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Gene effects for begomovirus resistance and plant architecture attributes in pumpkin (*Cucurbita moschata* Duchesne)

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Abstract: Knowledge of gene actions governing begomovirus resistance and plant architectural traits is a prerequisite for a successful hybrid breeding programme. Therefore, the gene actions associated with these traits were studied in two intervarietal crosses of *Cucurbita moschata* (C_1: Punjab Nawab × MVSR-6711 and C_2: Punjab Nawab × P-135). We used the generation mean analysis of six generations for this purpose. Significant differences between the generation means were observed for all the traits in both crosses. The parental lines differed significantly in most of the studied traits. The nature and magnitude of the gene effects of seventeen traits varied by trait and cross. A simple additive dominance model was adequate for the internode number, leaf length and width, petiole length, fruit weight and cavity diameter in C_1 and the number of fruits/plant in C_2. The non-allelic interaction was found to be significant for a majority of the traits including the per cent disease index of the squash leaf curl China virus, tomato leaf curl New Delhi virus and their mixed infections, which indicated, that recurrent selection in biparental progeny might be useful for the accumulation of genes with additive effects. Duplicate epistasis was observed for the vine, internodal and peduncle length in C_1 and the internode number, petiole and peduncle length, peduncle and fruit polar diameter in C_2. This information will help to establish a breeding program for the simultaneous improvement of virus resistance and yield traits in pumpkins.

Keywords: gene action; SLCCNV; scaling test; ToLCNDV; yield

The pumpkin (*Cucurbita moschata* Duchesne), is an economically important allogamous cucurbit crop grown in tropical and subtropical regions of the world (Dhatt et al. 2020). Globally, India is the second largest producer of pumpkins after China (FAO 2021). However, there is still a significant gap between the potential and the actual yields in the country. This could be attributed to biotic and abiotic stresses, lack of improved cultivars, and derisory marketing (Dhatt et al. 2020). Among the biotic stresses, viruses have an adverse effect on the growth and yield of the pumpkin (Muniyappa et al. 2003). The two begomovirus species *viz*., Squash leaf curl China virus (SLCCNV) and Tomato leaf curl New Delhi virus (ToLCNDV) are prevalent worldwide (Muniyappa et al. 2003; Dhillon et al. 2021) and host plant resistance is the cheapest, most invincible and ecological way to manage these diseases (Dhatt et al. 2020; Dhillon et al. 2021).

Plants of *C. moschata* have both vine and bushy growth habits (Wu et al. 2007). The differences in bush and vine phenotypes determine the architectural

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framework of the *C. moschata* plants, affecting the stem morphology, canopy formation, leaf morphology, leaf area, which, in turn, influence the yield (Wu et al. 2007). Presently, the thrust in pumpkin breeding is to improve the fruit yield with uniform fruit shape, size as well as biotic and abiotic tolerance with excellent keeping qualities (Hazra et al. 2007). Moreover, pumpkins have a wide range of genetic variability, but the genetic potential has meagrely been exploited in India (Hazra et al. 2007; Dhatt et al. 2020). Thus, to boost the pumpkin production, the cultivated areas or yield per unit area must be increased. However, due to defragmentation, urban advancements, industrialisation and the increasing population, there is a very low possibility of increasing the land under cultivation (Singh et al. 2019).

The germplasm available at the Punjab Agricultural University (PAU) Ludhiana, India represents a wide variability for the vine and bushy growth habits, yield as well as resistance against two begomovirus species (SLCCNV and ToLCNDV) and their mixed infection (MI-Sq/To; Dhatt et al. 2020; Verma 2022). However, to utilise the available variability, knowledge of the gene action governing the begomovirus resistance, plant architectural, yield and its contributing traits is a prerequisite to embarking on a successful hybrid development programme (Yadav et al. 2021; Omrani et al. 2022). Therefore, the focus of this research was to elucidate the gene action associated with various traits *viz.*, begomovirus resistance, plant architectural and yield traits through a generation mean analysis in *C. moschata*.

