Received: 01 Apr 2025 | Revised: 25 May 2025 | Accepted: 26 May 2025

Electronic Journal of Plant Breeding

Research Article

Determination of breeding approaches for improvement of economic traits in Indian muskmelon (*Cucumis melo* L.) through assessment of gene action

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Abstract
Muskmelon is an important cucurbitaceous vegetable due to its excellent taste, flavour, aroma and other quality traits present in its fruit. Architectural phenotypes of this crop have great potential to increase its fruit yield at the commercial level. Generation mean analysis was conducted in the year 2023 comprising five crosses of muskmelon (PMM-4A x Hara Madhu, PMM-4A x PMM-37, PMM-1 x Hara Madhu, PMM-32 x PMM-16, PMM-13 x PMM-16) derived from seven inbreds to study the gene action for implying correct breeding method to improve some important yield attributing traits. The results found in the present experiment suggest choosing specific breeding technique for a particular cross for improvement in a single character as both the type and intensity of gene action varied for a solitary trait in different crosses. Character-cross combination specified the role of simple additive gene for governing days to first female flower (Cross I and II) and total soluble solid content (Cross I, II, III and IV). Thus, simple pedigree method and selection in early generation could be adopted to improve these traits. Effect of dominance was observed in vine length (Cross-III) and number of fruits (Cross-II) where heterosis could be viable. Most of the cross combinations showed non allelic interaction in digenic level where duplicate epistasis was reported for all the traits like days to female flower (Cross III and IV), vine length (Cross I, II, IV and V), number of fruits per plant (Cross I and III), average fruit weight (Cross I,III, IV and V), fruit flesh thickness (Cross I, III,IV and V), fruit yield (Cross II and V) and TSS content (Cross V) indicating selection to be done in later generations at high intensity. Breeding methods like population improvement through biparental mating or recurrent selection would be effective to achieve sufficient improvement in these characters. On the contrary, the presence of complementary gene action in cross V for earliness, cross IV for number of fruits and cross II for fruit weight showed the significance of heterotic improvement.

Keyword: Gene action, Generation Mean Analysis, Muskmelon, Scaling test, Epistasis

INTRODUCTION

Identification of superior genotypes and development of new cultivars are the results of genetic recombination and further selection of plants exhibiting worthwhile phenotypes. The mode of gene action with the number of genes involved and its interaction with environment are the prerequisites in progress of quantitative genetic variation (Sprague, 1963). Determination of proper breeding technique for optimization of gene action more efficiently depends on the knowledge of the way genes act and interact (Fasoula and Fasoula, 1997). The type and magnitude of gene action, measured in terms of components of genetic variance are responsible for expression of quantitative traits in a breeding population and indispensable to choose the exact breeding strategy for improvement of such economic characters (Sharmila *et al*., 2007). Increase in the number of segregating generations with higher number of observational plants are the factors to enhance the accuracy of gene effect

https://doi.org/10.37992/2025.1602.022

(Cavalli, 1952) controlling the inheritance for yield and yield attributing traits (Gamble, 1962). Generation mean analysis (Hayman, 1958) is the most appropriate quantitative biometric approach (Mather and Jinks, 1982) to estimate the kind and extent of gene action based on the phenotypic performance of specific quantitative trait on maximum possible plant individuals in primary investigational breeding generations (Kearsey and Pooni, 1996). This method can assess the main genetic effect and most importantly their digenic epistatic interaction liable for inheritance of quantitative characters. It produces the mean genotypic value of an individual and can calculate the same for the families or generations (Pooni and Treharne, 1994) and ultimately enables the breeders to recognize the capability of the parents involved in crosses as well as the potential of crosses to be utilized either for heterotic exploration or pedigree method (Sharma and Sain, 2003).

Muskmelon (*Cucumismelo* L.; 2n=2x=24) is one of the commercial warm season vegetables of cucurbitaceae family grown all over the tropical and subtropical parts of the world with Asian origin (Schaefer *et al*., 2009; Sebastian *et al*., 2010) having centre of diversity from Mediterranean Sea to East Asia (Pitrat, 2008). Melon fruits are mostly consumed fresh and its economic importance lies in its refreshing sweetness and flavour, uniquely pleasant aroma, texture and nutritional enrichment (Lester, 2008;Weng *et al*., 2021). The pulp has low calorific value with appreciable quantity of ascorbic acid, folic acid and potassium with phenolics, flavonoids and tochopherols and thereby a good source of antioxidants (Lohani *et al*., 2023; Hiremata *et al.,* 2024). In addition, the orange fleshed cultivars are rich in beta carotene (Lester and Hodges, 2008; Laur and Tian, 2011). The crop is highly cross pollinated and most diverse species under genus *Cucumis* (Bates and Robinson, 1995) due to existence of wide morphological diversity specially in fruit traits like shape, size, firmness, rind pattern, skin fragrance, pulp colour and texture, aroma and sugar content (Mitchell *et al*., 2007; Pitrat, 2008; Fergany *et al*., 2011; Pitrat, 2016). Higher productivity, uniform fruit size and shape with admirable quality are the primary requirements for varietal release in this crop. There is an association between yield and several characters like days to anthesis, vine length, number of primary branches, number of fruits and average fruit weight (Lippert and Hall, 1982; Kultur *et al*., 2001; Abdalla and Aboul-Nasr, 2002; Taha *et al*., 2003). Thus, an insight in to the genetic control of these traits is of prime importance for yield improvement. Although fruit weight and other associated traits are reported (Lippert and Legg, 1972; Monforte *et al*., 2004; Feyzian *et al*., 2009) to be controlled both by simple additive and dominance effect, the complete information regarding the nature and extent of gene action in terms of genetic components of variance including the most important digenic epistatic interaction for expression and inheritance of the above said yield contributing traits in muskmelon are scarcely any (Zalapa *et al*., 2006). The present study was undertaken to gain information about gene action including non-allelic interaction regulating important yield attributing characters in Indian and to determine the appropriate breeding strategy for specific trait improvement.

