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Genetic Inheritance of Structural Traits in Tropical Carrot (*Daucus carota* L.)

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Abstract

The estimates of gene action and interactions in the inheritance of structural and economic traits in tropical carrot was evaluated through genetic analysis in a field study during 2011-15 at Indian Agricultural Research Institute (IARI), New Delhi, India. The four parental inbred lines, twelve F_1 and F_2 individuals and twenty four B_1 and B_2 generations were grown in the research field of Vegetable Research Farm, IARI, New Delhi, using randomized block design with three replications during the 2014-15 winter season. The six generation of structural traits inheritance were analyzed by using Mather and Jinks six parameter model. These experimental results revealed that the complimentary and duplicate type gene interaction was governed in plant height, top height, number of leaves, and plant weight. These epistatic effects can be exploited through development of hybrid cultivars by heterosis breeding. Although, these experimental results suggesting that frequency of gene dispersal between parents in earlier generation were higher for controlling inheritance of these traits with respective crosses. These genetic information is more helpful to find the inheritance nature and magnitude of gene interaction in order to formulate suitable breeding methodology for identifying the segregants with desirable structural and horticultural economic traits.

Keywords: *Carrot; Generation; Heterosis; Gene; Selection*

Introduction

Carrot is an important economical root crop and grown widely throughout the world. Its roots has purple, red, orange and yellow colour which are originated from oriental and occidental parts of world. It provides dietary sources of β-carotene, lycopene, anthocyanin, lutein, tocopherol, sugars phenolics, isocoumarines, terpenes and sesquiterpenes [1,2]. Recent consumption of carrot has steadily increased due to its nutritionally rich fresh and functional enrichment of processed products. The improved genetic background and nutritional profile such as improved flavours and more diverse pigments are of immense importance for the vegetable industry and consumers [3]. This genetic approach will help tackling malnutrition and supply good quality of carrot to the farmers, consumers and processing industry, thus, there is an urgent need of development of nutritional rich hybrids and cultivars. Hence, different genetic mechanism of phenotypically contrasting carrot genetic information needed for framing the plant architecture and horticultural economic traits for hybrid and cultivars. The main objective of carrot breeding programs is the bringing up high yielding and well adopted cultivar with desirable structural and economic traits. Breeding for such cultivars requires through understanding of genetic components of carrot. Many breeding procedures have been brought up for increasing yield of carrot but in order to bring up best hybrid combinations, a large population of carrot inbred lines are crosses to each other. Before the improvement of high yielding carrot cultivars and/or hybrids it is an important to study the economic components of gene interaction and effects. Generation mean analysis is an efficient technique to estimates of additive [d], dominance [h], additive × additive [i], additive × dominance [j] and dominance × dominance [l] gene action and effects in interacting and non-interacting crosses [4,5]. The sign of [h] and [l] gene effects are deciding the complimentary and duplicate type of epistatic gene interaction in mean population. The suitable breeding strategies of selection and hybrid exploitation are chosen based on type of epistasis noticed in the crosses. A large number of genetic analysis studies have been available for crop plants but very little emphasis on the structural traits such as plant height, top height, number of leaves, plant weight and foliage weight which are usually not considered for such studies but these genetic information will useful for the frame the plant architecture for substantial contribution towards carrot economic traits such as root length, root diameter, flesh thickness, root to top ratio. Thus, these experimental research studies have been conducted to know about gene action and interactions in the inheritance of structural traits in crosses between four phenotypical contrasting groups of carrot inbred lines i.e. inbred lines of yellow, purple, red and orange colour of root epidermal, phloem and xylem region. These research finding will bring up new information of genetic components of structural traits and would bring up new plant architectural and economic traits information. These genetic inheritance studies will helps in the precise understanding of gene interaction and breeding selection of potential parental lines or crosses. Furthermore, these breeding strategy will help accelerate to tropical carrot breeding with genesis of new carrot cultivars and hybrids.

Materials and Methods

Plant materials

The four inbred lines of White Pale, IPC-126, IPC-122 and PM were used in this study. The phenotypic characteristic feature of these lines were yellow, purple, red and orange coloured root epidermal layer, outer cortex (phloem) and inner cortex (xylem), respectively. Filial generation (F_1) were developed from these four inbred lines were self-pollinated to produce F_2 generations and backcrossed to get B_1 and B_2 generations for genetic analysis. The parental inbred lines, 25 F1, 300 F2 and 50 each of B1 and B2 tagged plants were taken for structural trait analysis.

Pollination program

Four different contrasting phenotypes of tropical carrot seeds were collected from the genetic bank maintained at the Division of Vegetable Science, IARI, New Delhi, India. These carrot seeds were sown during 2011-12 at Vegetable Research Farm, IARI, New Delhi, India. The carrot lines were chosen on the basis of root size, uniform colour of root epidermal, phloem and xylem and morphological characters. These selected lines were steckled and grown under net house for inbred line development. These carrot lines were selfed and harvested to get homozygous seeds. The harvested carrot inbred seeds were grown during 2012-13 for hybridization programme. The uniform root epidermal, phloem and xylem colour, size, shape roots of inbred lines were selected and grown under net house for crossing purpose. These selected inbred lines were crossed by manual emasculation and pollination with ten fertile inbred lines of cross combinations. The crossed F_1 seeds were harvested and sown during 2013-14. These F_1 carrot roots were harvested and advanced for F_2, B_1 and B_2 generation by selfing of F_1 plants, crossing with female and male parents, respectively. The harvested F_2, B_1 and B_2 seeds were grown during 2014-15 for F_2, B_1 and B_2 roots.

Experimental design

The experimental carrot field was laid out in Randomized Block Design with three replications. The P_1, P_2, F_1, F_2, B_1 and B_2 populations were grown for performance at the Vegetable Research Farm of Division of Vegetable Science, Indian Agricultural Research Institute, New Delhi New Delhi, India, located at an elevation of about 228m above MSL, 20°40′ north latitude and 77°13′ east longitude during the winter of 2013-14 and 2014-15. Each of these populations consist of 50 parental inbred lines (P_1 and P_2), 50 F1 individuals (3 block) and approximately 500 F_2 and 100 of each backcross (B_1 and B_2). Phenotypic data of roots were recorded on an individual plant of six populations for each cross where 20, 20, 25, 300, 50 and 50 plants were chosen from P_1, P_2, F_1, F_2, B_1 and B_2 generations of three cross combinations, respectively.

