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RESEARCH ARTICLE

Dissecting the genetic basis of fruit quality traits in muskmelon using crosses with *Cucumis melo* var. *callosus* and *C. melo* var. *momordica*

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Abstract

Fruit quality is an important component in muskmelon (*Cucumis melo* L.) breeding due to its direct influence on consumer preference and market value. The majority of commercial varieties of muskmelon are highly susceptible to various diseases and pests. Consequently, researchers increasingly rely on wild relatives as critical genetic resources for introgressing resistance in breeding programmes. In this context, the present study aimed to elucidate the genetic control of eight fruit quality traits: fruit length, fruit diameter, flesh thickness, cavity width, fruit shape index, average fruit weight, total soluble solids (TSS) and titratable acidity using generation mean analysis. Two inter-varietal crosses were developed involving wild relatives, DSM 132 (*C. melo* var. *callosus*) and DSM 19 (*C. melo* var. *momordica*), with a commercial variety, Hara Madhu, as the common recurrent parent. Six segregating populations (P_1, P_2, F_1, F_2, BC_1P_1, BC_1P_2) were evaluated across multiple seasons (2022–2024). Scaling and joint scaling tests revealed that the additive-dominance model alone was insufficient, suggesting the involvement of non-allelic interactions. Six-parametric model analysis showed that dominance (*h*) and dominance × dominance (*l)* interactions were most significant for most of the fruit quality traits. Duplicate epistasis was observed for most of the quality traits, including TSS, average fruit weight, flesh thicknessand titratable acidity, suggesting the potential for heterosis breeding or recurrent selection to improve these traits. Overall, the present findings provided insights into the genetic architecture of fruit quality traits in muskmelon and paved the way for the strategic use of wild relatives in breeding programmes.

Keywords: Duplicate epistasis, genetic studies, generation mean analysis, muskmelon, wild relatives

Introduction

Muskmelon (*Cucumis melo* L., 2n=24) is an important cucurbitaceous vegetable crop valued for its diverse and flavourful fruits. It is cultivated worldwide, with production of 29.54 mt from 1.09 m hectares in 2023 (FAOSTAT 2025). Globally, India ranks second in production after China, followed by Iran and Türkiye, with a production of 1.49 mt from 0.068 m ha and a productivity of only 22.03 t/ha (FAOSTAT 2025). Muskmelon possesses exceptional diversity for fruit traits, such as size, shape, colour, taste, and biochemical composition (Burger et al. 2006). Owing to such variation, defining fruit quality in melon is complex and varies across varietal groups (Fernandez-Trujillo et al. 2012). Non-sweet melon such as *C. melo* var. *callosus* (kachri) and var. *momordica* (phut) are consumed immature as vegetables or pickles, while sweet dessert types from *inodorus*, *reticulatus* and *cantalupensis* groups are eaten fresh due to high sugar and aroma. Generally, hot days and cool nights enhance melon sweetness, aroma and nutritional quality, whereas rainy seasons reduce it. Melon is also valued as a healthy food owing to its low calorie, fat and sodium content and richness in potassium and vitamins

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A and C (Choudhary et al. 2020). However, the cultivation of a few superior varieties has led to a narrow genetic base, making the crop more susceptible to pests and diseases such as *Fusarium* wilt, powdery mildew, downy mildew, ToLCNDV, etc. Wild relatives of melon, such as *C. melo* var. *callosus* and var. *momordica*, possess a reservoir of resistance genes, adaptability and distinct fruit quality traits absent in cultivated varieties (Dhillon et al. 2012; Pitrat 2013). Several of these accessions have contributed to the development of resistant breeding lines, for instance, DSM 11 (Choudhary et al. 2020) and KP4HM-15 for *Fusarium* wilt (Vashisht et al. 2015) and MR-1 for powdery and downy mildew (Cui et al. 2022). High genetic variability among wild accessions DSM 132 and DSM 19, along with clear differentiation between sweet and non-sweet melon types using microsatellite markers, has been reported earlier (Tara et al. 2023, 2024), highlighting their potential for genetic improvement. Moreover, these lines have been validated as reliable sources of ToLCNDV resistance, confirming their genetic uniqueness and breeding value (Padmanabha et al. 2024).

Despite their value, these wild relatives possess inferior quality traits, such as low sweetness and high acidity that interferes with sweetness in cultivated varieties (Choudhary et al. 2020). Moreover, selection based solely on phenotypic performance is ineffective for polygenic traits like TSS, acidity and fruit weight, which show continuous variation (Shashikumar et al. 2016). Hence, understanding the nature and magnitude of gene action is critical for efficient introgression of desirable traits into cultivated backgrounds. Generation mean analysis serves as a robust biometrical technique to dissect the inheritance of complex traits and guide suitable breeding strategies. Previous studies on generation mean analysis in melon have predominantly focused on cultivated types (Shashikumar et al. 2016; Ranjitha et al. 2023). However, the introgression of wild relatives such as *C. melo* var. *callosus* and *C. melo* var. *momordica* into elite *C. melo* var. *melo* background remains largely limited. Therefore, the present study aimed at the elucidation of the nature of gene action in the novel crosses to assess their potential for genetic improvement of fruit quality traits in melon.