MATERIALS AND METHODS

The investigational resources consisted of five crosses of muskmelon (PMM-4A x Hara Madhu, PMM-4A x PMM-37, PMM-1 x Hara Madhu, PMM-32 x PMM-16, PMM-13 x PMM-16) derived through manual pollination from seven inbred lines of diverse morphological background (**Table 1**). F_1 plants were selfed to generate F_2 seeds and backcrossed with both the parents to produce the seeds of B_1 and B_2. Therefore, a total of six populations were developed, each including two parents (P_1 and P_2), F_1, F_2, B_1 and B_2 generations. The developed generations with both the parents were grown under open field situation during 2023, at Vegetable Research Centre, Govind Ballav Pant University of Agriculture and Technology, Pantnagar, located at an elevation of 243.83 m above MSL, 29^0 North latitude and 79.3^0 East longitude under Tarai belt of Shiwalik ranges of Himalayas. The experiment was laid out in Randomized Block Design with three replications and healthy crop stand was maintained by following the recommended agronomic practices. The quantitative observations were taken from 10 plants in each parent, 20 plants in F_1, 40 plants in B_1 and B_2 and 120 plants in F_2 generations. The traits under observation were days to first female flowering, vine length (cm), number of fruits per plant, average fruit weight (g), fruit flesh thickness (cm), total fruit yield (q/ha) and total soluble solid (^{0}Brix). Five ripe marketable fruits were taken at random and total soluble solids were measured by digital refractometer (Atago Digital Refractometer by ATAGO CO. LTD, Tokyo, Japan).

Presuming the existence of non-homogenous variances in all the populations the generation mean analysis of six populations and scaling test were executed. The six generations were employed to conduct scaling test (Cavalli, 1952) in order to test the adequacy of six parameter model. Among the four scales (A, B, C and D) as described by Mather (1949) and Hayman and Mather (1955), the significance of A and B specifies the existence of all three types (additive x additive [i], additive x dominance [j] and dominance x dominance [l]) of non-allelic interaction. Significance of C scale indicates the presence of dominance x dominance [l] while D points to the additive x additive [i] epistatic interaction. The mean values of populations for all the generations were employed to estimate the components of genetic variances and evaluate the types of gene action for all the traits (Hayman, 1958; Mather and Jinks, 1971 and 1982). The mid parent [m], additive [d], dominance [h], additive x additive [i], additive x dominance [j] and dominance x dominance [l] are the components of six parameter or digenic interaction model. Student's 't' test was performed at 0.05 and 0.01 levels of probability

https://doi.org/10.37992/2025.1602.022

Table 1. Morphological features and source of muskmelon inbred lines

S.No.	Parent	Morphological trait	Source
1	PMM-4A	Andromonoecious, intermediate growth, elongated globe shaped fruit with pointed peduncle end, yellowish green rind colour and creamy white flesh with high TSS content	PCPGR, Pantnagar, Uttarakhand
2	Hara Madhu	Andromonoecious, viny growth, round shaped large fruit with prominent green suture, light yellow rind colour and light green crispy flesh with high TSS content	PAU, Ludhiana, Punjab
3	PMM-37	Andromonoecious, bushy growth habit, ovate shaped fruit with tapering peduncle end, creamy white rind colour and yellowish green thin flesh with low TSS content	PCPGR, Pantnagar, Uttarakhand
4	PMM-1	Andromonoecious, determinate type, round shaped fruit with yellow rind colour and creamy white medium flesh thickness with moderate TSS content	CIAH, Bikaner, Rajasthan
5	PMM-32	Andromonoecious, long vine, oval shaped fruit with yellowish green rind and greenish white thick mesocarp and high TSS content	CHES, Godhra, Gujarat
6	PMM-16	Andromonoecious, long vine, round shaped fruit with yellow rind and creamy white thick mesocarp and high TSS content	RARI, Durgapura, Rajasthan
7	PMM-13	Andromonoecious, long vine, ovate shaped fruit with prominent suture and truncated peduncle end, creamy white rind and light yellow thick mesocarp and high TSS content	RARI, Durgapura, Rajasthan

(Singh and Singh,1992) to estimate the significance of m, d, h, i, j and l. The presence of similar as well as dissimilar signs of [h] and [l] for a particular cross in a specific trait determined the complementary and duplicate gene action, respectively (Kearsey and Pooni, 1996). The software used for the statistical analysis was Plant Breeder Tools (PBT, 2013) developed by International Rice Research Institute, Philippines.

RESULTS AND DISCUSSION

All the traits under investigation significantly differed among six generations as revealed through the results of analysis of variance which represented the existence of adequate genetic variability as well as illustrated the feasibility for selection of desirable yield and its attributing characters in muskmelon. The progress of any plant breeding programme with the competence of selection and expression of heterosis largely depends upon the magnitude of genetic variability present in the plant population (Singh and Narayanan, 1993; Singh and Chaudhary, 1981). An insight in to the genetic mechanism controlling the expression and inheritance of character is most required for genetic improvement in any crop to develop superior genotypes with all desirable traits.