Horticultural operations

The experimental plot of parents, F_1, F_2, B_1 and B_2 consist of two, two, ten, three and three rows of 2.5m length each with spacing of 45 and 10cm between rows and plants, respectively. Before sowing of carrot seeds on the ridges, Pendimethalin at 3L a.i/ha were sprayed for control of weeds, after proper checking of moisture in the soil and an optimum moisture was maintained by irrigation up to half of the ridges in the experimental plots. The recommended fertilizer of NPK (40:60:60 Kg/ha) were applied during field preparations in the experimental plots. After thirty days of carrot sowing with earthing up and thinning, 40 Kg/ha of nitrogen dose was applied.

Structural traits

The research experiments involved the six basic generations of P_1, P_2, F_1, F_2, B_1 and B_2 of twelve crosses. The harvested carrot roots were observed for structural traits viz., plant length (cm), top height (cm), number of leaves, plant weight (g) and foliage weight.

Statistical analyses and structural traits analysis

The data collected from structural traits were subjected to study the genetic components in tropical carrot.

Generation mean analysis

The genetic components were estimated from mean values and standard errors for all generations by Mather and Jinks [6] and 't' test were used for significance of the scales and gene interactions effects. The test of adequacy of three and six parameter model was done by joint scaling test and individual scaling test of six generations [7]. The scaling test of A, B, C and D were done by Mather [8] and Hayman and Mather [9] method in which significance of 'A' and 'B' scale indicate that presence of three non-allelic interaction effects (additive × additive [i], additive × dominance [j] and dominance × dominance [l]), 'C' scale indicate the dominance × dominance [l] epistatic interaction effects and 'D' scale indicate the additive × additive [i] epistatic interaction effects. When the joint scaling test or three parameter model (mean [m], additive [d] and dominance [h]) of Cavelli [7] were significant, a six parameter were successfully used to test of fitness of appropriate genetic model as per Hayman [10], Mather and Jinks [4] and Mather and Jinks [6]. The six parameter or digenic interaction model consist of additive × additive [i] additive × dominance [j] and dominance × dominance [l] in addition to three parameter model. The significance of m, [d], [h], [i], [j] and [l] genetic effects were done by 't' test at the 0.05 and 0.01 levels of probability [11]. The type of epistatic gene interaction were determined by Kearsey and Pooni [12] as presence of similar sign of dominance [h] and dominance × dominance [l] effects when it is noted as complimentary epistasis while dissimilar sign of [h] and [l] effects then it is duplicate type of epistatic gene interaction. Genetic analysis were carried out separately for each cross using the plant breeder tools (PBT) [13] software developed by International Rice Research Institute, Department of plant breeding, genetics and biometrics. Philippines.

Results and Discussion

Structural traits

Plant length

The scaling test showed that scales A, B, C and D in White Pale × PM, IPC-126 × White Pale, PM × White Pale, IPC-122 × White Pale, IPC-122 × IPC-126, IPC-122 × PM crosses, A, B and C in White Pale × IPC-126 cross, A and C in White Pale × IPC-122 cross, B and C in PM × IPC-126, PM × IPC-122 crosses and scales C and D in IPC-126 × IPC-122 cross were significant and explained the presence of digenic gene interactions (Table 1). The epistatic gene interaction was presented in table 2. The positive dominance [h] and dominance × dominance [l] type of gene interactions was influencing the plant length along with negative effect of additive [d] gene in White Pale × IPC-126 and White Pale × IPC-122. Cukadar-Olmedo and Miller [13] and Edwards., et al. [14] stated in sunflower and wheat, respectively, in that the additive [d] gene of positive and negative sign depend on the female parent (P1). The dominance × dominance [l] type of gene interactions was significantly controlling than dominance [h] gene in the White Pale × PM, IPC-122 × White Pale and IPC-122 × PM crosses for this trait, in addition to these gene interactions, additive gene [d] also expressing in IPC-122 × PM cross. The value of [h] and [l] were increasing with favourable alleles in heterotic situations [16]. These similar research findings were reported in wheat [17], tomato [18] and sesame [19]. The additive [d], dominance [h], additive × dominance [j] and dominance × dominance [l] type of gene interactions was observed in the PM × IPC-126 and PM × IPC-122 crosses. The positive dominance [h], additive × dominance [j] and was significantly governing this trait in PM ×White Pale cross with negative additive [d] gene. The positive dominance [h], additive × additive [i] and dominance × dominance [l] type of gene interactions was significantly higher than the additive × dominance [j] type of gene interactions in the IPC-126 × White Pale and IPC-122 × White Pale crosses. The positive effects of dominance [h] and additive × additive [i] gene interactions was observed in IPC-126 × IPC-122 cross along with the negative effects of additive × dominance [j] gene interactions. The complimentary type of non-allelic gene interactions was observed due to same sign of dominance [h] and dominance × dominance [l] in all the crosses except IPC-126 × IPC-122 cross. In this non-allelic interaction inflates variation in F_2 populations with dominant effects, thus favours the hybrid exploitation through heterosis breeding [20-22]. Similar results were also reported in maize for plant height [23,24].