Materials and methods

Plant material and population development

The experimental material comprised one commercial muskmelon cultivar, Hara Madhu (*C. melo* var. *reticulatus*) and two wild *agrestis* melon breeding lines, DSM 132 (*C. melo* var. *callosus*, commonly known as *kachri*) and DSM 19 (*C. melo* var. *momordica*, commonly referred to as *phut*). The present experiment was conducted at the Vegetable Research Farm, ICAR-IARI, New Delhi, during the summer 2022 to *kharif* 2024 over six seasons. For the cross, I *i.e.*, Hara Madhu (P_1) and DSM 132 (P_2) were crossed to generate F_1 plants (summer 2022). The F_1 were sown (*kharif* 2022) to generate F_2 by selfing of F_1 and two backcross populations by backcrossing with P_1 (BC_1P_1) and P_2 (BC_1P_2). For cross II, *i.e.*, Hara Madhu (P_1) and DSM 19 (P_2) were crossed to generate F_1 hybrid (summer 2023) and in the following season (*kharif* 2023), F_1 seeds were sown to generate F_2, BC_1P_1 and BC_1P_2 populations.

Field evaluation

The experiment was conducted in a randomized completely block design (RCBD) with two replications. Standard package of practices was followed and each plant was self-pollinated to maintain genetic integrity and avoid cross-contamination. These six generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) for cross I were evaluated for three seasons, *i.e.*, summer 2023 (season I), *kharif* 2023 (season II) and summer 2024 (season III). For cross I, in season I, the number of individuals evaluated for phenotyping was: P_1 = 10, P_2 =10, F_1 = 30, F_2 = 150, BC_1P_1 = 44 and BC_1P_2 = 48, including both replications. In season II, the respective population sizes were: P_1 (10), P_2 (10), F_1 (18), F_2 (120), BC_1P_1 (40) and BC_1P_2 (38). In season III, P_1 (10), P_2 (10), F_1 (30), F_2 (154), BC_1P_1 (66) and BC_1P_2 (70). For cross II, six generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) were evaluated in the following two seasons in 2024, during summer (season I) and *kharif* season (season II). In season I, the population sizes were: P_1 (10), P_2 (10), F_1 (16), F_2 (136), BC_1P_1 (70) and F_2 (70), BC_1P_1 (40) and BC_1P_2 (38). These populations were grown in open field conditions during the spring-summer season and in net house conditions during the *kharif* season.

Data collection

The phenotypic traits were recorded for eight fruit quality parameters, namely, average fruit weight (g), fruit length (cm), fruit diameter (cm), flesh thickness (cm), cavity width (cm), total soluble solids (°Brix), fruit shape index (ratio of fruit length to fruit width) and titratable acidity. Sex expression was recorded as monoecious (M) and andromonoecious (A) during the peak flowering season in both the crosses. The data was recorded for three seasons for cross I and for two seasons in cross II.

Statistical and genetic analysis

Best linear unbiased estimates (BLUEs) were computed to account for the random effects of replications in segregating generations and the resulting values were used for genetic analysis using the 'lme4' package in Multi Environment Trail Analysis with R (META-R) v6.04 statistical software (Alvarado et al. 2020). The mean data of the six generations from the crosses Hara Madhu × DSM 132 (cross I) and Hara Madhu × DSM 19 (cross II) were subjected to generation mean analysis (GMA) to estimate genetic components. Initially, a scaling test was conducted to check for the presence of allelic and non-allelic interactions (epistasis). Further, these mean data were subjected to a joint scaling test to examine the competence of the simple additive–dominance model or to detect epistasis using the chi-square (χ2) test. The six-parameter or di-genic interaction model (Hayman, 1958) was used to estimate the gene effects whenever the χ2 and ABCD scaling test are inadequate. In case χ2 and ABCD scaling test are inadequate, a six-parameter model is used to estimate genetic effects. This six-parameter model represents mean effect (*m*), genetic effects including additive (*d*) and dominance (*h*) and gene interaction effects comprising additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*). To test the significance of the estimated scales (ABCD), joint scaling tests (*m, d, h*) and gene effects (*m, d, h, i, j, l*), students' t-test was used. The statistical analysis for the generation mean analysis was conducted using OP STAT software (Sheoran et al. 1998).

Results and discussion

The analysis of variance (ANOVA) for six generation means analysis in cross I (Hara Madhu × DSM 132) across three seasons revealed highly significant variations for all the traits studied, except for flesh thickness and fruit shape index in season II (Table 1). This lack of significance may be attributed to the fact that muskmelon, being primarily a summer crop, exhibits optimal trait expression under summer conditions. The combined (pooled) ANOVA for cross I showed a highly significant difference for all traits, except fruit shape index. The non-significance observed for fruit shape index in both season II and the pooled analysis may be due to similar fruit shapes of the parents, with Hara Madhu (P_1) having a round fruit shape and DSM 132 (P_2) having a flat, round fruit, resulting in limited variation for this trait in the segregating generations. For cross II (Hara Madhu × DSM 19), ANOVA across all seasons and pooled data revealed highly significant genetic variation for all studied traits, confirming sufficient variability for genetic analysis.

Mean performance of parents, hybrids and progenies

In cross I, P_1 exhibited superior performance, producing large fruits (867 g)with high sweetness (10.22 °Brix) (Table 2; Fig. 1), whereas P_2 (DSM 132) produced significantly smaller fruits (386.5 g) with low sweetness/sourness (4.56 °Brix)and higher acidity (0.32%). The F_1 hybrid displayed intermediate traits (429.4 g, 5.85 °Brix), reflecting partial dominance for P_1's quality traits and smaller size from P_2. The F_2 generation exhibited inbreeding depression, with reduced sweetness (5.39 °Brix) compared to F_1, although fruit weight increased, possibly due to genetic recombination. The backcross generations, BC_1P_1 and BC_1P_2, tended to resemble their respective recurrent parents, for instance, in BC_1P_1, traits such as average fruit weight (522.73 g) and TSS (6.36 °Brix) were more similar to P_1. Conversely, BC_1P_2 leaned towards P_2 with values like average fruit weight (456.25 g) and TSS (5.24 °Brix). Similar trends were observed across seasons, although overall means were lower under less favourable conditions.