MATERIAL AND METHODS

Description of experimental site and hybridisation programme. The present research work was carried out at the Vegetable Research Farm (VRF), Punjab Agricultural University (PAU), Ludhiana Punjab India during the main seasons (MSs; 2018, 2019, 2020) occurring from Feb–June and the rainy season (RS; 2019) from July–November. The breeding materials for the present study were the PAU released begomovirus resistant *C. moschata* variety Punjab Nawab (Dhatt et al. 2020) and the genetically diverse, but begomovirus susceptible lines *viz.*, P-135 and MVSR-6711 having a dark green smooth fruit colour and bushy growth habit, respectively. The two intervarietal crosses were developed through hand emasculation and pollination among the Punjab Nawab and MVSR-6711 as C_1 and the Punjab Nawab and P-135 as C_2 during the MS of 2018. Each F_1 was selfed as well as simultaneously backcrossed with both the parents to develop the F_2 and backcross populations {BC_1 (backcross with resistant parent) and BC_2 (backcross with susceptible parent)}, respectively during the MS 2019.

Artificial epiphytotic condition for screening against SLCCNV, ToLCNDV and MI-Sq/To. All six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the two populations were screened against SLCCNV, ToLCNDV and MI-Sq/To in RS using the whitefly mediated artificial inoculation method and phenotyped at 75DAS (Verma et al. 2022). The molecularly confirmed viral inoculum of each virus (Verma 2022) was maintained in three different insect proof enclosed structures on the most susceptible *C. moschata* variety Punjab Samrat. When sufficient whiteflies were maintained on the susceptible lines, the three set of nurseries containing all six generations of the two crosses were sown in pro trays and placed and transplanted inside the respective enclosed structures. The cultivar Punjab Samrat was planted as an infector row after five test rows to overrule the disease escape.

Experimental layout. The experimental material comprised of six generations of C_1 and C_2 was evaluated in a randomised complete block design in three replications. The data were recorded for SLCCNV, ToLCNDV and MI-Sq/To as per the disease rating scale (Verma 2022). However, the data for plant architectural and yield contributing traits for the generation mean analysis of the six generations of two crosses were collected during the MS 2020 under natural field conditions. The seeds were grown in pro trays and the seedlings were transplanted in enclosed structures (August 2019) and in natural conditions (March 2020) at a spacing of 3 m × 0.45 m. All the intercultural operations were carried out in accordance with the recommended package of practices (Anonymous 2021).

Data collection. The data for the percent disease index (PDI) of SLCCNV, ToLCNDV, MI-Sq/To and horticultural traits were recorded randomly on a single plant basis from each generation of C_1 and C_2 in all three replications. In the process of the random selection, the border plants were avoided. The total number of plants analysed were 60 plants each of parent and the F_1, 150 and 80 plants for the F_2 and backcross populations (BC_1 and BC_2), respectively. The disease reaction was scored at 75 days after sowing (DAS) on the symptom severity grade of 0 to 4 and the PDI was calculated as given by Mc-

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Kinney (1923). The plant architectural traits: vine length (VL, cm), internodal length (IL, cm), internodal number (IN), leaf length (LL, cm), leaf width (LW, cm), petiole length (PL, cm) and fruit yield traits: peduncle length (PDL, cm), peduncle diameter (PDD, cm), fruit weight (FW, kg), fruit polar diameter (FPD, cm), fruit equatorial diameter (FED, cm), cavity diameter (CD, cm), number of fruits per plant (NFPP) and yield per plant (YPP, kg) were recorded at the 50 percent flowering stage and full maturity, respectively.

Statistical analysis. Estimates of the PDI were transformed to arcsine values prior to the generation mean analysis. The significance of six generations within each cross for all the studied traits was tested using an analysis of variance (ANOVA) followed by the mean estimates and a comparison using SPSS Software (Ver. 22) using Tukey's honestly significant difference (HSD) method (IBM, Corp., Armonk, N.Y. USA). The PDI, plant architectural and yield trait data of the six generations were subjected to a scaling test (Mather 1949; Hayman & Mather 1955) and a generation mean analysis by utilising six parameter models (Hayman 1958; Jinks & Jones 1958).

RESULTS AND DISCUSSION

The analysis of variance of the six generations of two intervarietal crosses (C_1 and C_2) revealed significant mean squares for the PDI (SLCCNV, ToLCNDV and MI-Sq/To), plant architectural and fruit yield traits (Table S1 in the Electronic Supplementary Material). Thus, this highlighted the presence of sufficient genetic variability in the existing breeding material and the possibility of selection for different traits in *C. moschata* which is the first and foremost requirement for any crop improvement programme (Begna 2021).