Top height

The simple scale test revealed that significant of scales A, B, C and D in White Pale × IPC-126, White Pale × IPC-122, PM × IPC-122 crosses, A, B and C in PM × IPC-126 cross, A, C and D in IPC-126 × White Pale, IPC-126 × IPC-122, IPC-122 × IPC-126 crosses, A and C in IPC-122 × White Pale, IPC-122 × PM crosses, B and C in IPC-126 × PM cross and scale in C and D in PM × White Pale cross which are presented in table 1. The dominance [h], additive × additive [i] type of gene interactions was observed positively significant than dominance

Structural traits	Cross	Scaling Test				Joint Scaling Test		
		A ± SE	B ± SE	C ± SE	D ± SE	m ± SE	d ± SE	h ± SE
Plant height (cm)	White Pale × IPC-126	39.86** ± 2.18	37.59** ± 2.91	78.91** ± 3.27	-0.73 ± 1.90	70.35** ± 0.59	2.50** ± 0.60	2.21* ± 1.12
	White Pale × IPC-122	-5.45** ± 3.24	-4.42 ± 3.72	2.14** ± 3.27	-3.51 ± 2.56	76.59** ± 0.68	3.60** ± 0.71	6.77** ± 1.24
	White Pale × PM	21.76** ± 2.33	18.24** ± 2.62	20.18** ± 3.24	9.91** ± 2.09	67.04** ± 0.46	-3.83** ± 0.47	14.71** ± 0.86
	IPC-126 × White Pale	23.39** ± 4.40	11.98** ± 3.04	55.95** ± 3.68	-10.29** ± 2.68	73.92** ± 0.61	-2.63** ± 0.63	-4.42** ± 1.26
	IPC-126 × IPC-122	1.15 ± 3.13	-4.00 ± 3.55	26.11** ± 4.11	-14.48** ± 2.46	79.25** ± 0.78	-1.12** ± 0.81	1.91** ± 1.45
	IPC-126 × PM	16.82** ± 3.23	-2.38 ± 3.77	17.01** ± 3.31	-1.28 ± 2.69	71.54** ± 0.58	-7.25** ± 0.62	11.74** ± 0.97
	PM × White Pale	13.47** ± 3.06	8.42* ± 3.64	39.12** ± 3.76	-8.60** ± 2.60	67.51** ± 0.47	4.31** ± 0.48	11.51** ± 1.08
	PM × IPC-126	-6.74 ± 3.93	29.85** ± 2.80	22.93** ± 3.14	0.08 ± 2.62	69.95** ± 0.57	5.73** ± 0.61	14.23** ± 0.87
	PM × IPC-122	-3.71 ± 3.41	21.22** ± 3.27	25.73** ± 3.86	-4.11 ± 2.47	69.41** ± 0.68	4.94** ± 0.70	9.55** ± 1.32
	IPC-122 × White Pale	16.00** ± 3.85	8.15** ± 2.73	12.62** ± 3.76	5.77* ± 2.54	74.86** ± 0.68	-2.41** ± 0.71	6.24** ± 1.21
	IPC-122 × IPC-126	16.40** ± 3.53	14.79** ± 3.14	43.01** ± 3.90	-5.91* ± 2.37	76.37** ± 0.78	1.98* ± 0.81	-1.32** ± 1.45
	IPC-122 × PM	21.02** ± 3.22	21.09** ± 3.86	21.64** ± 3.87	10.23** ± 2.61	69.73** ± 0.68	-5.87** ± 0.70	8.39** ± 1.32
Top height (cm)	White Pale × IPC-126	32.31** ± 2.25	23.83** ± 2.61	65.06** ± 3.65	-4.46** ± 1.65	46.10** ± 0.58	2.05** ± 0.56	-6.08** ± 1.22
	White Pale × IPC-122	-10.39** ± 3.20	-12.61** ± 3.71	-8.11* ± 3.48	-7.44** ± 2.49	52.81** ± 0.64	4.03** ± 0.67	1.62** ± 1.23
	White Pale × PM	10.92** ± 2.80	11.10** ± 2.39	14.25** ± 3.17	8.88** ± 2.10	44.10** ± 0.47	-3.37** ± 0.48	7.63** ± 0.91
	IPC-126 × White Pale	10.34** ± 3.95	5.46 ± 3.62	41.48** ± 3.86	-12.84** ± 2.65	47.94** ± 0.59	-1.22* ± 0.60	-2.65* ± 1.28
	IPC-126 × IPC-122	-6.08* ± 2.90	-4.39 ± 3.12	13.66** ± 3.96	-12.06** ± 2.20	53.17** ± 0.70	1.43* ± 0.71	-2.32** ± 1.38
	IPC-126 × PM	-0.35 ± 2.55	-7.12** ± 3.31	-13.40** ± 2.99	-2.03 ± 2.29	47.03** ± 0.53	-5.12** ± 0.56	6.12** ± 0.96
	PM × White Pale	4.82 ± 3.61	-3.05 ± 3.08	22.01** ± 3.69	-10.12** ± 2.50	44.14** ± 0.48	3.50** ± 0.49	5.88** ± 1.11
	PM × IPC-126	-12.43** ± 3.24	13.75** ± 2.38	-12.11** ± 2.60	1.72 ± 2.12	46.21** ± 0.51	3.81** ± 0.55	6.84** ± 0.84
	PM × IPC-122	-14.93** ± 3.21	7.21* ± 3.61	11.82** ± 3.54	-9.77** ± 2.48	47.40** ± 0.62	5.64** ± 0.64	3.14* ± 1.22
	IPC-122 × White Pale	9.98* ± 4.36	4.61 ± 3.68	12.81** ± 4.05	5.89 ± 3.05	51.32** ± 0.66	-3.34** ± 0.68	-1.87** ± 1.26
	IPC-122 × IPC-126	10.92** ± 2.90	3.59 ± 2.77	29.08** ± 4.67	-7.28** ± 2.49	51.76** ± 0.70	-1.77** ± 0.70	-3.80** ± 1.34
	IPC-122 × PM	6.38** ± 2.55	3.65 ± 2.87	13.41** ± 3.79	-1.69 ± 2.10	47.32** ± 0.61	-6.22** ± 0.61	1.84** ± 1.22
No. of leaves	White Pale × IPC-126	0.73 ± 0.70	1.98* ± 0.79	-5.99* ± 2.37	4.35** ± 1.19	8.89** ± 0.22	1.17** ± 0.21	2.19** ± 0.38
	White Pale × IPC-122	3.24** ± 0.87	1.30 ± 0.74	-1.73** ± 1.31	3.14** ± 0.67	7.95** ± 0.20	-0.51** ± 0.19	3.09** ± 0.39
	White Pale × PM	4.63** ± 0.74	3.48** ± 0.76	3.35* ± 1.30	2.37** ± 0.61	7.55** ± 0.20	-0.40* ± 0.19	1.88** ± 0.41
	IPC-126 × White Pale	4.18** ± 0.72	1.69 ± 1.29	7.25** ± 1.41	-0.69 ± 0.91	8.20** ± 0.22	0.18 ± 0.23	3.18** ± 0.35
	IPC-126 × IPC-122	-1.28 ± 1.00	-1.39 ± 0.76	-4.68** ± 1.27	-0.49 ± 0.71	8.61** ± 0.21	-0.98** ± 0.21	2.44** ± 0.40
	IPC-126 × PM	2.22* ± 0.86	1.11 ± 0.83	-4.83** ± 1.38	2.08** ± 0.77	8.24** ± 0.21	-0.83** ± 0.21	3.45** ± 0.36

