(82.52)	H × H
	SVOK−1408 × Anushri	18.65 **		3.63**(81.40)	L × H

*, ** Significant at P ≤ 0.05 and P ≤ 0.01 level, respectively. SCA = specific combining effect;
*H = significant GCA effect of the parent in the desired direction; L = Non-significant GCA effect;
[a]PDI = Percent disease index; [b]DAS = Days after sowing.

All DC hybrids showed a notable, significant heterobeltiosis in terms of pod yield plant^{-1}. SVOK-1408 × Anushri and Radhika × Bindu showed higher heterobeltiosis compared to other DC hybrids. Positive estimates of heterosis for the days to 1st appearance of BYVMV disease indicate a delayed onset of the disease, which is desirable for obtaining more marketable pods plant^{-1}. For this trait, six DC hybrids showed positive heterosis over superior parent; SVOK-1408 × Singham showed the highest value. Heterosis estimates that are negative are desired for PDI of BYVMV. At 90 days after sowing, all DC hybrids exhibited negative heterosis compared to the better parent for PDI of BYVMV. SVOK-1408 × Anushri and Radhika × Bindu exhibited highest level of negative heterobeltiosis. High dietary fibre content in food plays a pivotal role in controlling gastrointestinal disorders and type 2 diabetes. It is preferable for the total dietary fibre content in okra pods to have a positive estimate of heterosis. The Radhika × Bindu and SVOK-1408 × Anushri hybrids had highest total dietary fibre content in okra pods, whereas all 8 DC hybrids showed positive heterobeltiosis.

Two DC hybrids SVOK-1408 × Anushri and Radhika × Bindu were found most promising in terms of days to 1st flowering, pod yield plant^{-1}, PDI of BYVMV, days to 50% flowering, pod length and total dietary fibre content based on heterobeltiosis manifestation.

Based on gca effects of parents, various heterotic cross combinations were examined, and four different types of combinations were found: H × H, H × L, L × H, and L × L (Table 7). As shown in Table 6, H denotes a parent that has a noticeable gca effect in the preferred direction, whereas L denotes a parent that has a non-significant gca effect.

High heterosis in DC hybrids of okra in present study may result from greater genetic diversity among the parental stocks. Okra pod yield was determined by the combined heterosis of its component traits. The lack of significant heterobeltiosis in most crosses for plant height, internodal length, number of branches plant^{-1}, pod diameter and number of seeds pod^{-1} may be explained by internal cancellation of heterotic components. Internal cancellation of heterosis components could account for the absence of significant heterobeltiosis in the majority of crossings for plant height, internodal length, number of branches plant^{-1}, pod diameter and number of seeds pod^{-1}. Breeders using SC hybrids as parental lines could find this useful in understanding why these traits do not develop. Earlier works using various single cross combinations and mating designs also revealed significant positive heterobeltiosis for pod yield and other economically important traits, and significant negative heterobeltiosis for days to 50% flowering, days to 1st flowering and PDI of BYVMV (Seth *et al.*, 2016).

Blood glucose control, hyperinsulinemia, and plasma lipid content are all improved by consuming a large amount of dietary fiber (DF), primarily the soluble kind, above the recommended limit of the American Diabetes Association (Chandalia *et al.*, 2000). According to a systematic evaluation of cohort studies on DF, the risk of cardiovascular disease was inversely correlated with total dietary fibre intake (Ma *et al.*, 2006). Positive heterosis for total dietary fibre content has also been reported in earlier studies using different parental lines and mating designs (Xavier *et al.*, 2019). H × H type cross combinations, such as Radhika × Bindu, showed both additive and additive × additive interactions for total dietary fibre content and pod yield plant^{-1}. These crosses are of great value since they allow for early generations to fix desired segregants. The H × L type cross combinations, such as Radhika × Bindu for PDI of BYVMV, or L × H type crossings, such as SVOK-1408 × Anushri for total dietary fibre content and PDI of BYVMV, on the other hand, indicate that at least one parent had a strong gca effect. This implies that the poor combiner may have complementary epistatic effects, while the good combiner may mostly have additive effects. Salimath and Bahl (1985) proposed that these two gene actions complement each other to maximise expression. The importance of non-additive gene expression was demonstrated by the considerable sca effects of crosses that fell into the L × L type, such as Radhika × Bindu for days to first flowering, pod length, pod weight, days to 50% flowering, and days to 1st appearance of BYVMV. Non-additive gene action is attributed to the superior performance of these combinations (Bhutia *et al.*, 2015).

A combination of honeycomb designs and pedigree or mass selection in the first segregating generations of two promising DC hybrids (SVOK-1408 × Anushri and Radhika × Bindu) can overcome heterosis in okra, where non-additive gene action is common for controlling most traits (Fig. 4). This approach enhances the effective-ness of selection and ultimately generates superior inbred recombinant lines. Recombinant lines produced from each promising DC hybrid are to be assessed based on a range of desirable traits, such as better yield, earliness, pod quality, and disease severity of BYVM, after all pedigree processes are finished (up to the F_5 generation). Highly productive recombinant lines can be developed by simultaneously selecting individual plants with better yield, suitable pod quality traits, and significant resistance to BYVMV disease.