In cross II, across seasons, P_1 (HM) produced large fruits (887 g), high sweetness (10.86 °Brix), moderate fruit length (10.82 cm) and thick flesh (2.53 cm) (Fig. 2). In contrast, P_2 (DSM 19) produced heavier fruits (998 g), longer fruit length (21.15 cm) and an elongated fruit shape, but with lower sweetness (6.34 °Brix). The F_1 hybrids in this cross exhibited reduced average fruit weight (773.13 g), intermediate fruit length (15.7 cm), lower sweetness (6.66 °Brix), and an oblong fruit shape. As in cross I, F_1 showed reduced mean values compared to F_2, indicating inbreeding depression. Both BC_1P_1 and BC_1P_2 generations aligned closely with their

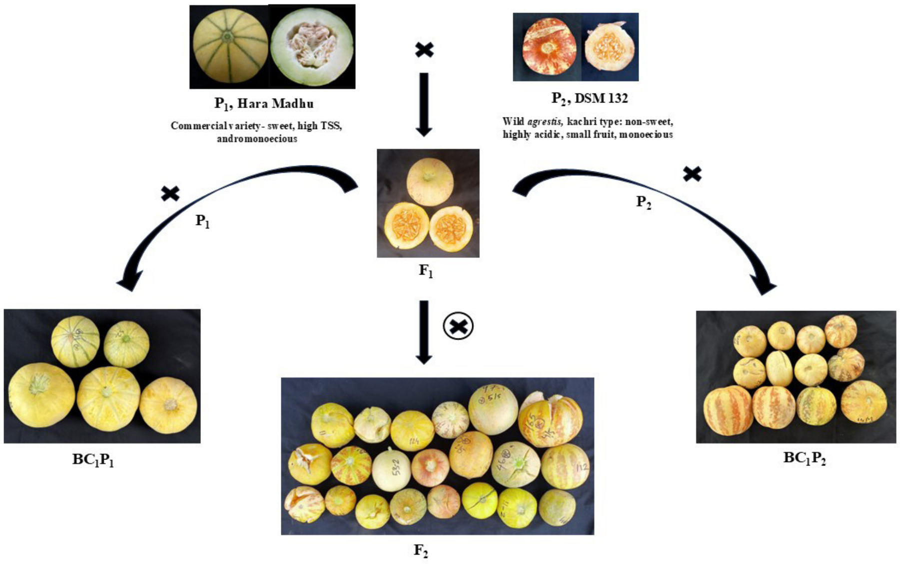

Fig. 1. Schematic representation of development of six basic generations by crossing Hara Madhu and DSM 132 (cross I), to generate F_1, F_2, BC_1P_1 and BC_1P_2

Table 1. Analysis of variance for fruit quality traits across seasons and pooled data in two muskmelon crosses

Mean sum of squares									
Source of variation	df	AFW	FL	FD	FT	CW	TSS	FSI	TA
Cross I-Hara Madhu × DSM 132									
Season I									
Genotype	5	66912.27**	5.11**	3.89**	0.29**	0.73**	10.37**	0.01**	0.01**
Replication	1	82.13	0.84	0.53	0.01	0.05	0.03	0.00	0.00
Error	5	1119.23	0.07	0.03	0.01	0.05	0.02	0.00	0.00
Source of variation	df	AFW	FL	FD	FT	CW	TSS	FSI	TA
Season II									
Genotype	5	32997.52**	2.45**	1.18**	0.04	0.42**	4.92**	0.01	0.01**
Replication	1	349.70	0.00	0.00	0.00	0.02	0.00	0.02	0.00
Error	5	418.19	0.06	0.08	0.02	0.03	0.07	0.02	0.00
Season III									
Genotype	5	68501.47***	5.06**	3.74**	0.31**	0.53**	10.91**	0.01**	0.01**
Replication	1	241.77	0.00	0.00	0.01	0.01	0.00	0.00	0.00
Error	5	465.04	0.03	0.04	0.01	0.03	0.04	0.00	0.00
Pooled									
Genotype	5	162369.96**	12.**	7.86**	0.52**	1.46**	25.34**	0.01	0.03**
Environment	2	21026.76**	1.79*	1.04*	0.20*	0.01*	3.45**	0.01	0.02**
G × E	10	3020.65**	0.31**	0.47**	0.06**	0.13*	0.43**	0.01	0.00
Pooled Error	15	10012.30	0.77	0.71	0.18	0.56	0.63	0.10	0.00
Cross II-Hara Madhu × DSM 19									
Season I									
Genotype	5	80095.42**	36.07**	5.99**	0.26**	1.74**	7.46**	0.33**	0.01**
Replication	1	22.16	0.00	0.05	0.02	0.02	0.00	0.00	0.00
Error	5	957.87	0.32	0.10	0.02	0.02	0.03	0.00	0.00
Season II									
Genotype	5	16667.23**	19.91**	0.65**	0.04**	0.23**	1.74**	0.35**	0.01**
Replication	1	330.23	0.01	0.23	0.00	0.18	0.02	0.00	0.00
Error	5	630.10	0.08	0.06	0.00	0.03	0.01	0.00	0.00
Pooled									
Genotype	5	84448.38**	53.86**	4.46**	0.23**	1.27**	8.03**	0.66**	0.01**
Environment	2	216626.82**	55.035**	13.39**	0.99**	1.44**	6.08**	0.08**	0.01**
G × E	10	12314.35**	2.13**	2.18**	0.06**	0.71**	1.17**	0.03**	0
Pooled Error	15	793.98	0.2	0.08	0.01	0.02	0.02	0	0

respective recurrent parents. These findings are consistent with earlier reports, where F_1 values were higher than F_2 due to inbreeding depression (Shashikumar et al. 2016).