	PM × White Pale	1.17 ± 0.97	2.02* ± 0.84	4.15** ± 1.12	-0.47 ± 0.63	7.74** ± 0.20	0.53* ± 0.20	2.23** ± 0.40
	PM × IPC-126	1.31* ± 0.66	2.35* ± 0.94	1.33** ± 1.05	1.16 ± 0.61	8.13** ± 0.20	0.90** ± 0.21	3.37** ± 0.36
	PM × IPC-122	3.59 ± 1.22	4.16 ± 0.76	4.59** ± 1.17	0.08 ± 0.73	7.61 ± 0.19	0.44** ± 0.20	2.48 ± 0.40
	IPC-122 × White Pale	0.59 ± 1.22	4.16** ± 0.76	4.59** ± 1.17	0.08 ± 0.73	7.61** ± 0.19	0.84** ± 0.20	2.48** ± 0.40
	IPC-122 × IPC-126	1.40* ± 0.68	4.07** ± 0.74	7.48** ± 1.05	-1.00 ± 0.54	7.49** ± 0.20	0.42* ± 0.20	3.45** ± 0.36
	IPC-122 × PM	4.63** ± 0.74	3.48 ± 0.76	3.35** ± 1.30	2.37 ± 0.61	7.55** ± 0.20	-0.40* ± 0.19	1.88** ± 0.41
Plant weight (g)	White Pale × IPC-126	433.50** ± 25.77	277.10** ± 30.39	782.10** ± 23.88	-35.75 ± 21.99	234.45** ± 3.84	-60.00** ± 3.99	203.40** ± 5.58
	White Pale × IPC-122	289.33** ± 32.91	401.44** ± 25.68	531.26** ± 30.86	79.75** ± 25.29	315.80** ± 2.33	6.77** ± 2.36	133.50** ± 4.50
	White Pale × PM	496.57** ± 24.40	308.71** ± 34.57	611.70** ± 29.99	96.79** ± 25.57	269.50** ± 2.14	-30.41** ± 2.16	205.78** ± 3.28
	IPC-126 × White Pale	330.50** ± 32.23	363.30** ± 29.67	758.22** ± 22.76	-32.21 ± 23.42	232.11** ± 3.83	64.17** ± 3.99	202.95** ± 5.85
	IPC-126 × IPC-122	231.30** ± 33.27	294.66** ± 32.70	451.00** ± 37.54	37.48 ± 29.19	279.13** ± 3.90	48.40** ± 3.94	220.57** ± 4.83
	IPC-126 × PM	318.90** ± 30.98	343.60** ± 24.27	639.70** ± 27.29	11.40 ± 23.02	216.64** ± 3.71	19.61** ± 3.77	265.19** ± 4.80
	PM × White Pale	309.33** ± 30.40	336.66** ± 33.81	636.43** ± 29.38	4.77 ± 26.69	272.09** ± 2.15	33.85** ± 2.17	205.35** ± 3.45
	PM × IPC-126	241.28** ± 30.31	314.08** ± 31.36	535.16** ± 25.75	10.10 ± 24.40	219.33** ± 3.69	-19.08** ± 3.76	252.62** ± 4.98
	PM × IPC-122	247.10** ± 37.54	331.60** ± .95	598.60** ± 29.10	-9.95 ± 27.38	281.16** ± 1.94	41.77** ± 1.96	193.30** ± 3.79
	IPC-122 × White Pale	343.77** ± 32.50	344.49** ± 29.15	719.73** ± 29.70	-15.73 ± 25.77	313.34** ± 2.33	-9.38** ± 2.36	141.91** ± 4.41
	IPC-122 × IPC-126	403.40** ± 20.86	318.20** ± 27.17	837.73** ± 27.04	-58.06** ± 20.72	246.89** ± 3.78	-67.68** ± 3.86	213.34** ± 4.98
	IPC-122 × PM	380.83** ± 24.85	333.08** ± 22.42	608.16** ± 27.42	52.87* ± 21.18	278.11** ± 1.94	-42.02** ± 1.95	195.95** ± 3.37
Foliage weight (g)	White Pale × IPC-126	-1.20** ± 3.76	-1.90 ± 4.16	9.96** ± 6.30	-6.53** ± 1.81	26.21** ± 1.29	2.50** ± 1.06	13.18** ± 2.59
	White Pale × IPC-122	12.17** ± 2.05	11.38 ± 1.72	18.38** ± 2.97	2.58 ± 1.06	34.24** ± 1.47	6.39** ± 1.37	-1.32** ± 2.82
	White Pale × PM	-6.91* ± 3.33	0.84 ± 3.59	-77.96** ± 16.33	35.94** ± 8.01	30.79** ± 1.15	2.08* ± 1.02	4.30* ± 2.16
	IPC-126 × White Pale	-2.30** ± 5.24	-2.40 ± 4.79	-4.83** ± 8.61	-1.93 ± 1.88	26.84** ± 1.39	-2.22** ± 1.11	11.45** ± 2.84
	IPC-126 × IPC-122	-3.80** ± 4.05	12.60** ± 4.46	-2.53** ± 8.31	5.66 ± 3.43	34.19** ± 1.57	3.98** ± 1.29	-2.99** ± 2.86
	IPC-126 × PM	-4.90** ± 4.02	1.60 ± 3.69	-4.36** ± 5.42	0.53 ± 1.93	31.27** ± 1.29	1.55** ± 1.18	2.09** ± 2.50
	PM × White Pale	-0.79** ± 3.55	-7.79* ± 3.36	-28.57** ± 6.12	9.99** ± 2.52	31.78** ± 1.14	-2.25* ± 1.00	5.11* ± 2.20
	PM × IPC-126	2.84** ± 3.43	-5.02 ± 3.99	-3.23** ± 5.28	0.52 ± 1.90	31.76** ± 1.21	-1.81** ± 1.11	1.12** ± 2.36
	PM × IPC-122	0.40 ± 3.67	11.90** ± 4.41	11.23** ± 5.93	0.53 ± 2.07	36.05** ± 1.38	2.12** ± 1.23	-5.60* ± 2.63
	IPC-122 × White Pale	11.59* ± 4.73	-6.15** ± 3.95	-1.76** ± 8.56	3.60 ± 3.29	33.15** ± 1.43	-4.48** ± 1.19	-1.20** ± 2.85
	IPC-122 × IPC-126	12.40** ± 4.36	-6.40** ± 3.93	7.86** ± 5.80	-0.93 ± 1.91	33.55** ± 1.42	-3.14* ± 1.28	-1.56** ± 2.69
	IPC-122 × PM	13.98** ± 4.36	2.48 ± 3.62	11.70* ± 5.67	2.38 ± 1.89	35.63** ± 1.35	-2.00** ± 1.22	-6.02* ± 2.60

