Agric Res J **60** (4) : 527-532, *August* 2023
DOI No. 10.5958/2395-146X.2023.00076.5

GENETIC EFFECTS ON FRUIT AND SEED TRAITS IN INTRA AND INTER-SPECIFIC HYBRIDIZATION DERIVED POPULATIONS INVOLVING HULL-LESS SEEDED PUMPKIN

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ABSTRACT

Sufficient understanding about genetic composition of the traits associated with yield and quality helps crop breeders to design their breeding program. The goal of this study was to estimate the main genetic effects on fruit and seed traits from crosses involving hulled and hull-less seeded parents. The intraspecific [LGR-121/VSR-5921 (*Cucurbita pepo*)] and interspecific [HLP-36/PVR-1343 (*C. pepo*/*C. moschata*)] hybridization derived six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) were evaluated using generation mean analysis. Significant differences were observed among all six generations for the fruit (3) and seed (5) traits under study. The additive-dominance model assessed through scaling test revealed adequacy only for seed number in intraspecific cross while, seed thickness and 100 seed weight in interspecific cross. Non-allelic interactions with duplicate type of epistasis were observed for remaining traits. - - It was observed - that most of the fruit and seed traits in intra and interspecific crosses expressed epistatic effects. Hence, improvement for these traits requires breeding methods like recurrent selection that can exploit non-additive variation in subsequent generations.

Keywords: *Cucurbita moschata*, *Cucurbita pepo*, Epistasis, Hull-less seed, Generation mean analysis.

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Genus *Cucurbita* consists of many economically important species but *Cucurbita pepo* and *C. moschata* are the two major species cultivated across the globe for their edible fruits and seeds. Pumpkin has been historically bred with a focus on improving yield and quality traits of fruits and seeds alongwith resistance against biotic and abiotic stresses (Dhatt *et al.*,2020). For varietal developmental programmes in pumpkin, most preferred traits for fruits are size, shape and weight along with hull-less seeds. - Hull-less seed trait is highly desirable for edible seed and baking industries as it allows direct utilization of the raw seed and excludes costly de-hulling process. Different seed characteristics such as seed length, seed width and seed size not only determine the seed yield but also affect fruit yield and quality (Paris and Nerson, 2003). Further, fruit size and shape are found to be correlated with seed characteristics in *Cucurbita* species (Nerson *et al.,* 2000; Nerson and Paris, 2001). However, there are no conclusive reports on the gene actions for fruit and seed traits in cucurbits (Guo *et al.,* 2020; Pan *et al.,* 2020).

In India, *C. moschata* is cultivated throughout the year due to high temperature tolerance and availability of virus resistance cultivars but lacks the crucial hull-less seed trait. In comparison, hull-less seeded varieties of *C. pepo* are restricted to spring season due to their sensitivity to high temperature and susceptibility to viral diseases. Therefore, for year round production and availability of fruits and hull-less seeds, both high temperature tolerance and virus resistance should be introgressed into hull-less *C. pepo* genotypes, or hull-less seed trait should be transferred to *C. moschata* genotypes. To develop desirable genotypes having all the required traits, the knowledge about gene(s) governing the traits and their effects is necessary. Concomitantly, information on the genetic control of traits will improve the accuracy of plant selection and reduce breeding time and cost. Genetic effects for various fruit and seed traits have been studied in intra-specific derived *Cucurbita* populations (-Ene *et al.,* 2019; Ketsakul *et al.,* 2020; Davoodi *et al.,* 2021; Hosen *et al.,* 2021). However, interspecific hybrids between *C. pepo* and *C. moschata* had been obtained with limited success and not used extensively- due to crossing barriers and linkage drag in pumpkin improvement programmes (-Kaur *et al.,* 2021). In this investigation, hull-less and hulled lines of *C. pepo* with different fruit traits were hybridized to develop intra-specific populations. Simultaneously, interspecific populations were developed by crossing the hull-less seeded *C. pepo* line with virus resistant line of *C. moschata*. To estimate the gene effects, generation mean analysis is a valuable tool (-Said, 2014; Patel *et al.,* 2021). Considering these facts, this study was devised to

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Date of receipt: 19.01.2022, Date of acceptance: 09.11.2022

understand the gene actions of fruit and seed traits among intra and interspecific crosses consisting of parents with different traits through generation mean analysis.