Generation means. The mean and standard error of the six generations of each cross combination for the different traits are presented in Table 1. In Tukey's multiple means comparison test, significant differences were observed between the parents for most of the studied traits. In all three virus conditions (SLCCNV, ToLCNDV and MI-Sq/To), a minimum average PDI was recorded in Punjab Nawab and a maximum average was recorded in P-135 and MVSR-6711 which was found to be statistically at par with the PDI of F_1, while it was intermediate in the BC_1 generation and F_2 generation of C_1 and C_2 had a PDI in a range of 77.92 to 79.23.

All the plant architectural and fruit yield traits of the begomovirus resistant parent, Punjab Nawab were higher than that of MVSR-6711 except for the NFPP. The differences were significant between the F_1 and F_2 for the VL, IL, PDD, FW, FPD, CD and YPP. The mean values in the backcross to Punjab Nawab (BC_1) were also similar to the recurrent parent for the LL, LW, PL, PDL, PDD, FPD, CD and NFPP and significantly different from BC_2 for each of these traits except the LL, LW and NFPP, suggesting the effectiveness of the backcross breeding method in improving these traits.

The parental lines showed highly significant divergence for the VL, LL, LW, PL, PDL, PDD, FPD, FED and CD in the plant architectural and yield traits of the C_2 cross. For the IL, LL, LW, PL, PDD, FW, FED, CD and YPP, the F_1 and F_2 exhibited significant differences, with the F_2 values lower than the F_1 ones except for the IN. The convergence of the means of the IL, FW, NFPP and YPP towards their respective recurrent parents in the backcrosses (BC_1 and BC_2), indicated the effectiveness of backcross breeding. Thus, a significant difference among parental, F_1, F_2, BC_1, and BC_2 generations allowed the genetic analysis of all the traits studied.

Gene effects. The results obtained on the estimates of the scaling tests (A, B, C and D) and the various gene effects (m, d, h, i, j and l) for the two crosses studied with respect to the various traits are presented in Tables 2 and 3.

Begomovirus resistance. The significance of scaling tests B and D indicated the presence of non-allelic interaction (additive × additive[i], additive × dominance[j] and dominance × dominance[l]) for the PDI in both crosses under SLCCNV, ToLCNDV and MI-Sq/To (Table 2 and 3). Based on the gene action, a significant additive effect [d] was found for the PDI in all three infection conditions, which indicated the importance of the progeny selection. Among the digenic interactions, significant [i] gene effects were noticed under SLCCNV, ToLCNDV and MI-Sq/To, which represents fixable genetic variance and, hence, the progeny *per se* selection would presumably be effective for enhancing the begomovirus resistance. The non-allelic interaction of the resistant gene(s) governing the leaf curl disease has previously been reported in chilli (Anandhi & Khader 2011) and tomato (Singh et al. 2015). Quantitative trait locus (QTL) with varying levels of dominant and epistatic effects governing the leaf curl disease have been mapped in the tomato (Wang et al. 2018), chilli

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Table 1. Estimates of the generation means of six generations for the begomovirus resistance, plant architectural and yield contributing traits in *Cucurbita moschata*