Analysis of generation means: The trait-mean values with their standard error analyzed under the present experiment for six generations of five cross combinations of muskmelon are presented in **Table 2**. Each inbred parental line involved in each cross showed significant differences for all the traits except days to first female flowering in cross-V; thus substantiating their utility in producing segregating populations. Among all, parent PMM 37 was found best for days to first flowering (38.66) and vine length (4.66 m) while in economic characters like number of fruits per plant (7.60), average fruit weight (1230.12 g) and total fruit yield (263.17 q/ha) PMM-1 was the most superior. Fruit flesh thickness and TSS content were found maximum in parent PMM-16 (4.53 cm) and PMM-4A (14.15^{0}Brix), respectively. Significant differences in mean values of quantitative characters among parental inbred lines confirmed their ability to produce segregating populations with broad genetic base. F_1 generations in all the five crosses showed a blended expression of significant positive heterosis over both mid and better parent for vine length, number of fruits per plant, average fruit weight, fruit flesh thickness and total fruit yield showing the existence of unidirectional dominance and therefore, higher trait mean due to accumulation of superior alleles ultimately enhancing the trait's phenotype as depicted by Bernardo, 2020 and also found by Zalapa *et al*., 2006 and Ranjitha *et al*., 2023, in muskmelon and Kere *et al*.,2013 in cucumber. Trait-mean values for days to first female flowering and TSS content resulted in both positive and negative significant way over the parental ones depicting the presence of bidirectional dominance as shown by Zalapa *et al*., 2006 in muskmelon for number of primary branches and Zdunic *et al*., 2008 regarding grain starch content in maize hybrids. F_1 generation showed intermediate performance for specific crosses in total soluble solid, fruit flesh thickness and vine length depicting the role of incomplete dominance for these traits to be expressed as reported by Panigrahi *et al*., 2023 and Kumari *et al*., 2015, in bitter gourd. On the contrary most of the crosses were found superior to the mid parent value for all the quantitative traits. Some exhibited superior performance than better parent in all quantitative traits except total soluble solids showing the effect of over dominance which can be exploited through heterosis breeding. Similar observations were reported by Dey *et al*., 2012 and Hossain *et al*., 2016 for earliness, vine length and fruit yield in bitter melon. F_2 generation

Table 2. Comparison of means of six generations for various characters in five crosses of muskmelon

Character	Populations					
	P_1	P_2	F_1	F_2	BCP_1	BCP_2
Days to first female flowering						
C-I	42.33(0.33)	39.00(0.21)	44.00(0.21)	41.00(0.10)	41.33(0.33)	39.33(0.33)