Table 1: *Estimates of scaling test and Joint scaling test of twelve carrot crosses for structural traits in tropical carrot (Daucus carota L.).*

Significant at A and B- Involves three type of non-allelic-gene interactions; Significant at C- Involves D×D;

Significant at D- Involves A × A; Significant at C and D- Involves A × A and D × D

*** = Significant (P ≤ 0.01) and * = Significant (P ≤ 0.05).*

× dominance [l] gene interactions with negative directions in the IPC-126 × White Pale, IPC-126 × IPC-122 and PM × White Pale crosses (Table 2). The positive and negative effects of dominance [h] and dominance × dominance [l] type of gene interactions was governing top height in IPC-126 × PM cross vise-versa in IPC-122 × White Pale cross. The non-fixable [h+l] effects was favouring dominance effects between parents [16, 20]. The magnitude of dominance [h], additive × additive [i] and dominance × dominance [l] type of gene interactions effects was positively controlling than negative directions of additive [d] in the White Pale × IPC-126 and White Pale × IPC-122 crosses, furthermore, additive × dominance [j] gene interactions was noticed in White Pale × IPC-126 cross. The negative values of [d] tends to association of favourable genes between the parents [25]. The additive [d] and dominance × dominance [l] gene interactions was positively significant than dominance [h] and additive × additive [i] type of gene interactions in the White Pale × PM cross. The additive [h] and additive × dominance [j] type of gene interactions was significantly expressed with positive directions in PM × IPC-126 cross. The importance of additive [d] and dominance [h] gene action was observed in some earlier studies [26,27], whereas non-additive effects [h+l] were reported by Ali., et al. [28] and Amawate and Behl [29]. The positive effects of dominance [h] and additive × additive [i] effects was observed significantly higher than negative effects of additive × dominance [j] gene interactions in IPC-122 × IPC-126 cross. The sign of [d] effects was decided by the female parent in the cross [14,15]. The positive effects additive [d], dominance [h] and dominance × dominance [l] type of gene interactions was governing top height in IPC-122 × PM cross. The significant values of [h] and [l] showed higher dominance effects in heterotic conditions [16,20].

		Gene interactions						
Structural traits	**Cross**	**m ± SE**	**d ± SE**	**h ± SE**	**i ± SE**	**j ± SE**	**l ± SE**	**Type of epistasis**
Plant height (cm)	White Pale × IPC-126	64.38** ± 0.55	-5.66** ± 1.54	14.44** ± 3.99	1.46 ± 3.80	-2.27 ± 3.36	75.98** ± 6.99	C
	White Pale × IPC-122	79.49** ± 0.63	-5.43* ± 2.23	13.97** ± 5.29	7.02 ± 5.13	-3.96 ± 4.72	11.90** ± 9.62	D
	White Pale × PM	72.46** ± 0.67	2.41 ± 1.59	-12.65** ± 4.28	-19.82** ± 4.18	-3.52 ± 3.34	59.84** ± 7.16	D
	IPC-126 × White Pale	68.32** ± 0.56	-1.18 ± 2.42	29.96** ± 5.55	20.58** ± 5.36	-11.41** ± 5.03	14.78** ± 10.39	C
	IPC-126 × IPC-122	76.31** ± 0.70	-1.50 ± 2.02	32.48** ± 5.15	28.96** ± 4.93	-5.15 ± 4.42	-31.81** ± 9.08	D
	IPC-126 × PM	75.04** ± 0.67	-0.90 ± 2.34	14.27** ± 5.48	2.57 ± 5.39	-19.20** ± 4.86	11.86** ± 9.93	C
	PM × White Pale	68.00** ± 0.70	-6.69** ± 2.18	34.94** ± 5.34	17.21** ± 5.19	-5.04 ± 4.47	4.68** ± 9.51	C
	PM × IPC-126	74.16** ± 0.64	9.60** ± 2.28	12.72* ± 5.33	-0.17 ± 5.25	36.60** ± 4.76	23.28* ± 9.66	C
	PM × IPC-122	71.60** ± 0.66	4.84* ± 2.08	19.55** ± 5.13	8.22 ± 4.94	24.93** ± 4.44	9.28* ± 9.17	C
	IPC-122 × White Pale	76.97** ± 0.70	-0.47 ± 2.12	-14.39** ± 5.24	-11.54* ± 5.09	-7.84 ± 4.51	35.70** ± 9.27	D
	IPC-122 × IPC-126	72.08** ± 0.62	-1.88 ± 2.01	15.35** ± 4.97	11.82* ± 4.74	-1.61* ± 4.41	19.36** ± 8.96	C
	IPC-122 × PM	72.62** ± 0.67	7.66** ± 2.24	-19.14** ± 5.42	-20.46** ± 5.23	-0.07 ± 4.75	62.58** ± 9.79	D
Top height (cm)	White Pale × IPC-126	38.86** ± 0.52	-6.14** ± 1.28	19.07** ± 3.63	8.92** ± 3.30	-8.48** ± 2.85	47.22** ± 6.30	C
	White Pale × IPC-122	53.89** ± 0.57	-4.73* ± 2.21	15.06** ± 5.15	14.89** ± 4.98	-2.22 ± 4.64	37.89** ± 9.50	D
	White Pale × PM	48.15** ± 0.63	3.41* ± 1.67	-8.99* ± 4.31	-17.77** ± 4.20	0.18 ± 3.50	39.79** ± 7.41	D
	IPC-126 × White Pale	42.73** ± 0.56	-0.54 ± 2.40	31.78** ± 5.53	25.68** ± 5.30	-4.88 ± 4.96	-9.88* ± 10.35	D
	IPC-126 × IPC-122	49.44** ± 0.65	-0.88 ± 1.76	22.50** ± 4.65	24.13** ± 4.40	1.69 ± 3.86	-34.60** ± 8.11	D
	IPC-126 × PM	50.46** ± 0.56	1.84 ± 2.00	9.84* ± 4.70	4.06 ± 4.59	-6.77 ± 4.17	-11.53** ± 8.54	D
	PM × White Pale	43.98** ± 0.64	-7.26** ± 2.15	29.58** ± 5.18	20.25** ± 5.00	-7.87 ± 4.42	-18.49* ± 9.36	D
	PM × IPC-126	50.41** ± 0.49	7.86** ± 1.87	2.88 ± 4.32	-3.44 ± 4.24	26.18** ± 3.94	14.76** ± 7.94	C