Generations	PDI			VL	IL	IN	LL	LW	PL	PDL	PDD	FW	FPD	FED	CD	NFPP	YPP
	SLCCNV	ToLCNDV	MI-Sq/To														
Punjab Nawab × MVSR-6711 (C_1)																	
Punjab Nawab	5.00 (6.00)^{a}	4.16 (5.00)^{a}	3.33 (4.00)^{a}	2.00^{e}	7.99^{e}	25.36^{c}	9.18^{ab}	12.54^{b}	15.18^{c}	7.34^{c}	2.12^{c}	1.21^{e}	10.69^{d}	14.91^{c}	12.68^{d}	1.26^{ab}	1.47^{e}
MVSR-6711	95.83 (85.00)^{d}	100.00 (90.00)^{e}	97.50 (87.00)^{e}	0.44^{a}	2.13^{a}	16.83^{a}	8.36^{a}	11.11^{a}	10.62^{a}	2.16^{a}	1.24^{a}	0.35^{a}	6.11^{a}	9.67^{a}	7.08^{a}	1.53^{c}	0.52^{a}
F_1	93.33 (82.00)^{d}	99.16 (89.00)^{e}	95.83 (85.00)^{e}	0.61^{b}	4.20^{b}	18.30^{ab}	10.84^{c}	12.97^{b}	12.78^{abc}	3.34^{b}	2.21^{c}	1.13^{de}	10.61^{d}	15.06^{c}	12.36^{d}	1.36^{bc}	1.35^{de}
F_2	78.26 (68.92)^{c}	78.54 (69.17)^{c}	79.23 (69.79)^{c}	0.82^{c}	5.21^{c}	19.55^{ab}	9.65^{abc}	12.92^{b}	13.57^{bc}	4.30^{b}	1.68^{b}	0.94^{c}	9.94^{c}	14.95^{c}	11.09^{c}	1.31^{b}	1.13^{c}
BC_1	55.55 (49.08)^{b}	54.44 (47.58)^{b}	52.08 (45.75)^{b}	1.43^{d}	6.89^{d}	20.43^{b}	10.40^{bc}	13.38^{b}	14.88^{c}	6.51^{c}	2.15^{c}	1.07^{d}	10.70^{d}	15.97^{d}	12.16^{d}	1.10^{a}	1.16^{cd}
BC_2	90.83 (79.00)^{d}	90.41 (78.50)^{d}	90.97 (79.16)^{d}	0.65^{b}	4.23^{b}	16.60^{a}	9.42^{abc}	12.73^{b}	11.63^{ab}	4.33^{b}	1.42^{a}	0.71^{b}	9.05^{b}	12.85^{b}	9.62^{b}	1.38^{bc}	0.88^{b}
Punjab Nawab × P-135 (C_2)																	
Punjab Nawab	5.00 (6.00)^{a}	4.16 (5.00)^{a}	3.33 (4.00)^{a}	2.00^{a}	7.99^{ab}	25.36^{a}	9.18^{a}	12.54^{a}	15.18^{a}	7.34^{a}	2.12^{a}	1.21^{ab}	10.69^{a}	14.90^{a}	12.68^{a}	1.26^{ab}	1.47^{ab}
P-135	97.50 (87.00)^{e}	99.16 (89.00)^{e}	98.33 (88.00)^{e}	2.220^{b}	8.66^{ab}	26.56^{ab}	11.41^{c}	16.62^{e}	17.65^{b}	10.88^{d}	3.02^{d}	1.31^{bc}	11.50^{b}	17.55^{c}	13.63^{b}	1.30^{b}	1.56^{ab}
F_1	95.00 (84.00)^{de}	98.33 (88.00)^{e}	96.66 (86.00)^{e}	2.16^{ab}	10.41^{c}	25.76^{a}	10.82^{c}	15.58^{d}	17.51^{c}	8.34^{abc}	2.81^{cd}	1.45^{c}	11.83b	18.01^{c}	13.58^{b}	1.23^{ab}	1.69^{b}
F_2	77.92 (68.75)^{c}	78.40 (68.92)^{c}	78.19 (68.88)^{c}	2.09^{ab}	7.52^{a}	27.86^{ab}	9.72^{ab}	13.59^{b}	16.12^{a}	7.81^{ab}	2.48^{b}	1.07^{a}	11.56^{b}	15.38^{ab}	12.47^{a}	1.19^{ab}	1.31^{a}
BC_1	50.00 (43.83)^{b}	51.25 (45.00)^{b}	51.53 (45.17)^{b}	2.30^{b}	9.07^{b}	28.86^{b}	9.94^{b}	14.81^{c}	18.99^{c}	8.81^{bc}	2.67^{bc}	1.19^{ab}	12.50^{c}	16.08^{b}	12.82^{a}	1.11^{a}	1.33^{a}
BC_2	92.08 (80.50)^{d}	92.78 (81.33)^{d}	92.22 (80.67)^{d}	2.22^{b}	7.80^{a}	28.96^{b}	10.95^{c}	14.51^{c}	16.38^{ab}	9.40^{c}	2.83^{cd}	1.15^{ab}	11.80^{b}	15.95^{b}	12.69^{a}	1.16^{ab}	1.41^{ab}

PDI – percent disease index; VL – vine length; IL – internodal length; IN – internode number; LL – leaf length; LW – leaf width; PL – petiole length; PDL – peduncle length; PDD – peduncle diameter; FW – fruit weight; FPD – fruit polar diameter, FED – fruit equatorial diameter; CD – cavity diameter; NFPP – number of fruits per plant; YPP – yield per plant; values with the different letters of the alphabet along each column are significantly different by Tukey's HSD test at $P = 0.05$