MATERIALS AND METHODS

Development of populations

The study was carried out at the Vegetable Research Farm, Department of Vegetable Science, Punjab Agricultural University, Ludhiana, India -during 2018 to 2020. The breeding materials for this study comprises of two hull-less seeded *C. pepo* lines (HLP-36 and LGR-121), one hulled line each of *C. pepo* (VSR-5921), and *C. moschata* (PVR-1343). The hull-less lines were intermated to hulled genotypes for generation of intraspecific (LGR-121 × VSR-5921, Cross-I) and interspecific (HLP-36 × PVR-1343, Cross-II) F_1 hybrids. Subsequently, these F_1s were selfed to produce F_2 and backcrossed to their parents P_1 (hull-less) and P_2 (hulled) to develop BC_1 and BC_2, respectively.

Experimental design and crop management

During spring 2020, all six generations including parents (P_1, P_2), first and second filial generations (F_1, F_2), backcrosses with both the parents (BC_1 and BC_2) were grown in a randomized complete block design with three replicates for each cross. Each replicates comprised of 15 plants for each of the parents, F_1, backcross generations and 45 plants for the F_2 generation. Seedlings were transplanted on both sides of beds, spaced 2 m × 60 cm. The standard agronomic practices recommended by PAU, Ludhiana (- were followed for optimum growth and development (Anonymous, 2021).

Data collection

For P_1, P_2, F_1, BC_1 and BC_2 populations of both crosses, data on fruit and seed traits were recorded on ten randomly selected plants per replicate and 30 random plants per replicate were selected for the F_2 population. Fruit weight (FWe) and 100 seed weight (100 SW) were measured in grams (g) with the help of weighing balance (-. Fruit polar diameter (FPD) and fruit equatorial diameter (FED) were measured along the polar and equatorial axis, respectively in centimetres (cm), whereas seed length (SL), seed width (SW), and seed thickness (ST) were measured at the longest, widest and thickest part of the seed, respectively in millimetres (mm) with the help of vernier calliper (-). The number of seeds per fruit (SN) was counted manually.

Statistical analysis

The data obtained for populations of both crosses were assessed for variability and non-allelic interactions. The analysis of variance and mean comparison of the traits were performed using SPSS Software version 22 (IBM, Corp., Armonk, N.Y. USA). To test the presence or absence of epistasis and to analyse the adequacy of the additive-dominance model, scaling test (A, B, C and D) proposed by Jinks and Jones (1958) were employed. These scales are computed by the linear combination of various means of populations involved as follows:

$$A = 2\overline{BC}_1 - \overline{P}_1 - \overline{F}_1,$$

$$B = 2\overline{BC}_2 - \overline{P}_2 - \overline{F}_1,$$

$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2,$$

$$D = 2\overline{F}_2 - \overline{BC}_1 - \overline{BC}_2$$

The significance of each scaling test was estimated using a t-test and respective standard error (SE).

The variance was calculated as: $V(A) = 4V(\overline{BC}_1) + V(\overline{P}_1) + V(\overline{F}_1)$, $V(B) = 4V(\overline{BC}_2) + V(\overline{P}_2) + V(\overline{F}_1)$, $V(C) = 16V(\overline{F}_2) + 4V(\overline{F}_1) + V(\overline{P}_1) + V(\overline{P}_2)$, and $V(D) = 4V\overline{F}_2 + V\overline{BC}_1 + V\overline{BC}_2$ where $V(\overline{P}_1)$ and $V(\overline{P}_2)$ are the mean variance of P_1 and P_2, respectively. $V(\overline{F}_1)$ is the mean variance of the derived progeny (F_1) while $V(\overline{BC}_1)$ and $V(\overline{BC}_2)$ are the mean variances of the backcross of the F_1 with the respective parents, P_1 and P_2. The mean variance of segregating F_2 generation was designated as $V(\overline{F}_2)$. The standard error (SE) was calculated from the square root of the respective variance as: $SE(A) = (VA)^{1/2}$, and Student's *t*-test was computed by dividing the value of the scale test with the SE as $t(A) = A/SE(A)$. A similar procedure was followed to determine the standard errors of B, C, D and their respective *t* values. The calculated *t* value(s) were compared with the tabulated value at 5% and 1% levels of significance. The significance of any of the scales implied the presence of interaction among non-allelic genes, while the non-significance of all the scales deciphered the absence of epistatic interactions (Hayman and Mather, 1955; Kearsey and Pooni, 1996).