	PM × IPC-122	47.19** ± 0.59	4.12 ± 2.17	22.94** ± 5.13	19.54** ± 4.96	22.14** ± 4.57	-27.26** ± 9.40	D
	IPC-122 × White Pale	50.91** ± 0.76	0.94 ± 2.64	-12.11* ± 6.25	-11.79 ± 6.11	-5.36 ± 5.48	26.39* ± 11.33	D
	IPC-122 × IPC-126	45.56** ± 0.93	-1.94 ± 1.65	12.89* ± 5.17	14.57** ± 4.98	-7.33* ± 3.66	-0.06 ± 8.10	C
	IPC-122 × PM	46.79** ± 0.68	5.58** ± 1.60	6.77** ± 4.41	3.37 ± 4.21	-2.73 ± 3.49	6.65** ± 7.46	C
No. of leaves	White Pale × IPC-126	11.68** ± 0.56	0.30 ± 0.41	-6.48** ± 2.42	-8.70** ± 2.39	1.25 ± 0.98	11.41** ± 2.90	D
	White Pale × IPC-122	10.18** ± 0.24	-0.32 ± 0.46	-2.98* ± 1.41	-6.28** ± 1.35	-1.94 ± 1.01	10.82** ± 2.26	D
	White Pale × PM	8.73** ± 0.23	0.07 ± 0.39	-1.80* ± 1.30	-4.75** ± 1.22	-1.14 ± 0.90	12.86** ± 2.04	D
	IPC-126 × White Pale	8.77** ± 0.30	-0.92 ± 0.67	4.41* ± 1.85	1.38 ± 1.82	-2.49 ± 1.44	14.48** ± 3.04	C
	IPC-126 × IPC-122	9.93** ± 0.23	0.92 ± 0.53	3.16* ± 1.48	0.98 ± 1.42	-0.11 ± 1.16	-13.65 ± 2.47	D
	IPC-126 × PM	10.37** ± 0.29	0.42 ± 0.51	-6.68** ± 1.60	-4.16** ± 1.55	-1.11 ± 1.13	7.49** ± 2.47	D
	PM × White Pale	8.53** ± 0.16	-0.22 ± 0.53	3.89** ± 1.34	0.94 ± 1.26	0.84 ± 1.16	2.25** ± 2.42	C
	PM × IPC-126	9.83** ± 0.18	-0.45 ± 0.48	1.13 ± 1.27	-2.33 ± 1.22	1.04 ± 1.08	6.00** ± 2.20	C
	PM × IPC-122	8.62** ± 0.18	1.13 ± 0.62	3.18 ± 1.53	-0.16 ± 1.46	3.56 ± 1.33	4.92 ± 2.77	C
	IPC-122 × White Pale	8.62** ± 0.18	1.13 ± 0.62	3.18* ± 1.53	-0.16 ± 1.46	3.56** ± 1.33	4.92 ± 2.77	C
	IPC-122 × IPC-126	8.41** ± 0.18	0.36 ± 0.39	5.73*8 ± 1.15	2.01** ± 1.09	2.67 ± 0.92	3.45** ± 1.91	C
	IPC-122 × PM	8.73** ± 0.23	0.07 ± 0.39	-4.75 ± 1.22	-1.80** ± 1.30	-1.14 ± 0.90	12.86** ± 2.04	D
Plant weight (g)	White Pale × IPC-126	191.22** ± 5.27	-48.20* ± 19.29	267.00** ± 44.33	71.50 ± 43.98	-156.40** ± 39.50	639.09** ± 80.80	C
	White Pale × IPC-122	268.93** ± 7.37	49.05* ± 20.55	-8.00 ± 50.79	-159.50** ± 50.59	112.11** ± 41.38	850.28** ± 87.82	D
	White Pale × PM	232.70** ± 7.31	-56.67** ± 20.97	114.15** ± 51.25	-193.59** ± 51.15	-187.85** ± 42.18	998.88** ± 89.10	D
	IPC-126 × White Pale	200.69** ± 4.87	-13.60 ± 21.30	266.92** ± 47.22	64.42 ± 46.85	32.80 ± 43.42	629.37** ± 88.20	C
	IPC-126 × IPC-122	289.00** ± 9.06	-5.32 ± 22.88	136.54* ± 58.59	-74.96 ± 58.38	63.36 ± 46.50	600.92** ± 98.95	C
	IPC-126 × PM	216.70** ± 6.37	19.60 ± 19.17	226.95** ± 46.29	-22.80 ± 46.04	24.70 ± 39.16	685.30** ± 81.39	C
	PM × White Pale	227.76** ± 7.14	-23.58 ± 22.55	200.69** ± 53.50	-9.55 ± 53.39	27.33 ± 45.31	655.54** ± 94.88	C
	PM × IPC-126	237.83** ± 5.92	29.15 ± 21.33	219.54** ± 49.06	-20.20 ± 48.80	72.80 ± 43.39	575.56** ± 89.12	C
	PM × IPC-122	242.22** ± 7.01	-2.00 ± 23.51	226.15** ± 54.89	19.90 ± 54.76	84.50 ± 47.18	558.79** ± 98.43	C
	IPC-122 × White Pale	226.56** ± 7.08	7.35 ± 21.53	192.46** ± 51.74	31.46 ± 51.55	0.71 ± 43.33	656.79** ± 91.12	C
	IPC-122 × IPC-126	183.56** ± 6.26	-5.60 ± 16.49	310.13** ± 41.75	116.13** ± 41.44	-85.20 ± 33.99	605.46** ± 71.32	C
	IPC-122 × PM	239.83** ± 6.64	20.37 ± 16.50	100.50* ± 42.51	-105.74* ± 42.37	-47.74 ± 33.24	819.66** ± 71.49	C
Foliage weight (g)	White Pale × IPC-126	31.63** ± 0.51	-0.60 ± 1.49	27.81** ± 4.69	13.06** ± 3.63	-0.70 ± 4.31	-16.16* ± 8.69	D
	White Pale × IPC-122	33.03** ± 0.66	-3.01 ± 2.62	0.46** ± 6.68	3.71* ± 5.88	12.46* ± 6.37	-3.06** ± 12.54	D
	White Pale × PM	50.99** ± 3.92	0.37 ± 1.62	-68.88** ± 16.19	-71.88** ± 16.03	7.75 ± 4.19	65.80** ± 17.56	D
	IPC-126 × White Pale	32.33** ± 0.48	0.20 ± 1.61	14.61** ± 5.64	3.86 ± 3.77	-0.10 ± 4.48	-8.56** ± 10.77	D