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Table 2. Scaling test and estimation of the gene effects for the begomovirus resistance, plant architectural and yield contributing traits in the Punjab Nawab × MVSR-6711 cross (C_1)

Parameter	PDI			VL	IL	IN	LL	LW	PL	PDL	PDD	FW	FPD	FED	CD	NFPP	YPP
	SLCCNV	ToLC-NDV	MI-Sq/To														
Scaling test																	
A	12.78 ± 6.39*	5.56 ± 5.82	5.00 ± 5.83	0.33 ± 0.24	1.58 ± 0.61**	−2.80 ± 2.18	0.79 ± 0.63	1.25 ± 0.76	1.80 ± 1.13	2.33 ± 0.71**	−0.03 ± 0.16	−0.18 ± 0.11	0.09 ± 0.48	1.97 ± 0.56**	−0.72 ± 0.56	−0.43 ± 0.14**	−0.49 ± 0.17**
B	−7.50 ± 3.23*	−18.33 ± 1.99**	−11.38 ± 2.85**	0.24 ± 0.06**	2.13 ± 0.35**	−1.93 ± 1.55	−0.35 ± 0.62	1.38 ± 0.75	−0.14 ± 0.93	3.16 ± 0.76**	−0.61 ± 0.16**	−0.06 ± 0.09	1.39 ± 0.51**	0.98 ± 0.64	−0.20 ± 0.54	−0.13 ± 0.18	−0.12 ± 0.12
C	25.56 ± 7.41**	11.67 ± 6.12	24.44 ± 6.89**	−0.38 ± 0.25	2.29 ± 1.15*	−0.60 ± 3.02	−0.52 ± 0.87	2.12 ± 1.18	2.91 ± 1.50	1.00 ± 1.02	−1.08 ± 0.24**	−0.05 ± 0.18	1.75 ± 0.82*	5.12 ± 1.11**	−0.12 ± 0.86	−0.30 ± 0.28	−0.18 ± 0.26
D	10.14 ± 4.12*	12.22 ± 4.04**	15.41 ± 3.96**	−0.47 ± 0.16**	−0.71 ± 0.61	2.07 ± 1.52	−0.48 ± 0.51	−0.26 ± 0.64	0.62 ± 0.87	−2.24 ± 0.70**	−0.21 ± 0.13	0.09 ± 0.09	0.13 ± 0.46	1.08 ± 0.63	0.39 ± 0.51	0.13 ± 0.12	0.21 ± 0.12
Genetic parameter																	
m	70.69 ± 8.34**	76.53 ± 8.13**	81.2 ± 8.00**	0.26 ± 0.33	3.65 ± 1.22**	25.23 ± 3.05**	7.80 ± 1.03**	11.30 ± 1.30**	14.14 ± 1.76**	0.26 ± 1.41	1.25 ± 0.27**	0.97 ± 0.19**	8.67 ± 0.93**	14.4 ± 1.26**	10.68 ± 1.02**	1.66 ± 0.24**	1.42 ± 0.23**
[d]	−45.42 ± 1.27**	−47.92 ± 0.86**	−47.08 ± 1.05**	0.78 ± 0.02**	2.93 ± 0.11**	4.26 ± 0.29**	0.41 ± 0.13**	0.71 ± 0.16**	2.28 ± 0.22**	2.59 ± 0.10**	0.44 ± 0.04**	0.43 ± 0.02**	2.2 ± 0.05**	2.61 ± 0.11**	2.79 ± 0.09**	−0.13 ± 0.06*	0.47 ± 0.04**
[h]	7.64 ± 21.74	−14.58 ± 20.89	−22.63 ± 20.57	1.87 ± 0.84*	5.66 ± 2.83*	−15.80 ± 7.90*	4.44 ± 2.72	4.84 ± 3.35	−0.93 ± 4.58	13.07 ± 3.62**	0.74 ± 0.71	−0.27 ± 0.48	3.15 ± 2.34	1.39 ± 3.07	−0.035 ± 2.59	−1.133 ± 0.62	−1.11 ± 0.59
[i]	−20.28 ± 8.25*	−24.44 ± 8.08**	−30.83 ± 7.93**	0.95 ± 0.33**	1.41 ± 1.22	–	–	–	–	4.49 ± 1.40**	0.43 ± 0.27	–	−0.26 ± 0.92	−2.16 ± 1.26	–	−0.26 ± 0.24	−0.42 ± 0.23
[j]	20.28 ± 6.54**	23.88 ± 6.04**	16.38 ± 6.01**	0.08 ± 0.23	−0.55 ± 0.65	–	–	–	–	−0.83 ± 1.03	0.58 ± 0.21**	–	−1.29 ± 0.63	0.99 ± 0.80	–	−0.30 ± 0.19	−0.37 ± 0.17*
[l]	15.00 ± 14.16	37.22 ± 13.11**	37.22 ± 13.21**	−1.53 ± 0.52**	−5.12 ± 1.68**	–	–	–	–	−9.99 ± 2.26**	0.22 ± 0.46	–	−1.21 ± 1.49	−0.78 ± 1.88	–	0.83 ± 0.42*	1.03 ± 0.39**
Epistasis	no epistasis	no epistasis	no epistasis	duplicate	duplicate	–	–	–	–	duplicate	no epistasis	–	no epistasis	no epistasis	–	no epistasis	no epistasis