Estimation of gene effects for fruit quality traits through generation mean analysis

The mean data from both crosses, including individual seasonal data and pooled data across six generations and seasons, were subjected to scaling (A, B, C and D) and joint scaling tests (Table 3). Non-significant allelic interactions were observed for titratable acidity (season I) and flesh thickness (season II) in cross I, as well as for fruit shape index (season I and pooled) and titratable acidity (season II) in cross II. The remaining seasons showed significant allelic interactions. Therefore, fruit shape index (FSI) and titratable acidity (TA) demonstrated inconsistent model fit across seasons and crosses, with some datasets conforming to the six-parameter model and others indicating complex epistatic interactions. This suggests a quantitative and environment-dependent inheritance pattern for these traits. In contrast, the remaining traits across both crosses and all seasons consistently deviated from the additive-dominance model, reflecting the involvement of non-allelic gene interactions and epistasis. These findings reaffirm

Table 2. Generation mean analysis for fruit quality traits across seasons and pooled data in two muskmelon crosses

	AFW	FL	FD	FT	CW	TSS	FSI	TA
Cross I-Hara Madhu × DSM 132								
Season I								
P_1	867 ± 20.77	10.1 ± 0.17	11.65 ± 0.18	2.55 ± 0.05	6.38 ± 0.11	10.22 ± 0.17	0.865 ± 0.01	0.15
P_2	386.5 ± 12.61	6.32 ± 0.20	8.96 ± 0.21	1.56 ± 0.03	5.73 ± 0.18	4.56 ± 0.08	0.71 ± 0.01	0.32 ± 0.01
F_1	429.4 ± 8.71	7.55 ± 0.16	8.75 ± 0.18	1.59 ± 0.05	5.39 ± 0.10	5.85 ± 0.10	0.86 ± 0.01	0.21
F_2	504.3 ± 10.11	8.16 ± 0.15	9.37 ± 0.14	1.66 ± 0.03	5.71 ± 0.09	5.39 ± 0.07	0.87 ± 0.01	0.22
BC_1P_1	522.73 ± 18.16	9.22 ± 0.43	10.4 ± 0.33	1.82 ± 0.07	6.2 ± 0.24	6.36 ± 0.10	0.88 ± 0.02	0.19
BC_1P_2	456.25 ± 21.6	7.39 ± 0.39	8.2 ± 0.46	1.56 ± 0.07	4.89 ± 0.26	5.24 ± 0.10	0.91 ± 0.03	0.27 ± 0.01
Season II								
P_1	702 ± 13.97	9.13 ± 0.24	10.39 ± 0.21	1.74 ± 0.07	6.59 ± 0.14	8.4 ± 0.15	0.88 ± 0.01	0.17 ± 0.01
P_2	328 ± 9.75	5.71 ± 0.13	8.12 ± 0.22	1.34 ± 0.03	5.3 ± 0.16	3.93 ± 0.11	0.71 ± 0.01	0.39 ± 0.00
F_1	405.94 ± 4.85	6.97 ± 0.14	8.5 ± 0.15	1.47 ± 0.03	5.51 ± 0.10	5.04 ± 0.08	0.82 ± 0.01	0.27 ± 0.01
F_2	417.27 ± 9.93	7.29 ± 0.15	8.73 ± 0.16	1.5 ± 0.03	5.53 ± 0.11	4.98 ± 0.07	0.84 ± 0.01	0.29 ± 0.01
BC_1P_1	426.3 ± 11.18	7.92 ± 0.25	9.05 ± 0.20	1.57 ± 0.03	5.62 ± 0.16	5.12 ± 0.10	0.87 ± 0.01	0.26 ± 0.01
BC_1P_2	401.83 ± 11.36	7.3 ± 0.22	8.61 ± 0.17	1.48 ± 0.04	5.46 ± 0.13	4.48 ± 0.06	0.85 ± 0.02	0.34 ± 0.01
Season III								
P_1	887 ± 32.49	10.82 ± 0.24	11.97 ± 0.28	2.53 ± 0.08	6.61 ± 0.12	10.86 ± 0.14	0.91 ± 0.01	0.12
P_2	390 ± 16.12	6.06 ± 0.12	8.52 ± 0.17	1.51 ± 0.04	5.4 ± 0.14	4.39 ± 0.12	0.71 ± 0.01	0.3 ± 0.01
F_1	467.55 ± 7.98	7.81 ± 0.14	9.4 ± 0.2	1.77 ± 0.04	5.87 ± 0.15	5.75 ± 0.10	0.84 ± 0.01	0.24
F_2	463.86 ± 10.49	7.6 ± 0.13	8.87 ± 0.14	1.62 ± 0.03	5.79 ± 0.31	5.41 ± 0.08	0.87 ± 0.01	0.21
BC_1P_1	501.48 ± 13.47	8.37 ± 0.20	9.32 ± 0.18	1.7 ± 0.04	5.64 ± 0.11	5.82 ± 0.07	0.9 ± 0.02	0.17
BC_1P_2	408.63 ± 9.5	7.29 ± 0.14	8.11 ± 0.12	1.47 ± 0.03	5.06 ± 0.09	5.11 ± 0.07	0.91 ± 0.02	0.24
Pooled								
P_1	754.49 ± 23.01	9.46 ± 0.21	10.44 ± 0.31	2.06 ± 0.07	6.04 ± 0.17	9.46 ± 0.12	0.88 ± 0.00	0.16 ± 0.00
P_2	381.62 ± 20.59	6.48 ± 0.43	8.66 ± 0.14	1.50 ± 0.03	5.49 ± 0.10	4.36 ± 0.08	0.76 ± 0.05	0.33 ± 0.02
F_1	436.33 ± 2.85	7.50 ± 0.05	8.84 ± 0.05	1.59 ± 0.02	5.53 ± 0.04	5.50 ± 0.04	0.85 ± 0.00	0.24 ± 0.00
F_2	460.16 ± 3.70	7.73 ± 0.05	8.96 ± 0.05	1.59 ± 0.01	5.59 ± 0.06	5.25 ± 0.03	0.87 ± 0.00	0.24 ± 0.00
BC_1P_1	476.59 ± 7.58	8.21 ± 0.13	9.24 ± 0.10	1.64 ± 0.02	5.60 ± 0.06	5.58 ± 0.04	0.88 ± 0.01	0.21 ± 0.00
BC_1P_2	419.80 ± 5.80	7.58 ± 0.08	8.54 ± 0.07	1.51 ± 0.02	5.28 ± 0.05	4.96 ± 0.04	0.90 ± 0.01	0.27 ± 0.00
Cross II- Hara Madhu × DSM 19								
Season I								
P_1	887 ± 32.49	10.82 ± 0.24	11.97 ± 0.28	2.53 ± 0.08	6.61 ± 0.12	10.86 ± 0.14	0.91 ± 0.01	0.12
P_2	998 ± 62.02	21.15 ± 0.63	10.26 ± 0.25	1.87 ± 0.11	5.69 ± 0.26	6.34 ± 0.11	2.06 ± 0.05	0.23 ± 0.01
F_1	773.13 ± 23.16	15.7 ± 0.48	9.63 ± 0.27	1.92 ± 0.06	5.61 ± 0.17	6.66 ± 0.14	1.64 ± 0.04	0.17
F_2	536.25 ± 16.46	11.67 ± 0.27	8.04 ± 0.14	1.62 ± 0.04	4.77 ± 0.09	6.05 ± 0.06	1.47 ± 0.03	0.19
BC_1P_1	481.78 ± 12.16	9.48 ± 0.23	7.43 ± 0.11	1.51 ± 0.03	4.16 ± 0.09	5.89 ± 0.06	1.31 ± 0.03	0.18
BC_1P_2	676.36 ± 32.27	14.51 ± 0.59	7.97 ± 0.19	1.75 ± 0.05	4.37 ± 0.12	5.97 ± 0.07	1.84 ± 0.06	0.22
Season II								
P_1	608 ± 19.54	7.35 ± 0.17	8.29 ± 0.19	1.69 ± 0.05	5.01 ± 0.12	7.79 ± 0.11	0.89 ± 0.01	0.17
P_2	669.5 ± 22.74	15.71 ± 0.59	7.43 ± 0.22	1.44 ± 0.05	4.41 ± 0.11	5.52 ± 0.13	2.12 ± 0.06	0.28