	IPC-126 × IPC-122	34.63** ± 1.49	-0.80 ± 1.67	-15.33* ± 7.44	-11.33 ± 6.86	-16.40** ± 5.32	20.13** ± 10.67	D
	IPC-126 × PM	32.46** ± 0.47	0.00 ± 1.68	1.18** ± 4.62	-1.06 ± 3.86	6.50 ± 4.74	-2.23** ± 8.63	D
	PM × White Pale	38.39** ± 0.99	0.00 ± 1.54	-17.48** ± 5.55	-19.98** ± 5.04	-7.00 ± 4.08	11.40** ± 8.70	D
	PM × IPC-126	32.43** ± 0.48	-0.18 ± 1.63	11.69** ± 4.52	-1.05 ± 3.80	-7.87 ± 4.53	-1.12* ± 8.42	D
	PM × IPC-122	33.06** ± 0.61	0.00 ± 1.66	-17.81** ± 4.95	-1.06 ± 4.15	-11.50* ± 5.07	13.36** ± 8.92	D
	IPC-122 × White Pale	34.06** ± 1.42	0.37 ± 1.66	-11.46** ± 7.32	-7.21 ± 6.59	-17.74** ± 4.91	12.65** ± 10.85	D
	IPC-122 × IPC-126	32.53** ± 0.48	-0.40 ± 1.65	-11.13** ± 4.70	1.86 ± 3.82	-18.80** ± 5.30	14.13** ± 8.80	D
	IPC-122 × PM	32.70** ± 0.48	0.00 ± 1.63	-12.01** ± 4.63	-4.76 ± 3.79	-11.50* ± 5.03	21.22* ± 8.65	D

Table 2: *Estimation of type of gene interaction and its effects of the best fit model on generation means for structural traits in twelve different crosses of tropical carrot (Daucus carota L.) evaluated at Indian Agricultural Research Institute during winter 2014-15.*

m = Mean, [d] = Additive effects, [h] = Dominance effects, [i] = Additive × additive effects, [j] = *Additive × dominance effects, [l] = Dominance* × dominance effects.

*** = Significant (P ≤ 0.01) and * = Significant (P ≤ 0.05).*

Number of leaves

The scaling test of A, B, C and D in White Pale × PM cross, A, B and C in PM × IPC-126, IPC-122 × IPC-126 crosses, A, C and D in IPC-126 × PM, White Pale × PM, White Pale × IPC-122 crosses, C and D in White Pale × IPC-126 cross, A and C in IPC-126 × White Pale, IPC-126 × IPC-122, IPC-122 × PM, PM × IPC-122 crosses, B and C in IPC-122 × White Pale cross were highly significant values which explained the presence of digenic interactions (Table 1). The dominance [h] and dominance × dominance [j] type of gene interactions effects was governing number of leaves in the IPC-126 × White Pale, IPC-126 × IPC-122, PM × White Pale, PM × IPC-126 and PM × IPC-122 crosses. The positive effects of dominance × dominance [l] gene interactions was highly significant than negative effects of dominance [h] and additive × additive [i] for this trait in the White Pale × IPC-126, White Pale × IPC-122 and White Pale × PM, IPC-126 × PM, IPC-122 × PM crosses (Table 2). Higher positive values of [h] effects causing due to heterozygosity of genes present in the parents [12]. The effects of [h] and [l] were significant and positive tends to increase the dominant phenotype in F2 generations which led to positive heterosis [25]. The dominance [h], additive × dominance [j] and dominance × dominance [l] gene interactions was highly conditioning for number of leaves in IPC-122 × White Pale cross whereas in IPC-122 × IPC-126 cross, dominance [h], additive × additive [i] and dominance × dominance [l] type of gene interactions was highly expressed for this trait. Further it was noticed that the non-fixable [h+l] effects was controlling than fixable effects [d+i] almost in all crosses. The similar type of gene interaction and effects had been reported in cotton [30], melon [31], wheat [17], tomato [18], maize [23,24], and sesame [19]. Prevalence of epistatic gene interaction can be visualized that considerable genetic diversity exists in the F2 and its derived population.