Components of generation means

In the determination of gene effects, six generation mean components *viz*., general mean [m], additive [d], dominant [h]; additive × additive [i], additive × dominant [j] and dominant × dominant [h] were computed using the formulae suggested by Jinks and Jones (1958) as follows:

$$[m] = 0.5\overline{P}_1 + 0.5\overline{P}_2 + 4\overline{F}_2 - 2\overline{BC}_1 - 2\overline{BC}_2,$$

$$[d] = 0.5\overline{P}_1 - 0.5\overline{P}_2,$$

$$[h] = 6\overline{BC}_1 + 6\overline{BC}_2 - 8\overline{F}_2 - \overline{F}_1 - 1.5\overline{P}_1 - 1.5\overline{P}_2,$$

$$[i] = 2(\overline{BC}_1 - \overline{BC}_2) - 4\overline{F}_2,$$

$$[j] = 2\overline{BC}_1 - \overline{P}_1 - 2\overline{BC}_2 + \overline{P}_2,$$

$$[l] = \overline{P}_1 + \overline{P}_2 + 2\overline{F}_1 + 4\overline{F}_2 - 4\overline{BC}_1 - 4\overline{BC}_2,$$

For the traits with atleast one significant scaling

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test, all six parameters were explored, whereas when all four scaling tests were non-significant, the gene effect estimation was limited to three *viz*., [m], [d], and [h]. All of these genetic parameters were tested for significance with a t-test following a similar procedure for the calculation of variance and SE.

RESULTS AND DISCUSSION

Variation in means of generations for fruit and seed traits in intra and interspecific populations

The analysis of variance calculated among six generation means for fruit and seed traits revealed significant variability in each cross combination implying the possibility for genetic analysis (Table 1). Significant differences were observed between the two parents for all of the studied traits, except for SW in intraspecific and FPD and 100 SW in the inter-specific cross (Table 2). In the intraspecific cross, FPD, FED, and FWe of hull-less parent (LGR-121) were higher than that of hulled parent (VSR-5921) by 116.99, 171.14, and 34.88% respectively. But in the interspecific cross, FED and FWe of hulled parent (PVR-1343) were greater than the hull-less parent (HLP-36) by 28.44 and 71.86% respectively. Among seed traits, SL of hull-less parents was significantly higher than those of hulled parents but ST was more in hulled parents in both crosses (Table 2). In the intraspecific cross, SN and 100 SW were significantly better in hull-less parent while in an interspecific cross only SW was better in hull-less parent and SN higher than a hulled parent.

The differences were non-significant between F_1 and F_2 for FWe, FPD, FED, SW, ST, SN, and 100 SW in cross-I (intraspecific cross), suggesting additive gene effect governing these traits (Table 2). The F_2 mean was higher than that of the F_1 for SL, indicating a possibility for transgressive segregation. Also, in the interspecific cross (cross-II), differences between F_1 and F_2 mean values were non-significant for FED, SL, SW, ST, SN and 100 SW indicating additive gene effect. For FPD and FWe, F_2 values were significantly lower than F_1 that could be due to interspecific hybridization (Table 2). Further, the, F_1 values for traits such as FPD, FED, SW, SN and 100 SW were statistically similar to better parent LGR-121 while for ST with VSR-5921 among the intraspecific cross, respectively. While for the traits FWe and SL, F_1 values were significantly better than the inferior parent (VSR-5921) but lower than the better parent (LGR-121). In interspecific cross F_1, SL was statistically similar to hull-less parent (HLP-36) and SW and ST were better than the hulled parent (PVR-1343). For traits such as FWe and FED, F_1 was similar with inferior parent (PVR-1343) while for SN and 100 SW F_1 was statistically inferior to both the parents that -could be attributed to fertilization barriers driven by interspecific hybridization.

