

GENETIC ANALYSIS OF YIELD COMPONENTS IN PEA UNDER DIFFERENT POWDERY MILDEW CONDITIONS

MUHAMMAD ABUBAKKAR AZMAT¹, ASIF ALI KHAN² AND MUHAMMAD SHABAN^{1*}

¹Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad-Pakistan (Burewala Campus)

²Institute of Plant Breeding and Biotechnology, Muhammad Nawaz Shareef University of Agriculture, Multan-Pakistan

*Corresponding author's email: drshaban@uaf.edu.pk

Abstract

Genetic analysis of 11 yield traits were performed using six generations of four biparental crosses, each involving powdery mildew resistant (It-96; No.267) and susceptible parents (Climax; PF-400) in pea. Scaling assays revealed that all three forms of non-allelic interactions were present (additive \times additive [i], additive \times dominance [j] and dominance \times dominance [l]) for almost all yield contributing traits. Moreover, it was found that only simple additive dominance model was not fit for these traits. Generation mean analysis has confirmed the influence of both additive and non-additive genetic effects in controlling the inheritance of all traits. Additive genetic effects [d] were controlling the inheritance of majority traits. With few exceptions, it was found that additive genetic effects [d] were smaller than the corresponding dominant genetic effects [h]. In most of the traits, [d] genetic component was smaller than [i], [j] and [l] genetic components, again suggesting the role of additive and non-additive genes in controlling their inheritance. Smaller than unity degree of dominance suggested the presence of partial dominance in determining their genetics. Significant positive mid parent heterosis, inbreeding depression and high heritability estimates were prevalent for most of yield related traits. Keeping in view the interplay of different genetic components in controlling the inheritance of different yield related traits and powdery mildew resistance in pea, back cross breeding method is recommended to have high yielding genotypes with powdery mildew resistant background.

Key words: Degree of dominance, Genetic analysis, Genetic components, Heterosis, Heritability

Introduction

Owing to high nutritional value and palatability, pea is the most popular legume crop. It is a cool season crop grown for its green pods and seeds in different parts of the world. The domestication of pea is traced back in Harappa-Pakistan, and in the northwest part of India in 2250-1750 BC, when it was grown as pulse crop (Allchin, 2017). Including Pakistan, the area under pea crop is increasing throughout the world but the mean yield is almost stagnant (Din *et al.*, 2019; Greveniotis *et al.*, 2021). The yield is a complex trait that is affected by genetic effects, biotic and abiotic factors (Rana *et al.*, 2020), the growing location and the agro-tech practices (Liliane & Charles, 2020).

The yield related traits contribute to overall yield, which can be used successfully in breeding programs to improve the green pod and seed yield in pea (Aman *et al.*, 2021). The expression of these traits is influenced by genetic effects and numerous environmental factors (Bueckert *et al.*, 2015; Giri *et al.*, 2020). Understanding the type and scope of genetic impacts is essential for the selection of suitable breeding strategy for the development of high yielding pea cultivars.

Generation mean analysis is first order statistics used for reliable, precise and robust assessment of genetic components in the quantitatively inherited traits. The generation mean analysis makes use of the data of six generations including two parental genotypes (P_1 and P_2), their F_1 progeny (non-segregating generations) and three segregating generations (F_2 , BC_1 and BC_2) to provide information on main genetic effects influencing the expression of different quantitative traits *viz.*, dominance, additive and their digenic interactions (Fahad *et al.*, 2018). The generation means analysis evaluates the genetic influences on biochemical and physiological variables in

addition to yield traits (Pujar *et al.*, 2021), and the inheritance of different diseases (Shashikumar *et al.*, 2010; Salegua *et al.*, 2021). The generation means analysis has been used to study the inheritance of yield contributing traits in different crop species such as barley (Madhukar *et al.*, 2018) and cotton (Giri *et al.*, 2020).