F_1	553.13 ± 24.39	13.19 ± 0.38	8.41 ± 0.16	1.48 ± 0.05	5.15 ± 0.13	5.66 ± 0.12	1.57 ± 0.04	0.20 ± 0.01
F_2	446.5 ± 11.66	9.31 ± 0.39	6.93 ± 0.16	1.29 ± 0.03	4.33 ± 0.11	5.45 ± 0.08	1.36 ± 0.05	0.22 ± 0.01
BC_1P_1	445.08 ± 7.94	8.41 ± 0.18	7.41 ± 0.12	1.40 ± 0.02	4.52 ± 0.10	6.01 ± 0.07	1.14 ± 0.02	0.2
BC_1P_2	490.23 ± 9.95	11.19 ± 0.30	7.86 ± 0.14	1.48 ± 0.03	4.86 ± 0.11	5.29 ± 0.05	1.44 ± 0.04	0.25
Pooled								
P_1	670.86 ± 28	9.44 ± 0.15	9.10 ± 0.36	1.87 ± 0.08	5.22 ± 0.20	8.65 ± 0.22	1.00 ± 0.03	0.16
P_2	727.89 ± 40.92	16.70 ± 0.66	8.36 ± 0.18	1.60 ± 0.04	4.82 ± 0.09	5.91 ± 0.04	1.95 ± 0.05	0.25
F_1	615.07 ± 13.46	13.60 ± 0.27	8.46 ± 0.16	1.63 ± 0.02	5.00 ± 0.11	6.10 ± 0.06	1.56 ± 0.02	0.19
F_2	510.19 ± 11.12	10.72 ± 0.19	7.71 ± 0.09	1.52 ± 0.02	4.59 ± 0.05	5.83 ± 0.05	1.40 ± 0.02	0.21
BC_1P_1	467.99 ± 8.16	9.04 ± 0.16	7.43 ± 0.07	1.46 ± 0.02	4.40 ± 0.05	5.82 ± 0.04	1.25 ± 0.02	0.2
BC_1P_2	562.56 ± 17.66	12.30 ± 0.36	7.71 ± 0.10	1.56 ± 0.03	4.54 ± 0.06	5.65 ± 0.04	1.61 ± 0.04	0.23