In cross-I, both backcross populations (BC_1 and BC_2) converged to their respective parents for FWe, FPD, SW, ST, SN and 100 SW. The convergence was complete for BC_1 as all traits were similar with parent LGR-121, but for BC_2 traits such as FED and SL differed significantly from parent VSR-5921 suggesting partial convergence. In cross-II, the means of both the backcrosses for FPD, FED, SL, SW, and ST converged on their respective recurrent parents indicating the complete convergence and effectiveness of backcrossing for improving the traits. For FWe and SN, BC_2 did not converge on their recurrent parent PVR-1343, similarly, for 100 SW, BC_1 suggested partial convergence due to significant differences with recurrent parent (HLP-36). This variability for fruit and seed traits in generations is in accord with the variation

Table 1. Analysis of variance for fruit and seed traits

Source	df	FWe	FPD	FED	SL	SW	ST	SN	100 SW
Cross-I									
Replication	2	520.875	0.859	0.257	0.094	0.075	0.009	37.701	0.713
Generation	5	61373.120*	20.707*	6.245*	5.617*	0.799*	0.231*	595.355*	3.505*
Error	10	478.816	0.847	0.307	0.057	0.115	0.017	115.517	0.303
CV%		5.740	10.240	5.510	1.970	4.450	6.410	9.820	7.180
Cross-II									
Replication	2	2927.667	0.567	0.605	0.005	0.023	0.022	24.740	0.242
Generation	5	126647.500*	4.743*	5.258*	1.274*	1.288*	0.040*	1721.283*	3.098*
Error	10	1245.535	0.932	0.339	0.165	0.107	0.007	59.167	0.206
CV%		4.880	7.880	4.820	3.210	4.470	4.540	7.560	8.160

FWe = Fruit weight per fruit; FPD = Fruit polar diameter; FED = Fruit equatorial diameter; SL = Seed length; SW = Seed width; ST = Seed thickness; SN = Seed number per fruit; 100 SW = Hundred seed weight; * = significant at $p<0.05$.

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Table 2. Comparison of means of the generations derived from intra and interspecific crosses of *Cucurbita*

	Fwe	FPD	FED	SL	SW	ST	SN	100 SW
Cross-I								
LGR-121	508.349^{c}	12.557^{c}	10.999^{bc}	13.711^{d}	7.674^{ab}	1.600^{a}	124.067^{b}	7.738^{b}
VSR-5921	187.489^{a}	5.787^{a}	7.647^{a}	10.332^{a}	6.759^{a}	2.243^{c}	89.767^{a}	5.737^{a}
F_1	445.354^{b}	10.208^{bc}	11.680^{c}	11.382^{b}	7.522^{ab}	2.300^{c}	111.100^{ab}	8.634^{b}
F_2	471.148^{bc}	9.336^{b}	10.842^{bc}	12.333^{c}	7.854^{b}	2.205^{bc}	111.144^{ab}	8.636^{b}
BC_1	464.948^{bc}	10.023^{bc}	9.823^{b}	13.666^{d}	8.341^{b}	1.840^{ab}	124.033^{b}	7.978^{b}
BC_2	209.801^{a}	6.013^{a}	9.468^{b}	11.313^{b}	7.540^{ab}	2.174^{bc}	96.300^{ab}	7.292^{ab}
Cross-II								
HLP-36	644.407^{b}	13.085^{b}	11.155^{a}	13.428^{b}	7.714^{bc}	1.685^{a}	108.500^{b}	6.445^{c}
PVR-1343	1107.485^{d}	12.735^{b}	14.328^{c}	11.677^{a}	6.369^{a}	1.972^{b}	140.033^{c}	6.826^{c}
F_1	643.210^{b}	13.245^{b}	11.190^{a}	13.295^{b}	7.795^{bc}	1.942^{b}	73.867^{a}	4.215^{a}
F_2	502.623^{a}	9.921^{a}	11.072^{a}	12.480^{ab}	8.127^{c}	1.962^{b}	81.522^{a}	5.108^{ab}
BC_1	687.085^{bc}	12.794^{b}	11.646^{ab}	12.711^{ab}	7.115^{ab}	1.814^{ab}	93.933^{ab}	4.814^{ab}
BC_2	752.178^{c}	11.735^{ab}	13.005^{bc}	12.299^{ab}	6.908^{ab}	1.960^{b}	112.233^{b}	6.016^{bc}

FWe = Fruit weight per fruit; FPD = Fruit polar diameter; FED = Fruit equatorial diameter; SL = Seed length; SW = Seed width; ST = Seed thickness; SN = Seed number per fruit; 100 SW = Hundred seed weight. Values with the different letters of the alphabet along each column are significantly different by Tuckey's Honset Significance

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reported in *Cucurbita* germplasm by various authors (Du *et al.,* 2011; Barboza *et al.,* 2012; Liu *et al.,* 2013; Darrudi *et al.,* 2018).