PDI – percent disease index; VL – vine length; IL – internodal length; IN – internode number; LL – leaf length; LW – leaf width; PL – petiole length; PDL – peduncle length; PDD – peduncle diameter; FW – fruit weight; FPD – fruit polar diameter; FED – fruit equatorial diameter; CD – cavity diameter; NFPP – number of fruits per plant; YPP – yield per plant; m – mean effect; [d] – additive effect; [h] – dominance effect; [i] – additive × additive effect; [j] – additive × dominance effect; [l] – dominance × dominance effect; *,**statistically significant at $P < 0.05$, 0.01, respectively

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(Thakur et al. 2020) and pumpkin (Saez et al. 2020). Thus, the knowledge of the resistance spectrum of gene(s) and the gene action should be considered for the successful implementation of a resistance breeding programme.

Plant architectural traits. The combined analysis of the six generations for the IN, LL, LW and PL in C_1 signified the adequacy of the additive dominance model due to the insignificance of the scaling tests (Table 2). On the basis of the gene action, both the additive [d] and dominance [h] gene effects were significant for the IN. However, the higher magnitude of the dominance gene effects illustrated the exploitation of the heterosis breeding. A significant [d] gene effect was observed for the LL, LW and PL, which suggested the use of the selections in the early generations for the improvement of these traits.

Epistatic interactions were present for the VL and IL in both the crosses and for the IN, LL, LW and PL in C_2 as depicted from the significance of either of the four scaling tests (Table 2 and 3). The estimates of the genic effects revealed the significance of [d] and [h] with the preponderance of the latter in both the crosses for the VL and IL as well as for the IN, LL, LW and PL in C_2 only. Among the digenic interactions, [i] as well as [l] were operative for the VL in both the crosses as well as for the PL in C_2, however, the magnitude of the dominance × dominance was higher than the others. The significant positive effects for pooled [h] and negative estimates for [l] showed the presence of duplicate types of gene interactions, which means dominant genes with small cumulative effects controlled the inheritance of the VL in both the crosses, the IL in C_1 as well as the IN and PL in C_2 (Table 2 and 3). Therefore, the selection should be delayed until a high level of gene fixation is attained and population improvement methods would be more effective to break the undesirable linkage and accumulate desirable genes (Pujar et al. 2022). The significant contribution of the epistasis in controlling the inheritance of the VL and IL in pumpkins was earlier reported by Mohanty et al. (1999); Pandey and Rao (2010); Almeida et al. (2020); Yadav et al. (2021) and in the summer squash by Kaur et al. (2018). A significant [d], [h] [i] gene model was found for the LL and LW in C_2. Thus, the improvement in these traits can be achieved through progeny selections, however, the different signs of [d] and [h] and significance [j] for the LW indicated that one should perform the selections in later generations (Bhardwaj & Vikram 2004).

Yield traits. The additive dominance model was found to be adequate for the FW and CD in C_1 as well as for the NFPP in C_2. However, only the [d] gene effect was found to be significant for the FW and CD in C_1. Thus, for these traits, the simple pedigree method with selection in early generation should be preferred.