C-II	42.33(0.33)	38.66(0.33)	45.33(0.12)	42.00(0.10)	43.66(0.33)	40.33(0.33)
C-III	42.33(0.12)	39.00(0.21)	36.33(0.12)	33.00(0.10)	43.66(0.12)	40.66(0.25)
C-IV	44.33(0.33)	39.33(0.45)	35.33(0.33)	32.66(0.16)	43.33(0.33)	41.33(0.45)
C-V	39.33(0.12)	39.33(0.45)	35.66(0.12)	32.00(0.10)	41.00(0.21)	41.00(0.43)
Vine length (m)						
C-I	2.56 (0.02)	2.99 (0.02)	3.03 (0.03)	3.6 (0.01)	3.20 (0.05)	3.91 (0.01)
C-II	2.56(0.02)	4.66(0.01)	3.95(0.02)	3.74(0.00)	3.54(0.01)	4.43(0.01)
C-III	3.46(0.03)	2.99(0.02)	3.24(0.01)	3.11(0.00)	3.76(0.03)	3.14(0.03)
C-IV	4.24(0.02)	3.41(0.01)	4.03(0.02)	3.76(0.00)	4.03(0.01)	4.25(0.02)
C-V	4.16(0.04)	3.41(0.01)	4.36(0.03)	4.18(0.02)	4.82(0.03)	4.41(0.03)
Number of fruits per plant						
C-I	5.87 (0.24)	6.37 (0.66)	6.53 (0.35)	6.99 (0.41)	7.01 (0.35)	6.89 (0.33)
C-II	5.87 (0.24)	5.35 (0.24)	7.56 (0.26)	7.27 (0.44)	6.83 (0.27)	7.01 (0.32)
C-III	7.60 (0.23)	6.37 (0.66)	7.53 (0.87)	9.17 (1.09)	7.47 (0.54)	9.23 (0.48)
C-IV	5.27 (0.37)	7.24 (0.32)	8.22 (0.54)	7.91 (0.46)	8.12 (0.47)	8.99 (0.59)
C-V	7.00 (0.58)	7.24 (0.32)	10.34 (0.46)	9.89 (0.48)	11.43 (0.87)	10.63 (0.49)
Average fruit weight (g)						
C-I	792.77 (20.30)	858.69 (19.90)	1414.56 (83.64)	682.99 (9.97)	753.88 (28.31)	582.78 (40.11)
C-II	792.77 (20.30)	762.45 (90.56)	1314.83 (28.34)	561.92 (13.14)	689.28 (38.02)	424.00 (35.35)
C-III	1230.12 (45.06)	858.69 (19.90)	1230.49 (36.76)	723.81 (66.15)	732.76 (14.45)	540.80 (77.66)
C-IV	833.83 (33.34)	993.22 (37.06)	1347.59 (94.93)	851.37 (66.80)	699.37 (26.37)	450.65 (15.49)
C-V	1149.11 (26.40)	993.22 (37.06)	1012.78 (25.62)	1102.93 (23.1)	986.42 (31.63)	953.37 (28.39)
Fruit flesh thickness (cm)						
C-I	2.63(0.09)	3.98(0.04)	3.76(0.02)	3.15(0.02)	2.86(0.07)	4.08(0.05)
C-II	2.63(0.09)	3.45(0.08)	3.78(0.01)	3.30(0.00)	2.81(0.08)	3.76(0.07)
C-III	3.20(0.05)	3.98(0.04)	3.55(0.01)	3.20(0.00)	3.45(0.05)	4.15(0.04)
C-IV	4.08(0.04)	4.53(0.04)	4.33(0.02)	3.96(0.02)	4.28(0.05)	4.70(0.02)
C-V	4.40(0.09)	4.53(0.04)	4.85(0.01)	4.26(0.01)	4.61(0.07)	5.73(0.41)
Total fruit yield (q/ha)						
C-I	202.77 (4.49)	205.61 (10.93)	206.45 (8.56)	201.88 (11.51)	206.73 (13.12)	252.97(11.10)
C-II	202.77 (4.49)	200.19 (12.57)	218.82 (10.81)	215.45 (10.01)	216.45 (10.66)	198.60(10.26)
C-III	263.17 (13.01)	205.61 (10.93)	260.84 (10.96)	209.25 (12.01)	193.69 (11.61)	203.58(6.00)
C-IV	207.60 (7.46)	240.58 (6.00)	228.22 (12.43)	196.57 (10.88)	202.87 (11.38)	217.98(10.49)
C-V	241.50 (7.08)	240.58 (6.00)	246.06 (10.66)	192.94 (12.92)	205.61 (10.93)	218.98(12.42)
Total Soluble Solid (^{0} Brix)						
C-I	14.15 (0.08)	10.28 (0.04)	10.03 (0.59)	11.00 (0.35)	10.96 (0.33)	8.33(0.08)
C-II	14.15 (0.08)	8.92(0.10)	7.76(0.31)	7.86(0.12)	9.36(0.46)	7.22(0.12)
C-III	11.46 (0.20)	10.28 (0.04)	11.09 (0.86)	10.42 (0.24)	9.46(0.38)	9.37(0.35)
C-IV	10.11 (0.15)	9.25(0.10)	9.36 (0.20)	10.80 (0.20)	8.92(0.08)	9.46(0.38)
C-V	8.32(0.22)	9.25(0.10)	7.75(0.16)	8.00(0.20)	7.46(0.20)	7.76(0.31)