Estimation of scaling tests and gene effects in intra and interspecific crosses

The individual scaling tests were significant for FWe, FPD, FED, SL and SW in both the intra and inter specific crosses indicating inadequacy of additive-dominance model and presence of non-allelic interactions for these traits (Table 3). At least one scaling test was significant for ST and 100 SW in cross-I and for SN in cross-II displaying variability in adequacy of the additive dominance model. The differences in fruit and seed size of the parents involved in the crosses and interspecific hybridization in cross-II that effect the fruit and seed setting could be the reasons for the variation confirmed through the significant scaling tests. Nevertheless, the significant scaling tests indicated the traits were influenced with non-allelic interactions that hindered the progress through normal selection. On the contrary, SN in cross-I, ST and 100 SW in cross-II revealed adequacy of the additive dominance model signifying the absence of epistatic effects. Our results are concurrent with the findings of Davoodi *et al.* (2021), who also observed the inadequacy of additive-dominance model for most of the fruit and seed traits in *Cucurbita* populations.

Table 3. Scaling tests for fruit and seed traits in intra and interspecific crosses of *Cucurbita*

	FWe	FPD	FED	SL	SW	ST	SN	100 SW
Cross-I								
Scale test A	-23.806	-2.720**	-3.034**	2.240**	1.487**	-0.219	12.900	-0.415
Scale test B	-213.240**	-3.970**	-0.390	0.913*	0.798*	-0.194	-8.267	0.214
Scale test C	298.047**	-1.416	1.362*	2.526**	1.939**	0.376	8.544	3.801**
Scale test D	267.546**	2.636**	2.393**	-0.313	-0.173	0.395*	1.956	2.001*
Cross-II								
Scale test A	86.553*	-0.742	0.946*	-1.300*	-1.279**	0.001	5.500	-1.032
Scale test B	-246.338**	-2.510**	0.492	-0.374	-0.349	0.006	10.567	0.991
Scale test C	-1027.821**	-12.624**	-3.575*	-1.773*	2.835**	0.309	-70.178**	-1.267
Scale test D	-434.018**	-4.686**	-2.507**	-0.050	2.232**	0.151	-43.122**	-0.613

FWe = Fruit weight per fruit; FPD = Fruit polar diameter; FED = Fruit equatorial diameter; SL = Seed length; SW = Seed width; ST = Seed thickness; SN = Seed number per fruit; 100 SW = Hundred seed weight; * = significant at $p<0.05$; ** = significant at $p<0.01$. Significance levels are shown based on the t-test compared to table t.

Table 4. Estimates of genetic effects for fruit and seed traits in intra and interspecific crosses of *Cucurbita*

	FWe	FPD	FED	SL	SW	ST	SN	100 SW
Cross-I								
[m]	883.011**	14.445**	14.109**	11.395**	6.871**	2.711**	110.828**	10.739**
[d]	160.430**	3.385**	1.676**	1.690**	0.457**	-0.321**	17.150**	1.001**
[h]	-1209.794**	-16.199**	-10.640**	3.766	3.282*	-1.614*	0.994	-6.309
[i]	-535.092**	-5.273**	-4.786**	0.626	0.346	-0.789**		-4.002*
[j]	189.434**	1.250**	-2.643**	1.327*	0.688	-0.025		-0.629
[l]	772.137**	11.962**	8.210**	-3.779**	-2.631**	1.203*		4.203
Cross-II								
[m]	7.910	3.539	7.728**	12.453**	11.505**	2.130**	38.022	5.410**
[d]	-231.539**	0.175	-1.587**	0.875**	0.672**	-0.144**	-15.767**	-0.191
[h]	1343.550**	15.825**	9.915*	-0.733	-9.802**	-0.482	138.156*	-0.011
[i]	868.036**	9.371**	5.014**	0.099	-4.463**		86.244**	
[j]	332.891**	1.768*	0.454	-0.926	-0.931*		-5.067	
[l]	-708.250**	-6.119**	-6.453**	1.575	6.091**		-102.311**	