The non-allelic interaction model was found to be adequate for explaining the gene action in the majority of the fruit yield traits in both intervarietal crosses (Tables 2 and 3), as earlier reported by Pandey and Rao (2010). This reveals that not only the additive and dominance, but also other types of gene interaction may likely contribute to the genetics of various yield traits in pumpkins. The [i] gene interaction was observed to be significant for the PDL in both crosses as well as for the PDD, FW, FPD and FED in C_2. While the [l] gene interaction was found to be significant for the PDL, NFPP and YPP in C_1 as well as for the PDL, PDD and FPD in C_2. These significant interactions showed duplicate epistasis for the PDL in both crosses as well as for the PDD and FPD in C_2 which is substantiated by the earlier study of Kaur et al. (2018). Hence, recurrent selection can effectively be utilised to improve these characteristics.

The significant additive[d] and [i] gene interaction for the FW in C_2 suggests the effectiveness of the selection in later generations (Table 3). Based on the gene effects, significant [d] + [l] and [d] + [j] + [l] gene models were found for the NFPP and YPP, respectively, in C_1 (Table 2). Contrary, the significance of the scaling test for the FPD, FED in C_1 as well as for the CD and YPP in C_2 indicated the implementation of six parameter models (Table 2 and 3). However, none of the non-allelic interactions ([i], [j] and [l]) were significant, indicating higher order epistatic interactions (Sharma & Saini 2002).

Thus, selection for improved recombinant effects for these traits is possible through pedigree breeding by delaying the selection to later generations (Omrani et al. 2022). The information on the gene effects of begomovirus resistance, plant architectural, and fruit yield traits will help plant breeders in selecting the appropriate breeding programme. Furthermore, it will also help in the development of a strategy for mapping the population development required for identifying the linked molecular marker, facilitating marker assisted breeding for simultaneous improvement of virus resistance and yield traits in pumpkins.

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Table 3. Scaling test and estimation of the gene effects for the begomovirus resistance, plant architectural and yield contributing traits in the Punjab Nawab × P-135 cross (C_2)