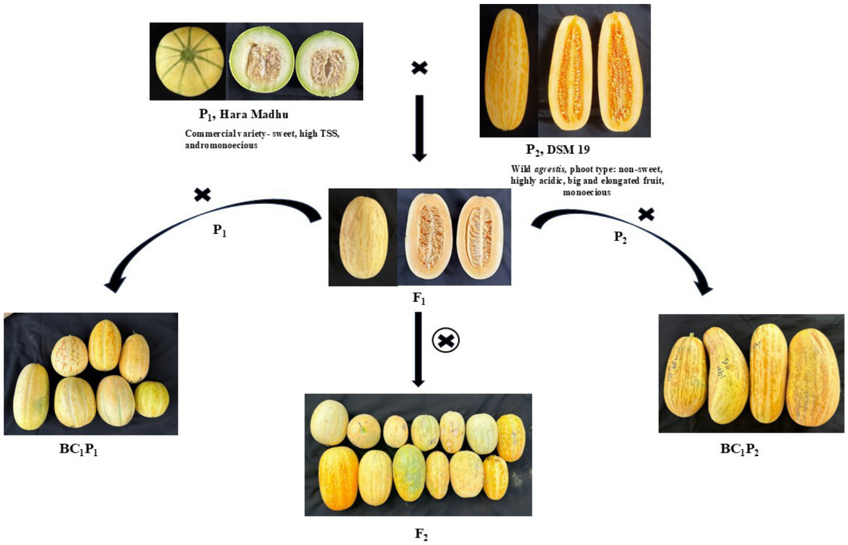

Fig. 2. Schematic representation of development of six basic generations by crossing Hara Madhu and DSM 19 (cross II), to generate F_1, F_2, BC_1P_1 and BC_1P_2

the quantitative nature of trait expression in muskmelon and align with earlier reports by Zalapa et al. (2006), Pornsuriya and Pornsuriya (2009), and Shashikumar et al. (2016). Therefore, a six-parametric model or digenic gene interaction model (*m, d, h, i, j* and *l*) was employed to detect epistasis. The mean effect (*m*) was significant for both crosses and all traits studied across all seasons, indicating that the traits are quantitatively inherited.

In cross I, dominance effects (*h*) for average fruit weight were significantly negative across all seasons and in the pooled data, indicating strong non-additive gene action. Additive effects (d) varied in direction between seasons, suggesting genotype × environment interaction. In cross II, the dominance effect (*h*) was also significantly negative, while the additive effect (*d*) remained non-significant across all seasons. Previous studies in muskmelon have reported the involvement of both additive and non-additive gene actions for this trait (Akrami and Arzani 2019). The dominance × dominance interaction (*l*) was consistently significant and positive throughout, reinforcing the role of duplicate epistasis. In cross II, significant negative dominance effect (*h*) and additive × dominance (*i*) effects, along with positive dominance × dominance interaction (*l*), further reinforced duplicate epistasis as the major governing interaction for average fruit weight. Previous studies reported complementary epistasis (Sakulphrom et al. 2017), while Zalapa et al. (2006) highlighted the involvement of both dominance and epistatic effect. Similarly, the occurrence of both duplicate and complementary epistasis in different crosses was also reported (Shashikumar et al. 2016).

In cross I, fruit length showed no significant gene or epistatic effects during seasons I and II. In contrast, season

Table 3. Estimation of genetic effects and epistasis for fruit quality traits across seasons and pooled data in two muskmelon crosses

		Scaling test				Six parameter model							
	Traits	A	B	C	D	*m*	*d*	*h*	*i*	*j*	***l***	χ2	Epistasis
Cross I- Hara Madhu × DSM 132													
Season I	AFW	237.01**	182.31**	549.07**	-64.88*	471.5	-25.33	-241.71**	129.75*	-54.7	289.57*	73.89**	D
	FL	0.88*	0.47	2.00**	-0.33	7.87**	-0.33	-1.56	0.65	-0.42	0.7	9.76**	-
	FD	1.49**	0.47	3.57**	-0.81	9.09**	-0.6	-0.39	1.62	-1.02	0.34	28.45**	D
	FT	0.64**	0.46*	1.26**	-0.08	1.64**	-0.17	-0.61*	0.16	-0.19	0.94*	44.23**	D
	CW	0.4	0.80*	1.41**	-0.1	5.55**	0.21	-0.35	0.21	0.41	1	20.35**	-
	TSS	3.95**	4.23**	8.15**	0.02	5.52**	0.07	-4.37**	-0.03	0.28	8.21**	206.35**	D
	FSI	-	-	-	-	-	-	-	-	-	-	-	-
	TA	-0.01	-0.02	-0.05	0.01	0.22**	0.001	0.07**	-0.02	-0.004	-0.01	3.38*	-
Season II	AFW	134.71**	255.81**	385.81**	2.35	428.92**	60.42*	-284.44**	-4.7	121.10*	395.22**	67.13**	D
	FL	-0.46	1.52*	1.38*	-0.16	7.35**	0.85*	-1.69	0.33	1.98*	0.73	9.21**	-
	FD	0.47	2.17**	0.83	0.91	9.05**	0.84	-3.57**	-1.82	1.7	4.46**	10.23**	D
	FT	0.07	0.16	0.03	0.1	1.56**	0.05	-0.47*	-0.21	0.1	0.44	2.42	-
	CW	0.3	1.77**	0.34	0.87*	5.83**	0.64	-2.79**	-1.73*	1.47*	3.80**	14.59**	D
	TSS	2.40**	3.23**	5.71**	-0.04	5.01**	0.38	-3.48**	0.09	0.83	5.54**	175.16**	D
	FSI	-	-	-	-	-	-	-	-	-	-	-	-
	TA	-0.05*	-0.06*	-0.12**	0.003	0.29**	0.002	0.12**	-0.01	-0.02	-0.10*	13.26**	D
Season III	AFW	421.01**	280.75**	715.76**	-7	458.58**	-56.95**	-383.96**	14	-140.26*	687.76**	155.10**	D
	FL	2.78**	1.64**	5.33**	-0.45	7.51**	-0.70**	-2.27**	0.91	-1.14*	3.51**	50.53**	D
	FD	3.54**	2.67**	5.70**	0.25	8.96**	-0.28*	-2.87**	-0.51	-0.87	6.72**	59.92**	D
	FT	0.91**	0.77**	1.75**	-0.03	1.62**	-0.06	-0.61**	0.06	-0.14	1.62**	78.28**	D
	CW	1.00**	0.89**	-0.14	1.02	5.98**	-0.06	-2.52*	-2.04	-0.11	3.93**	18.84**	D
	TSS	5.27**	4.45**	10.03**	-0.16	5.42**	-0.53**	-4.56**	0.31	-0.82	9.40**	510.68**	D
	FSI	-	-	-	-	-	-	-	-	-	-	-	-
	TA	-0.02	-0.02	-0.12**	0.04**	0.23**	0.01	0.04*	-0.08**	0.01	0.04	42.07**	-
Pooled	AFW	285.84**	231.06**	539.84**	-11.47	450.90**	-25.29*	-314.32**	22.94	-54.79*	493.96**	103.86**	D
	FL	1.23**	1.05**	2.95**	-0.34*	7.58**	-0.23	-1.61**	0.68*	-0.18	1.59*	27.86**	D
	FD	1.45**	1.43**	2.80**	0.036	8.936**	-0.11	-1.69**	-0.073	-0.023	2.949**	17.04**	D
	FT	0.46**	0.46**	0.91**	0.01	1.588**	-0.039	-0.51**	-0.02	0	0.948**	32.52**	D