FWe = Fruit weight per fruit; FPD = Fruit polar diameter; FED = Fruit equatorial diameter; SL = Seed length; SW = Seed width; ST = Seed thickness; SN = Seed number per fruit; 100 SW = Hundred seed weight; [m] is the mean effect of all generations in a cross, [d], [h], [i], [j], and [l] are the effects of genetic parameters *viz*., additive, dominance, additive × additive epistasis, additive × dominance epistasis and dominance × dominance epistasis, respectively. * = significant at $p<0.05$; ** = significant at $p<0.01$. Significance levels are shown based on the t-test compared to table t.

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The estimation of gene effects was predicted through three or six parameter models (Table 4). The significant [m] value for majority of the traits revealed the statistically different mean values among different generations and implied that unbiased information was generated through first-degree statistics in both the crosses. The perusal of data from cross-I suggested only additive gene effect in SN revealed through three parameter model. All six components of gene action were significant for the fruit traits including FWe, FPD and FED. Additive gene effects along with additive × dominance and dominance × dominance epistatic interaction for SL, both additive and dominant gene effects along with additive× additive and dominance × dominance gene effects were significant for ST. In the case of SW, both additive and dominant gene effects together with dominant × dominant gene interaction were significant. Only additive gene effects with additive × additive digenic epistatic interaction were significant for 100 SW. For traits such as FWe, FPD, FED and ST duplicate epistasis was revealed by opposite signs of dominant effects and dominant × dominant gene interaction. The negative sign associated with additive × additive gene interaction for all three fruit traits along with ST and 100 SW suggested dispersion of genes among parents for these traits.

In - cross-II, the estimation of various gene effects reveals the significance of only additive gene effects for SL and ST, non-significance of both additive and dominant gene effects in 100 SW. All gene effects including genetic interactions were significant for fruit traits such as FWe, FPD and FED except additive × dominant gene interaction in FED. Both additive and dominant along with additive × additive and dominant × dominant gene interactions were significant for SN. In SW all gene effects along with interactions were significant and the negative sign associated with additive × additive interaction revealed dispersion of genes in parents for the trait. The traits-, FWe, FPD and FED revealed duplicate epistasis besides SW and SN similar to cross-I. The involvement of epistasis for fruit yield and seed traits components that hinders the efficiency of simple selection measures in early generations has been reported in cucurbits (Kaur *et al.,* 2018; Riahi *et al.,* 2020; Davoodi *et al.,* 2021). However, the variation present in segregating populations decreases with selfing and generation advancement. Therefore, selection should be delayed to later generations to attain a high level of gene fixation and break undesirable linkages (Mather and Jinks, 1982; Ramli *et al.,* 2016).

The results in the present study disclosed that the nature and magnitude of genetic effects and interactions governing the inheritance of fruit and seed traits in intra and interspecific pumpkin populations. Both fixable and non-fixable gene effects along with the duplicate type of epistasis were present in a majority of traits. For these types of crosses, mild selection during the earlier generation followed by intense selection in later generations is preferred. Therefore, the methods that exploit non-additive gene effects and deal with non-allelic interactions -are also employed such as recurrent selection, followed by concentrated selection

in later generations or biparental mating. Multi-parent crossing in earlier segregating generations or diallel selective mating could also be promising for the genetic improvement of fruit and seed traits. -It can be concluded that the methods which maintain considerable variability and heterozygosity in later generations developed through selective mating in early generations could be followed for the improvement of traits with epistatic effects.

Acknowledgements

Authors gratefully acknowledge Confederation of Indian Industry, Department of Science and Technology and Beauscape Farms for supporting the research through Prime Minister's fellowship for Doctoral Research.

Authors' contribution

Conceptualization of research work and designing of experiments (ASD); Execution of field/lab experiments and data collection (KSG, NV, BK); Analysis of data and interpretation (KSG, NV, JSK, MS, OPM); Preparation of manuscript (KSG, JSK , MS,OPM, BK, ASD).

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