C-I = PMM-4A x Hara Madhu, C-II = PMM-4A x PMM-37, C-III = PMM-1 x Hara Madhu, C-IV = PMM-32 x PMM-16, C-V = PMM-13 x PMM-16 showed wide variation for all the traits for inbreeding depression as well as transgressive segregation in both positive and negative directions. In the mean values of the characters like days to first female flowering, vine length and number of fruits per plant F_2 progeny fell outside the range of either parents concluding the role of positive or negative complementary effect of additive alleles, epistatic interactions of unique parental elements, over dominance, or any amalgamations of these mechanisms towards inheritance of these traits in muskmelon (De los Reyes, 2019). Inbreeding depression was found more in traits like average fruit weight, fruit flesh thickness, total fruit yield and total soluble solid content and scattered in specific crosses for days to first female flowering and vine length. This could be due to the occurrence of maximum segregation of desirable alleles producing higher frequency of inferior segregants in particular crosses (Angadi, 2015; Rao, 2017). Although being a quality trait, the TSS content showed slight degree of inbreeding depression. Mackay *et al*., 2021 reviewed the same outcome in muskmelon. These results depicted the role of heterotic effect and non-additive gene action in the inheritance of these traits. Both the backcross progenies (B_1 and B_2) showed differences for their parental involvement and the results also revealed that their performance tended towards the respective parents in most of the studied characters (Habiba *et al*., 2016) depicting the presence of both additive and dominance gene action. The present results analyzing the generation means could also not specify the gene action and pattern of inheritance of the studied traits precisely. Therefore, these findings are not enough evidence in support of performing simple selection methods for improving these economic characters in muskmelon.

Analysis of interaction through scaling test: The test of adequacy of scale through scaling test (Hayman, 1958) is a way to distinguish interacting and non-interacting crosses or in other words, to discover the competence of simple additive dominance model or presence of non-allelic interaction. In this method, four tests (A, B, C and D) for scale effects have been employed. When the scale is adequate, the values of A, B, C and D would be non-significant detecting the adequacy of simple additive dominance gene action and absence of epistasis. If the scales are significant, A and B specify additive × dominance (j), C designates dominance × dominance (l) while D denotes additive × additive (i) type of gene interactions for particular traits in the crosses. The results of the scaling tests (**Table 3**) revealed that none among the five crosses had non-significant scale value for any of the seven quantitative characters indicating the inadequacy of simple additive dominance model and presence of digenic or higher order epistasis depicting moderate difficulty for trait improvement. Days to first female flowering, number of fruits per plant and fruit flesh thickness showed significance for each scale for all the crosses indicating the presence of all three types of non-allelic interactions demonstrating the complexity for inheritance of these traits. The same result was also observed for cross I (PMM-4A x Hara Madhu) and IV (PMM-32 x PMM-16) for vine length and cross IV and V (PMM-13 x PMM-16) for average fruit weight. Similar findings were recorded by Senthil *et al.,* 2024 in mungbean, Zalapa *et al*., 2006 and Javanmard *et al*., 2018 in muskmelon and Tiwari *et al*., 2011 in cucumber.