We proposed another breeding approach to develop the okra S3 MAGIC population (Fig. 5). Following a funnel breeding scheme, a total of 450 individuals of the MAGIC population will be obtained. Initially, we crossed four promising commercial F_1 hybrids, namely SVOK-1408 (AB), Anushri (CD), Radhika (EF), and Bindu (GH), in pairs (ABCD and EFGH). This led to the creation of two double-cross or four-way hybrids, ABCD, as well as EFGH. One hundred and fifty individuals of each of the two four-way hybrids will be inter-crossed using a chain pollination strategy. For double cross hybrids, this technique will ensure a full combination of all the original genomes without selective mating. By following

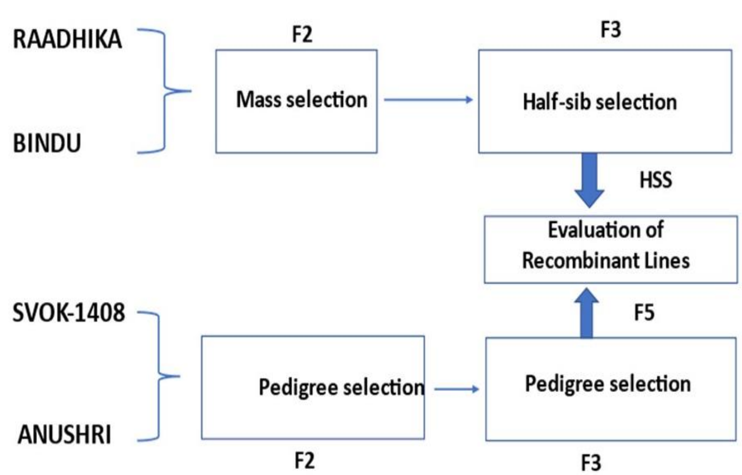

Fig. 4: Combination of honeycomb design and pedigree/mass selection in the initial segregating generations of two promising DC hybrids

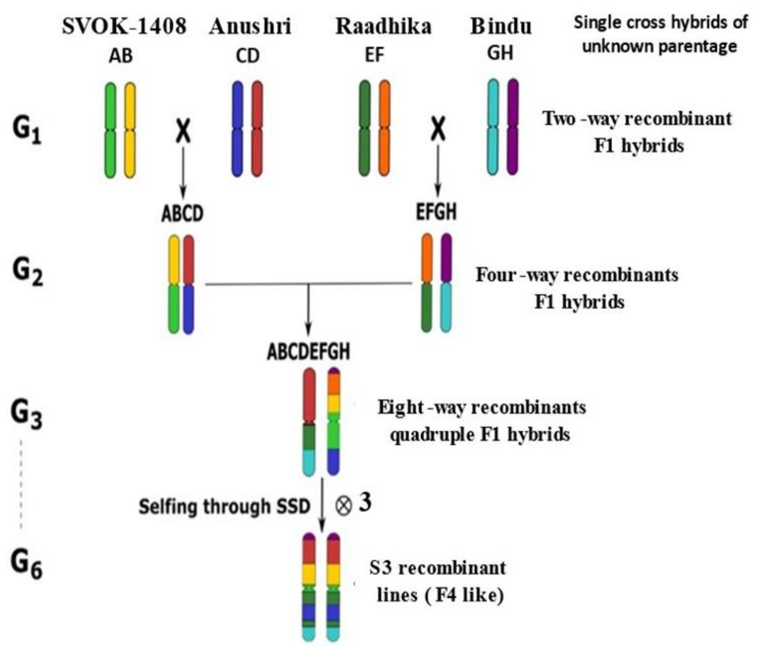

Fig. 5: Representative scheme on the development of MAGIC populations utilizing double-cross hybrids in okra

this approach, we will obtain around 300 quadruple F_1 hybrids. Subsequently, these hybrids will be self-pollinated to generate 450 F_2 populations. In the selection process, we will focus on identifying plants with higher yield potential, better pod quality and resistance to BYVMV disease. Selection will be performed using the single-seed descent approach, starting with the F_2 generation and continuing through subsequent populations up to F_4. By employing this approach, we could able to develop a stable line against BYVMV disease. The resulting MAGIC population in okra can be efficiently employed in future breeding initiatives.

Conclusions: The majority of attributes were controlled by non-additive gene action, which indicated that heterosis breeding would be an effective breeding approach for okra trait improvement. Developing BYVMV-resistant DC hybrids in okra by utilizing commercial SC hybrids, and finding reliable heterotic combiners are important breakthroughs in this study. Two promising DC hybrids, "Radhika × Bindu" and "SVOK-1408 × Anushri" can be employed in segregating generations with suitable breeding strategies to isolate the MAGIC population that can be utilized effectively in future breeding programs. Despite the successful establishment of multi-parent populations in other crops, okra has not yet benefited from such a population. Therefore, the creation of a multi-parent population in okra would be a significant milestone in the field of okra breeding.

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