Plant weight

The scales of A, B, C and D in White Pale × IPC-122, White Pale × PM, IPC-122 × IPC-126, IPC-122 × PM crosses and A, B and C in White Pale × IPC-126, IPC-126 × White Pale, IPC-126 × IPC-122, IPC-126 × PM, PM × White Pale, PM × IPC-126, PM × IPC-122, IPC-122 × White Pale, IPC-122 × IPC-126, IPC-122 × White Pale crosses were significant (Table 2). The magnitude of dominance × dominance [l] gene interactions was higher than dominance [h] gene actions in the IPC-126 × White Pale, IPC-126 × IPC-122, IPC-126 × PM, PM × White Pale, PM × IPC-126, PM × IPC-122, IPC-122 × White Pale and IPC-122 × PM crosses for plant weight. The significant and positive [h] and [l] showed the dominant phenotype in the mean population [20]. The dominance [h], additive × additive [i] and dominance × dominance [j] type of gene interactions was controlling this trait in IPC-122 × IPC-126 cross. The positive effect of dominance [h] and dominance × dominance [l] gene interactions was exhibited for plant weight in the White Pale × IPC-126 and White Pale × PM cross. Higher allele effects of dominance was conditioning the expression of heterosis [32]. The positive effect of additive [d], additive × dominance [j] and dominance × dominance [l] type of gene interactions was effectively expressing than the negative effects of additive × additive [i] type of gene interactions in the White Pale × IPC-122 cross. The effects of [d+i] was significant and positive indicated that higher frequency of gene dispersal between the parents which restrict conventional selection in the earlier generations of combinations [20,32].

Foliage weight

The scales of A, B, C and D in PM × White Pale cross, A, C and D in White Pale × IPC-126 cross, A, B and C in White Pale × IPC-122, IPC-122 × White Pale, IPC-122 × IPC-126 crosses, A, C and D in White Pale × PM cross, A and C in IPC-126 × White Pale, PM × IPC-126, IPC-122 × PM crosses, B and D in IPC-126 × IPC-122, PM × IPC-122 crosses and scales in B and C in PM × IPC-122 cross was significant, thus shows epistatic gene interaction (Table

2). The dominance × dominance [l] gene interactions was positively significant than the dominance [h] and additive × dominance [j] gene interactions for foliage trait in the IPC-126 × IPC-122, PM × IPC-122, IPC-122 × White Pale, IPC-122 × White Pale, IPC-122 × IPC-126 and IPC-122 × PM crosses. The dominance [h] and additive × dominance [l] gene interactions was governing majorly for this trait in the IPC-126 × White Pale and PM × IPC-126 with positive and negative directions, respectively. The negative effects of dominance [h] and additive × additive [i] gene interactions was expressing for foliage weight with positive directions of dominance × dominance [l] interactions in the White Pale × PM and IPC-126 × PM crosses (Table 3). The higher values of [h] and [l] was increasing heterosis directions with positive and negative, respectively [20]. These results are in close conformity with the results reported by Karami., et al. [33], Ramalingam and Sivasamy [34] in sesame and cotton respectively for foliage weight. The dominance [h] and additive × additive [j] type of gene interactions was significantly conditioning with positive directions than negative directions of dominance × dominance [l] type of gene interactions for this trait in the White Pale × IPC-126 and White Pale × IPC-122 crosses. Jinks and Jones [35] reported that higher magnitude of [h] and [l] effects were influencing the heterosis when [i] and [l] are reinforce the effects of dominance in complimentary type epistasis. The linkage between [i] and [l] effects resulted into biased epistatic effects, however, this basic genetic mechanism cannot be ignored [36]. Sprague [37] suggested that undesirable linkage of [i] and [l] was eliminated through intermating of selector followed by selection of useful recombinants.

Conclusion

The complex structural traits studied in the present experiment shown that additive [a], dominance [h], additive × additive [i], additive × dominance [j] and dominance × dominance [l] gene effects were detected in the twelve crosses of six generation. The complimentary type of epistatic gene interactions were governed in the plant height (White Pale × IPC-126, White Pale × IPC-122, IPC-126 × White Pale, IPC-126 × PM, PM × IPC-126, PM × IPC-122 crosses), top height (White Pale × IPC-126, White Pale × IPC-122, PM × IPC-126 and IPC-122 × PM crosses), number of leaves (IPC-126 × White Pale, PM × White Pale, PM × IPC-126, PM × IPC-122, IPC-122 × White Pale and IPC-122 × IPC-126 crosses), plant weight (White Pale × IPC-126, White Pale × PM, IPC-126 × White Pale, IPC-126 × IPC-122, IPC-126 × PM, PM × White Pale, PM × IPC-126, IPC-122 × White Pale, IPC-122 × IPC-126, IPC-122 × PM crosses), whereas duplicate type of non-allelic gene interactions were evidenced in the plant height (IPC-126 × IPC-122 cross), top height (White Pale × PM, IPC-126 × PM and IPC-122 × White Pale crosses), number of leaves (White Pale × IPC-126, White Pale × IPC-122, White Pale × PM, IPC-126 × IPC-122, IPC-126 × PM and IPC-122 × PM crosses), plant weight (White Pale × IPC-122 cross), foliage weight (all crosses). These epistatic parameter results clearly depicted that nature and magnitude of gene action and effects would help to understand the behavior of non-allelic gene interaction effects, frequency of allele association and dispersion between the parents with respective crosses by identifying the positive and negative sign of additive [a+i] and non-additive gene effects [h+l]. Thus, these complimentary and duplicate type of gene interaction and effects of structural traits are assist the fixing of favourable allele in the earlier [d+i] and later [h+l] generations followed by heterosis and recurrent selection breeding strategy, respectively. These genetic analysis of complex structural traits will give sufficient genetic information for understanding with adoptive effective breeding approach for framing the plant architecture of carrot which indirectly influencing the yield attributable traits. Hence, hybrid exploitation by non-fixable effects due to increase the positive proportion of dominance [h] and dominance × dominance [l] gene effects wherein complimentary epistatic had evidenced crosses. The higher frequency of gene dispersal alleles between parents were detected in duplicate non-allelic gene interaction, thereby, selection would be restricted in earlier generation and favours the homozygosity of alleles till advanced generation through intermating of selected parents followed by cyclic recurrent selection and mass selection with respective crosses. The genetic information of nature and magnitude of gene action would help to adopt sound breeding strategy for targeted structural traits and thus, increase the frequency favourable genes in the carrot populations and also it can serve as a potential sources of superior inbred lines for future carrot improvement program.

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