Gene action: The investigation through six parameter model (Jinks and Jones, 1958) revealed the inadequacy of simple additive and dominance gene effect in most of the crosses for inheritance of each quantitative trait and presence of all kinds of epistatic interactions (**Table 4**). The significance of mean [m] for all the quantitative characters denotes that the combined input of overall mean, locus effects and interaction of fixed loci was noteworthy and the traits were quantitatively inherited. Only days to first flowering for C-II (PMM-4A x PMM-37) showed the adequacy of both simple additive (d) and dominance (h) genetic components for inheritance. Thus, improvement of earliness in flowering could be achieved by selection of transgressive segregants through adopting pedigree method followed by heterosis breeding (Pandey and Rai, 2006). Total soluble solids [C-II and C-III (PMM-1 x Hara Madhu)] resulted in competence of only additive genetic component significantly. Therefore, breeding strategy should be simple pedigree method and selection in early generation for effective improvement of TSS. These findings are in congruence with Pandey and Rai, 2006 in pumpkin, Kere *et al*., 2013 and Delaney and Lower and 1987 in cucumber. Significant and positive values of h were recorded for days to first flowering (C-II, III), vine length (C-III), number of fruits per plant (C-I, II, IV), average fruit weight (C-II), total fruit yield and total soluble solids (C-V). Fruit flesh thickness showed the same for all the crosses indicating the predominance of dominant gene effect. Thus, selection should be delayed for these traits till heterozygosity is reduced in population (Rathod *et al*., 2021).

The results of present study further indicated that all the three types of non-allelic interactions with predominance of additive x additive (i) and dominance x dominance (l) effects. The pattern of gene action varied for the same trait in different cross combinations. Days to first female flowering showed both kind of non-allelic interaction. Crosses III and IV indicated earliness as additive genetic component was significant and negative, denoting the efficiency of pedigree selection to select desirable segregants (Mistry *et al*., 2016). They also expressed duplicate epistasis since the signs of h and l were in opposite directions advocating the intensity of selection to be mild for earlier and strong in later generations. Cross V reported both h and l in negative direction suggesting complementary gene action and indicating dominance at the loci towards early flowering, implying desirable heterosis in negative direction for producing individuals with earliness. These findings are in conformity with the findings of Shahi *et al*., 2006 and Choudhary and

Table 3. Significance of scaling test and identification of interacting and non-interacting crosses in muskmelon

Character	Scaling test				Character	Scaling test			
	A	B	C	D	A	B	C	D	
Days to first female flowering					Vine length (m)				
C-I	-3.66** (±0.77)	-4.33** (0.73)	-5.33** (0.72)	1.33* (0.51)	-0.61** (0.12)	-0.01 (0.05)	0.60** (0.09)	0.61** (0.06)	
C-II	-0.33 (0.75)	-3.33** (0.75)	-3.66** (0.68)	3.56 (0.32)	-0.63** (0.04)	0.18** (0.03)	-0.08 (0.07)	0.18** (0.02)	
C-III	8.66** (0.30)	6.00** (0.56)	-22.00** (0.55)	-18.33** (0.35)	-0.05 (0.08)	-0.10 (0.08)	-0.55** (0.06)	-0.20** (0.05)	
C-IV	7.00** (0.81)	8.00** (1.06)	-23.66** (1.08)	-19.33** (0.65)	-0.21** (0.04)	0.05 (0.05)	-1.66** (0.06)	-0.75** (0.03)	
C-V	7.00** (0.47)	7.00** (0.99)	-22.00** (0.68)	-18.00** (0.53)	0.54** (0.08)	-1.28** (0.07)	0.25 (0.13)	0.49** (0.06)	
Number of fruits per plant					Average fruit weight (g)				
C-I	3.60** (0.34)	3.00** (0.29)	-7.40** (0.21)	-7.00** (0.21)	-699.55** (103.03)	-1107.68** (117.59)	-1748.59** (174.32)	-29.32 (52.99)	
C-II	0.53* (0.25)	-1.06** (0.26)	-1.46** (0.30)	-0.46* (0.18)	-952.39** (85.35)	-12.56.29** (118.34)	-2187.55** (121.96)	10.56 (58.20)	
C-III	-1.20** (0.30)	-0.73** (0.15)	2.46** (0.19)	2.20** (0.15)	-968.09** (64.94)	-884.35** (183.51)	-1504.33** (292.68)	174.06 (154.10)	
C-IV	-0.86* (0.31)	-0.86** (0.27)	0.66 (0.35)	1.20** (0.21)	-782.68** (113.56)	-1349.52** (106.52)	-1026.75** (331.56)	552.73** (137.05)	
C-V	0.60* (0.22)	-3.06** (0.17)	2.73** (0.22)	2.60** (0.12)	-882.08** (123.52)	-1251.02** (117.52)	-1214.15** (301.43)	642.52** (128.45)	
Fruit flesh thickness (cm)					Total fruit yield (q/ha)				
C-I	-0.66** (0.17)	0.41** (0.11)	-1.55** (0.14)	-0.65** (0.09)	-43.76 (27.96)	58.92* (24.54)	-32.69 (49.68)	-23.92 (28.72)	
C-II	-0.78** (0.19)	0.30 (0.16)	-0.45** (0.13)	0.01 (0.10)	-32.71 (23.27)	-190.79** (26.45)	-123.35* (49.78)	50.07 (25.69)	
C-III	0.15 (0.13)	0.76** (0.09)	-1.48** (0.07)	-1.20** (0.07)	154.57** (25.43)	-28.95 (28.38)	154.65** (50.75)	14.51 (27.36)	
C-IV	0.15 (0.12)	0.53** (0.07)	-1.41** (0.12)	-1.05** (0.07)	84.77** (28.42)	-12.43 (24.79)	115.48* (46.56)	21.57 (25.38)	
C-V	-0.01 (0.17)	2.08* (0.82)	-1.56** (0.11)	-1.81** (0.41)	155.84** (25.72)	59.05* (28.59)	77.52 (50.02)	-68.68* (26.77)	
Total Soluble Solid (^{0} Brix)									
C-I	0.67 (0.89)	0.65 (0.61)	-5.92** (12.83)	-2.30** (0.78)					
C-II	-1.18 (0.98)	-0.52 (0.41)	-6.7** (0.80)	-2.50** (0.53)					
C-III	-2.17* (0.92)	0.75 (1.15)	-3.01 (2.15)	-0.79 (0.75)					
C-IV	-2.20** (0.49)	-3.16** (0.28)	-7.09 (0.94)	-0.86 (0.47)					
C-V	-0.01 (0.17)	2.08* (0.82)	-1.56** (0.11)	-1.81** (0.41)					