Cont...

	CW	0.55	0.61	0.47*	0.35	5.68**	-0.04	-1.19*	-0.7	0.07	1.86**	10.43**	D
	TSS	4.16**	3.90**	7.85**	0.11	5.32**	-0.20*	-4.57**	-0.21	-0.26	8.27*	421.64**	D
	FSI	-	-	-	-	-	-	-	-	-	-	-	-
	TA	-0.04**	-0.05**	-0.10**	0.01	0.24**	0.003	0.11**	-0.01	-0.001	-0.08**	21.97**	D
Cross II- Hara Madhu × DSM 19													
Season I	AFW	487.471**	406.682**	-108.987	501.57**	807.89**	-13.38	-1210.05**	-1003.14**	-80.79	1897.292**	93.29**	D
	FL	8.861**	8.903**	8.025**	4.87**	14.062**	-0.03	0.735	-9.739**	0.04	27.503**	128.17**	-
	FD	5.985**	5.947**	8.429**	1.751**	8.933**	0.25	-5.26**	-3.5	-0.04	15.434**	244.69**	D
	FT	0.99**	1.054**	1.734**	0.155	1.755**	0.07	-0.97**	-0.31**	0.06	2.355**	74.73**	D
	CW	3.197**	3.382**	3.711**	1.434**	5.215**	0.2	-3.74**	-2.87**	0.19	9.447**	199.45**	D
	TSS	5.063**	5.227**	8.873**	0.708**	6.36**	0.04	-5.81**	-1.42**	0.16	11.707**	1305.16**	D
	FSI	0.062	0.05	-0.307	0.21	1.578**	-0.03	0.762**	-0.42	-0.01	0.531	3.24*	-
	TA	-0.08**	-0.04*	-0.025	-0.05**	0.182**	0.02	0.191**	0.091**	0.046*	-0.21**	23.84**	D
Season II	AFW	312.08**	322.38**	478.44**	78.01*	495.80**	17.58	-111.76*	-156.02*	10.3	790.48**	106.72**	D
	FL	5.90**	1.63	1.56	2.98**	10.95**	-1.85*	1.63	-5.97*	-4.27**	13.49**	32.02**	-
	FD	1.52**	1.26**	0.96	0.91*	7.55**	0.08	-2.46**	-1.82*	-0.25	4.60**	25.77**	D
	FT	0.42**	0.34**	0.64**	0.06	1.36**	-0.02	-0.32*	-0.12	-0.09	0.87**	31.39**	D
	CW	0.66**	0.62**	0.13	0.57**	4.68**	0.08	-1.55**	-1.15**	-0.05	2.43**	21.29**	D
	TSS	1.86**	1.84**	4.03**	-0.17	5.48**	0.04	-1.68**	0.34	-0.02	3.36**	153.02**	D
	FSI	0.46**	-0.03	0.11	0.16	1.44**	-0.24**	0.75**	-0.33	-0.49*	0.76*	16.07**	C
	TA	0.03	0.01	0.003	0.02	0.22**	-0.01	0.06	-0.04	-0.02	0.08	5.77**	-
Pooled	AFW	386.09**	411.84**	585.17**	106.38**	552.15**	10.04	-157.59*	-212.76**	25.75	1010.70**	41.95**	D
	FL	5.37**	5.18**	5.59**	2.48**	11.68**	0.05	2.32	-4.96*	-0.19	15.51**	36.01**	-
	FD	2.04**	2.14**	3.13**	0.53	7.94**	0.002	-1.80*	-1.05	0.1	5.24**	19.35**	D
	FT	0.39*	0.44**	0.79**	0.02	1.54**	0.01	-0.36*	-0.03	0.05	0.85**	14.92**	D
	CW	0.93*	1.06**	1.22*	0.38*	4.73**	0.02	-1.15**	-0.77*	0.12	2.76**	14.95**	D
	TSS	2.87**	3.05**	5.45**	0.24	5.91**	-0.01	-3.23**	-0.47	0.18	6.39**	127.40*	D
	FSI	0.18	0.19	0.07	0.16	1.46**	0.02	0.64**	-0.31	0.01	0.68*	5.54*	C
	TA	-0.04**	-0.02	0.002	-0.03**	0.20**	0.02	0.15**	0.06**	0.03	-0.12**	10.96**	D

III and the pooled analysis showed significant negative effects for the dominance effect (*h*), whereas the additive × dominance interaction (*l*) showed a significant positive effect, indicating duplicate epistasis. In cross II, no epistatic interactions were detected. Similar gene interactions controlling fruit length, primarily due to duplicate epistasis, have also been reported earlier in muskmelon.