Parameter	PDI			VL	IL	IN	LL	LW	PL	PDL	PDD	FW	FPD	FED	CD	NFPP	YPP
	SLCCNV	ToLC-NDV	MI-Sq/To														
Scaling test																	
A	0.00 ± 6.06	0.00 ± 5.85	3.05 ± 5.82	0.45 ± 0.19*	−0.27 ± 0.59	6.60 ± 1.66**	−0.11 ± 0.51	1.51 ± 0.73*	5.30 ± 1.06**	1.92 ± 0.48**	0.41 ± 0.15**	−0.27 ± 0.14*	2.48 ± 0.43**	−0.75 ± 0.53	−0.61 ± 0.46	−0.27 ± 0.14	−0.48 ± 0.20*
B	−8.33 ± 2.90*	−11.94 ± 2.21**	−10.56 ± 2.61**	0.07 ± 0.14	−3.48 ± 0.51**	5.60 ± 1.61**	−0.32 ± 0.46	−3.17 ± 0.5**	−2.39 ± 1.09*	−0.43 ± 0.57	−0.17 ± 0.19	−0.46 ± 0.13**	0.28 ± 0.45	−3.66 ± 0.59**	−1.82 ± 0.51**	−0.20 ± 0.15	−0.42 ± 0.23
C	19.17 ± 7.31*	13.61 ± 6.40*	17.78 ± 6.78**	−0.15 ± 0.29	−7.40 ± 0.86**	8.00 ± 3.14*	−3.34 ± 0.72**	−5.96 ± 0.96**	−3.36 ± 1.62*	−3.70 ± 0.79**	−0.85 ± 0.26**	−1.12 ± 0.22**	0.39 ± 0.55	−6.97 ± 0.81**	−3.57 ± 0.74**	−0.26 ± 0.24	−1.16 ± 0.35**
D	13.75 ± 4.10**	12.78 ± 4.02**	12.64 ± 4.00**	−0.33 ± 0.16*	−1.83 ± 0.50**	−2.10 ± 1.62**	−1.45 ± 0.41**	−2.15 ± 0.53**	−3.13 ± 0.79**	−2.59 ± 0.47**	−0.55 ± 0.14**	−0.19 ± 0.09*	−1.18 ± 0.38**	−1.27 ± 0.50*	−0.57 ± 0.41	0.10 ± 0.09	−0.12 ± 0.16
Genetic parameter																	
m	78.75 ± 8.27**	77.22 ± 8.09**	76.11 ± 8.06**	1.44 ± 0.33**	4.67 ± 1.00**	21.76 ± 3.26**	7.38 ± 0.83**	10.27 ± 1.07**	10.14 ± 1.61**	3.92 ± 0.95**	1.47 ± 0.29**	0.88 ± 0.18**	8.72 ± 0.78**	13.67 ± 1.01**	12.01 ± 0.82**	1.48 ± 0.20**	1.26 ± 0.33**
[d]	−46.25 ± 1.16**	−47.50 ± 0.96**	−47.50 ± 0.97**	−0.10 ± 0.03**	−0.33 ± 0.12**	−0.60 ± 0.28*	−1.11 ± 0.12**	−2.04 ± 0.19**	−1.23 ± 0.23**	−1.76 ± 0.11**	−0.45 ± 0.06**	−0.05 ± 0.02*	−0.40 ± 0.07**	−1.32 ± 0.12**	−0.47 ± 0.09**	−0.01 ± 0.05	−0.04 ± 0.06
[h]	−19.58 ± 21.17	−16.38 ± 20.77	−12.22 ± 20.66	1.90 ± 0.81*	5.65 ± 2.56*	20.40 ± 7.89**	5.91 ± 2.14**	7.95 ± 2.81**	16.53 ± 4.25**	11.11 ± 2.44**	2.68 ± 0.75**	0.21 ± 0.49	8.25 ± 2.05**	2.48 ± 2.61	0.28 ± 2.12	−0.91 ± 0.51	−0.23 ± 0.85
[i]	−27.50 ± 8.19**	−25.55 ± 8.03**	−25.27 ± 8.00**	0.66 ± 0.32*	3.65 ± 1.00**	4.20 ± 3.25	2.91 ± 0.82**	4.31 ± 1.05**	6.27 ± 1.59**	5.19 ± 0.94**	1.10 ± 0.28**	0.37 ± 0.18*	2.37 ± 0.77**	2.55 ± 1.00*	1.14 ± 0.81	–	0.25 ± 0.32
[j]	8.33 ± 6.18	11.94 ± 6.03*	13.61 ± 5.97*	0.37 ± 0.22	3.20 ± 0.73**	1.00 ± 2.00	0.21 ± 0.63	4.68 ± 0.87**	7.70 ± 1.28**	2.34 ± 0.70**	0.58 ± 0.24**	0.19 ± 0.14	2.20 ± 0.61**	2.91 ± 0.76**	1.21 ± 0.617	–	−0.05 ± 0.26
[l]	35.83 ± 13.59**	37.50 ± 13.11**	32.77 ± 13.17*	−1.18 ± 0.51*	0.08 ± 1.63	−16.40 ± 4.96**	−2.48 ± 1.37	−2.64 ± 1.83	−9.17 ± 2.89**	−6.68 ± 1.55**	−1.34 ± 0.48**	0.36 ± 0.35	−5.14 ± 1.31**	1.85 ± 1.65	1.28 ± 1.38	–	0.66 ± 0.57
Epistasis	no epistasis	no epistasis	no epistasis	duplicate	no epistasis	duplicate	no epistasis	no epistasis	duplicate	duplicate	duplicate	no epistasis	duplicate	no epistasis	no epistasis	-	no epistasis

PDI – percent disease index; VL – vine length; IL – internodal length; IN – internode number; LL – leaf length; LW – leaf width; PL – petiole length; PDL – peduncle length; PDD – peduncle diameter; FW – fruit weight; FPD – fruit polar diameter; FED – fruit equatorial diameter; CD – cavity diameter; NFPP – number of fruits per plant; YPP – yield per plant; m – mean effect; [d] – additive effect; [h] – dominance effect; [i] – additive × additive effect; [j] – additive × dominance effect; [l] – dominance × dominance effect; *,**statistically significant at $P < 0.05$, 0.01, respectively

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CONCLUSIONS

The current study concluded that the genetic background of the parental lines involved in the different crosses influenced the nature and magnitude of the genes controlling various traits. Among the studied traits, yield and the contributing traits were, in general, more complex and highlighted the polygenic control where selection should be delayed to later generations. On the other hand, begomovirus resistance was governed by the additive and additive × additive gene effects suggesting the effectiveness of the selection even in early generations. Therefore, the progeny *per se* selection would be a highly effective approach in a such case, leading to development of inbreds and their utilisation in future resistance and hybridisation programmes.

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