C-I = PMM-4A x Hara Madhu, C-II = PMM-4A x PMM-37, C-III = PMM-1 x Hara Madhu, C-IV = PMM-32 x PMM-16, C-V = PMM-13 x PMM-16; A, B, C and D are the tests to measure scale effect; *Significant at 5% levels of probability, **Significant at 1% levels of probability.

Singh, 2010 in cucumber and Bohn and Davis, 1957 in muskmelon. Both additive and dominance gene effects were found negatively significant in vine length (C-I and II) decreasing the heterosis in positive direction. Only cross-V was found having positively significant d value depicting the role of simple selection for its improvement (Rathod *et al*., 2021). Crosses-III and IV both showed significant h and i effect for vine length in desired direction. Cross-III depicts the significance for heterotic improvement as the h value is higher than i whereas Cross-IV established the role of simple selection since i value surpassed h. All the non-allelic interactions reported in vine length

Table 4. Estimates of gene effects in five crosses of muskmelon through six parameter model

Character	[*m*]	[*d*]	[*h*]	[*i*]	[*j*]	[*l*]	Epistasis
Days to first female flowering							
C-I	41.00**(±0.10)	1.98**(0.47)	0.66(1.07)	-2.56*(1.03)	0.33(0.51)	10.66**(2.02)	--
C-II	42.00**(0.10)	4.68**(1.06)	3.13**(0.47)	--	1.50(0.52)	3.66(2.00)	--
C-III	33.00**(0.10)	-3.00**(0.28)	30.23**(0.72)	34.56**(0.70)	1.33(0.30)	-51.33**(1.25)	Duplicate
C-IV	32.66**(0.16)	-2.14**(0.56)	32.16**(1.37)	38.66**(1.30)	-0.50(0.63)	-53.66**(2.50)	Duplicate
C-V	32.00**(0.10)	1.08(0.96)	-33.03**(1.09)	36.00**(1.06)	--	-51.09**(2.06)	Complementary
Vine length (m)							
C-I	3.86** (0.01)	-0.69** (0.05)	-0.63** (0.13)	-1.32** (0.13)	-0.30(0.06)	1.79**(0.25)	Duplicate
C-II	3.86**(0.00)	-1.22**(0.01)	-0.36**(0.05)	-0.181**(0.04)	-0.40(0.02)	0.81**(0.09)	Duplicate
C-III	3.75**(0.00)	-0.10(0.05)	0.81**(0.11)	0.38**(0.11)	0.02(0.06)	-0.25(0.23)	--
C-IV	3.76**(0.00)	-0.21**(0.02)	1.20**(0.06)	1.50**(0.06)	-0.13(0.02)	-1.34**(0.11)	Duplicate
C-V	5.50**(0.02)	0.98**(0.04)	-0.38**(0.14)	-0.99**(0.13)	0.91(0.05)	1.43**(0.22)	Duplicate
Number of fruits per plant							
C-I	9.60**(0.02)	0.71**(0.21)	11.16**(0.44)	13.98**(0.43)	0.30(0.21)	-20.60**(0.87)	Duplicate
C-II	11.93**(0.04)	1.69**(0.15)	2.01**(0.38)	1.01*(0.36)	0.80(0.17)	-0.40(0.70)	--
C-III	12.40**(0.02)	-1.46**(0.14)	-1.30**(0.32)	-3.45**(0.31)	-0.26(0.16)	6.33**(0.62)	Duplicate
C-IV	13.06**(0.06)	-0.98**(0.17)	2.11**(0.45)	-2.40**(0.43)	-0.79(0.12)	3.06**(0.79)	Complementary
C-V	16.60**(0.02)	3.53**(0.11)	-0.23(0.26)	-4.28**(0.24)	1.83(0.12)	5.68**(0.50)	--
Average fruit weight (g)							
C-I	884.35**(106.93)	-32.96(14.21)	-1335.60**(319.30)	-58.62(105.98)	408.12*(102.22)	1865.81*(262.59)	Duplicate
C-II	896.95**(125.60)	113.32(47.16)	1785.01**(359.10)	-21.16(116.40)	303.91(140.29)	2229.89**(290.87)	Complementary
C-III	1344.18*(312.29)	233.83*(50.57)	-2340.84*(727.34)	-347.92(308.17)	-83.81(187.59)	2200.26**(430.67)	Duplicate
C-IV	1973.81*(275.23)	-34.69(24.92)	-3863.76**(577.74)	-1105.29(274.09)	566.84**(78.86)	3237.51**(353.36)	Duplicate
C-V	1693.81**(225.03)	-137.69(49.80)	-3920.96**(569.14)	-1805.49(256.88)	677.37**(82.86)	3329.43**(342.16)	Duplicate
Fruit flesh thickness (cm)							
C-I	3.15**(0.02)	-1.21**(0.08)	1.75**(0.20)	1.30**(0.19)	-0.54(0.10)	-1.05**(0.38)	Duplicate
C-II	3.30**(0.00)	-0.95**(0.10)	0.70**(0.22)	-0.03(0.21)	-0.54(0.12)	0.51(0.45)	--
C-III	3.20**(0.00)	-0.70**(0.07)	2.35**(0.15)	2.40**(0.14)	-0.30(0.08)	-3.31**(0.30)	Duplicate
C-IV	3.96**(0.02)	-0.41**(0.06)	2.12**(0.15)	-2.10**(0.14)	-0.19(0.06)	-2.78**(0.27)	Duplicate
C-V	4.26**(0.01)	-1.11*(0.41)	4.01**(0.83)	3.63**(0.83)	-1.05(0.41)	-5.70**(1.66)	Duplicate
Total fruit yield (q/ha)							
C-I	173.82*(57.58)	-18.90**(3.75)	95.65(138.96)	47.85(57.45)	-102.68*(35.18)	-63.02(84.82)	--
C-II	333.11**(51.82)	-30.19*(6.67)	-395.91*(123.28)	-100.14(51.39)	158.08**(31.63)	323.64**(75.94)	Duplicate
C-III	260.46**(55.16)	-31.72*(6.95)	-10.68(133.17)	-29.02(54.72)	183.52**(35.16)	-96.60(82.15)	--
C-IV	225.56**(51.27)	-58.16**(7.16)	-13.28(126.30)	-43.14(50.77)	97.19*(34.95)	-29.19(78.95)	--
C-V	56.34(54.31)	-69.45**(9.04)	501.09**(131.45)	137.36(53.55)	96.78*(36.41)	-352.26**(80.61)	Duplicate
Total Soluble Solid (^{0} Brix)							
C-I	5.32**(1.56)	4.64**(0.06)	5.98(3.52)	4.60(1.56)	-0.01(0.69)	-3.28**(2.28)	--
C-II	4.31**(1.07)	4.83**(0.06)	6.75(3.05)	4.99(1.07)	-0.66(0.96)	-3.30(2.07)	--
C-III	8.87**(1.50)	5.99**(0.11)	0.47(3.60)	1.60(1.50)	-2.91(0.82)	-0.18(2.68)	--
C-IV	8.41**(0.95)	5.25**(0.08)	-3.63(2.17)	1.73(0.94)	0.96(0.48)	3.62*(1.30)	--
C-V	4.26**(0.01)	-1.11(0.41)	4.01**(0.83)	3.63**(0.83)	-1.05(0.41)	-5.70**(1.66)	Duplicate

C-I = PMM-4A x Hara Madhu, C-II = PMM-4A x PMM-37, C-III = PMM-1 x Hara Madhu, C-IV = PMM-32 x PMM-16, C-V = PMM-13 x PMM-16; m, [*d*], [*h*], [*i*], [*j*] and [*1*] denote mean, additive effect, dominance effect, additive x additive, additive x dominance and dominance x dominance, respectively. *Significant at 5% levels of probability, **Significant at 1% levels of probability.