For fruit diameter, exhibited non-significant effects in cross I during season I, similar to fruit length. However, in the subsequent seasons and in the pooled data, significant negative dominance (*h*) and significant positive dominance × dominance (*l*) epistatic interactions were observed. In cross II, this trait exhibited significant negative (*h*) and significant (*l*) effects, further supporting the role of non-additive gene interactions. These consistent patterns across seasons indicated the predominance of duplicate epistasis in controlling fruit diameter, which corroborates earlier findings by Sakulphrom et al. (2017). In cross I, flesh thickness was influenced by a negative dominance effect (*h*) and a positive dominance × dominance epistatic interaction (*l*) across all seasons except in season I. A similar pattern was noted in cross II. Duplicate epistasis was thus evidentin both crosses, aligning with previous findings in muskmelon (Sakulphrom et al. 2017; Javanmard et al. 2018).

For cavity width, no significant genetic effects were observed in season I of cross I. In both season III and the pooled dataset, only *h* and *l* remained significant withopposite interactions, indicating the presence of duplicate epistasis. A similar trend was observed in cross II. Total soluble solids (TSS) in cross I was strongly influenced by a significant negative dominance effect (*h*) and significant positive dominance × dominance epistatic interaction (*l*) across all seasons and in the pooled dataset. Additive effects were non-significant in seasons I and II but showed a significant negative effect in season III and in the pooled dataset. A similar trend was observed in cross II, with non-significant additive effects acrossall seasons. These results indicate the prevalence of duplicate epistasis in both crosses, consistent with earlier findings in muskmelon for this trait (Javanmard et al. 2018). The influence of dominant gene effects on TSS was also highlighted by Kamer et al. (2014), while Javanmard et al. (2018) reported the significance of additive gene action for this trait.

Fruit shape index (FSI) was non-significant in cross I; therefore, this trait was not considered for genetic analysis. In cross II, the dominance effect (*h*) was consistently positive and significant across all seasons, indicating the presence of dominant gene action favouring higher FSI. Season I showed no significant epistasis, while season II and pooled data showed complementary epistasis, primarily driven by dominant gene effects and their interactions (*h* and *l*), reinforcing the role of non-additive gene action in shaping FSI. Varying results were reported for the fruit shape index in muskmelon, and additive gene action.

In cross I, titratable acidity consistently exhibited a significant dominance effect (*h*) across all seasons and the pooled data, indicating the predominance of non-additive gene action. While nosignificant epistasis was detected in season I, the presence of significant negative dominance × dominance (*l*) in season II and in pooled data suggests the occurrence of duplicate epistasis. Similarly, in cross II, duplicate epistasis was observed in season I and in the pooled analysis. These results partially corroborate Silva et al. (2022), who reported that a major gene with additive and dominance effects, together with polygenes contributing additive effects, governed pH and titratable acidity. Their study also involved a cross between the cultivated variety 'Vedrantais' and the wild accession 'AC-16 (*C. melo* var. *acidulus*), highlighting the significance of wild relatives in acidity-related genetic studies. However, their analysis was based on additive-dominant mixed models, which did not partition digenic interactions. By contrast, our study employed a six-parameter or digenic interaction model, allowing the detection of duplicate epistasis, which provides new insights into the complex genetic architecture of acidity traits. The historical understanding of melon acidity inheritance has evolved with the discovery of the So gene for acidity flavour governed by a monogenic dominant gene, as reported by Harel Beja et al. (2010). Following this, subsequent studies mapped this gene to chromosome 8 and rechristened as *PH* gene (Cohen et al. 2014). More recent investigations, however, have reported polygenic and complex inheritance. For instance, Lee and Kim (2006) reported dominance for higher acidity with polygenic effects, while Zhang et al. (2010) demonstrated the involvement of two primary genes plus polygenes. Our present findings of duplicate epistasis further support this evolving understanding by revealing that non-allelic interactions also play an essential role in regulating titratable acidity, adding an additional layer of complexity to the inheritance of this important fruit quality trait.

Improving fruit quality traits remains a major breeding goal in muskmelon to satisfy customer preferences, industry norms and dietary requirements. Traits such as average fruit weight, flesh thickness, total soluble solids and low titratable acidity content are all quantitatively inherited and governed by complex gene interactions, as revealed in the present study. Understanding the nature of gene action is therefore critical for designing effective breeding strategies. The predominance of non-additive gene action and duplicate across several traits highlights the importance of dominance and gene interactions, indicating that simple selection in early generations may be ineffective. For traits under strong dominance control, heterosis breeding or recurrent selection would be more appropriate, whereas additive traits could be improved through conventional selection.

Although this study primarily focused on phenotypic inheritance using generation mean analysis, the results are consistent with QTL mapping and marker studies identifying genomic regions controlling key fruit quality traits in muskmelon. For example, SSR markers have differentiated *C. melo var. cantalupensis* and *momordica* populations for horticultural traits (Singh et al. 2015), while SNP-based QTL mapping has been used to dissect fruit quality variation (Pereira et al. 2018). Together, these findings reaffirm the polygenic and environment-dependent nature of fruit quality traits. Future work should focus on validating the parental lines used in this study with linked molecular markersand conducting multi-season evaluations to identify stable genetic effects. Integrating conventional breeding with molecular tools will accelerate the development of nutrient-rich, high-quality muskmelon varieties with broad adaptability and consumer appeal.

Author's contribution

Conceptualization of research (HC, RKY, GPM, AK); Designing of the experiments (HC, RKY, GPM, AUS); Contribution of experimental materials (HC, RKY); Execution of field/lab experiments and data collection (KKT); Analysis of data and interpretation (IG, KKT, DCM, HC); Preparation of the manuscript (HC, KKT, IG, AK, AUS).

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