were of duplicate type demonstrating the approach of population improvement through bi-parental mating or recurrent selection to be more efficient for accumulation of desirable genes and also to break unwanted linkages. The results agree with the findings of Mistry *et al*., 2016 in brinjal for plant height, Sanandia *et al*., 2010, in sponge gourd, Munshi and Verma, 1998 in muskmelon, Delaney and Lower, 1987 in cucumber, Panigrahi *et al*., 2023 in bitter gourd and Kaur *et al*., 2018 in summer squash for vine length. Among the economic traits, number of fruits per plant showed a combination of non-allelic interaction and effect of both genetic components. Based on the results, it could be inferred that bulk or pedigree method would be effective for improvement of this trait (Rathod *et al*., 2021) as both d and h are significant in desirable direction (crosses-I and II). Since additive effect is larger than dominance, the character needs selection in early segregating generation (Javanmard *et al*., 2018). The dominance x dominance type (l) of non-allelic interaction influenced the inheritance of fruit number (Celine and Sirohi, 1998) in crosses III, IV and V suggesting to adopt recurrent selection or heterosis breeding to improve this trait. Prevalence of both duplicate (C-I and III) and complementary (C-IV) type of epistasis advocates the implementation of population improvement and heterosis breeding respectively, for improvement of this character. The observations are in agreement with the findings of Tiwari *et al*., 2011;Sun *et al*., 2006 and Shahi *et al*., 2006 in cucumber, Rani *et al*., 2013 and Tewari *et al*., 1998 in bitter gourd, Chadha *et al*., 1972 and Jose *et al*., 2005 in muskmelon. The trait average fruit weight directly contributes towards fruit yield of individual plant in muskmelon. The results of the studied crosses showed the control of dominant gene effect in governing this character (Mistry *et al*., 2016, Selvakumar *et al*., 2021). There is an indication of contribution of recessive alleles from male due to expression of dominance component with negative sign for all the crosses except cross-II. In this trait, only cross-III showed the effect of additive genetic component in desirable direction whereas cross-II resulted in dominance gene action. The negative sign of additive x additive interaction shows dispersion of alleles in parents. Many dominant genes in a progressive way have small effects in controlling the expression of this particular trait as all the crosses showed epistasis with prevalence of dominance and dominance x dominance gene interaction which is also the same reason behind inability of isolating recombinant lines expressing improvement in this character (Aravindkumar, 2004). Therefore, all the cross combinations were valuable foundation of complementary dominant genes and interallelic gene combinations for exploiting this trait through hybrid vigour. Hence, heterosis breeding and population improvement through recurrent selection for specific combining ability would be the options to be taken on to exploit dominant variances and the epistasis with elevated intensity of dominant interactions (Mohanty *et al*., 1999; Chandrakumar, 2006; Kaur *et al*., 2018). Regarding fruit flesh thickness, each cross showed dominance gene action in the desirable direction but the interaction of dominance x dominance resulted significantly in the undesirable direction. The duplicate epistasis revealed the hindrance of improvement through selection as it decreases the variation in F_2 and subsequent generations. As a consequence, the selection should be delayed to later generation to achieve a high level of homozygosity and gene fixation. This finding is in agreement with the observations of Kaur *et al*., 2018 in bitter gourd, Mohan *et al*., 2012 in ash gourd, Sirohi and Ghoruri, 1993 and Mohanty *et al*., 1999 in pumpkin and Aravindkumar, 2004 and Javanmard *et al*., 2018 in muskmelon and Selvakumar *et al*., 2021 in carrot. Fruit yield showed the positive and significant response of additive x dominance with negative directional values of dominance x dominance gene interaction in combination with duplicate epistasis disclosing the role of selection in later generations, hybrid vigour and population improvement through biparental mating or recurrent selection in efficient accumulation of desirable genes and/or to split unwanted linkages for improvement of this character. These observations agree with the reports of Kaur *et al*., 2018 and Rathod *et al*. 2021 in bitter gourd, Pandey and Rai, 2006 in pumpkin, Delaney and Lower, 1987, Tiwari *et al*., 2011 and Kere *et al*., 2013 in cucumber and Bohn and Davis, 1957; Chadha *et al*., 1972; Jose *et al*., 2005, and Javanmard *et al*., 2018 in muskmelon. Total soluble solid (TSS) is an extremely important quality trait. In our experiment, this trait was observed to be influenced by additive genetic variance and all the crosses reported no epistasis except C-IV with duplicate type of digenic interaction. Most of the crosses showed dominance x dominance interaction in undesirable direction depicting the inefficiency of heterosis. Based on the results it could be concluded that simple selection in earlier generations would be effective (Javanmard *et al*., 2018; Silva *et al*., 2022) to get progenies with higher TSS content.

The results obtained in the present experiment recommend implementation of specific breeding strategy for a particular cross combination in order to get improvement in a single trait as both the type and intensity of genetic component of variance varied for controlling a solitary character in different crosses. Simple selection in earlier generation through pedigree breeding could be adopted to improve the characters governed by additive gene effect. Dominance with complementary type of non-allelic interaction could be exploited through heterosis breeding or by recurrent selection for specific combining ability. Traits governed by both additive and non-additive type of genetic components are challenging to improve through direct selection. Therefore, recombination breeding followed by selection in later generations would be the way of achievement in this case. Recurrent selection would be an option of population improvement by mitigating the exposure of deleterious recessive alleles from selected selfed progeny. Despite having high degree of dominance and dominance x dominance interactions the hybrid vigour could not be exploited due to the presence of duplicate epistasis for most of the traits under this study. In such crosses, selecting a superior plant in earlier generations should be lenient whereas in later generations the same should be intense as it assesses the improvement through selection. Therefore, to make use of non-additive gene effect and to tackle non-allelic interactions, breeding strategies like restricted recurrent selection through intermating carried among improved segregates, followed by selection or biparental or diallel selective mating or multiple crosses during the initial segregating generations would be effective to get desirable genotype with improved traits. Furthermore, targeted crossing among selected individuals in early segregating generations could be done to maintain substantial heterozygosity and therefore, all three kinds of gene effects would concurrently be utilized in an efficient way through adopting few cycles of recurrent selection, followed by pedigree method which will ultimately generate more variability in later generations for selecting individuals having improved yield, quality and architectural traits.

ACKNOWLEDGEMENT

The authors gratefully acknowledge the facilities provided by Department of Vegetable Science, College of Agriculture, Govind Ballav Pant University of Agriculture and Technology, Pantnagar-263145, U.S. Nagar, Uttarakhand, India

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