Powdery mildew (*Erysiphe pisi*) is the major limitation to green pod and seed yield of pea in Pakistan and wherever conducive environmental conditions prevail in the world (Azmat *et al.*, 2012; Villegas-Fernández *et al.*, 2021). The incorporation of powdery mildew resistance gene in high yielding pea cultivars is the most appropriate solution to manage the menace. It is general observation that powdery mildew resistant pea genotypes are inferior in yield and yield contributing traits and vice versa. The linkage and pleiotropic effects have been reported to be associated with yield penalties of disease resistance (Brown, 2002). Hence, the hybridization between contrasting pea genotypes with reference to yield and powdery mildew response can be used to break the linkage between disease resistance genes and the genes negatively affecting the yield, resulting in new high yielding genetic combinations with powdery mildew resistant background.

This research was done to evaluate the additive, dominance and digenic epistatic interactions affecting different yield related traits and overall yield in pea.

Material and Methods

Plant material and development of generations: Four pea genotypes cv. Climax, cv. PF-400 (high yielding and powdery mildew susceptible), It-96 and No.267 (low yielding and powdery mildew resistant) were crossed. The F_1 plants of the four crosses *i.e.* Climax \times It-96, Climax \times No.267, PF-400 \times It-96 and PF-400 \times No.267 were used to develop BC_1 , BC_2 and F_2 seeds of each cross.

Sowing and evaluation of segregating and non-segregating generation in the field:

The segregating (F_2 , BC_1 and BC_2) and non-segregating (P_1 , P_2 and F_1) generations were sown in a well-prepared field (well-drained silt loam soil, pH 7.4) at the Vegetable Research Institute, Faisalabad, Pakistan (longitude 73°74' East, latitude 30°31.5' North), during Rabi planting season. The experiment was laid out in a Randomized Complete Block Design with three replications of each of the six generations of the four crosses. Plants were spaced 10 cm apart from one another in seed beds that were 75 cm broad. At a rate of 40-40-25 kg/ha, a composite NPK fertilizer was applied to the soil. The experimental material received irrigation following 7 to 10 days interval, and manual weeding was done on a regular basis. All other cultural and agronomic practices were kept similar across the growing plots to minimize the experimental error (Azmat *et al.*, 2011).

For the parents and F_1 (non-segregating generations), data were recorded on 10 randomly selected competitive plants in each replication for each trait. For F_2 and backcross generations (Segregating generations), the data for all the traits were recorded from 60 and 25 randomly selected competitive plants respectively in each replication. The data on the individual plants in each generation were recorded at appropriate time for 11 yield related parameters *viz.*, node bearing 1st flower, total number of nodes, number of productive nodes, number of productive branches, number of pods/plant, pod length, pod width, number of seeds/pod, weight of pods/plant and 100 seed weight (fresh and dry) as described by Azmat *et al.*, (2011).

Assessment of genetic basis of inheritance: The data regarding above mentioned yield related traits measured at plant maturity were subjected to the analysis of variance using Genstat (12.0) software (Amhakhian *et al.*, 2021). The genetic basis of variation for the traits was estimated from the data collected on the six generations (P_1 , P_2 , F_1 , BC_1 , BC_2 , and F_2) of the four crosses. The generation means analysis was performed using a computer program written by Dr. H.S. Pooni, School of Biological Sciences, University of Birmingham, U.K and used as described by Raza *et al.*, (2019). Means and variances of the parents, BC_1 , BC_2 , F_1 and F_2 generations used in the analysis were calculated from individual plant data pooled over replications.

A weighted least square analysis was performed on the generation means commencing with the simplest model using parameter “m” only. Further models of increasing complexity (md, mdh, mdhi, mdhij and mdhijl) were fitted if chi-square value was significant, where (m) representing mean, (d) additive, (h) dominance (i) additive/additive, (j) additive/dominance and (l) dominance/ dominance genetic effects. The most accurate model was one with non-significant chi-square values coupled with significant estimates of all parameters. In the model fitting, P_1 was chosen as the parent with the greater value for each attribute.

Results

The yield traits in segregating and non-segregating generations were significantly different among the crosses (Table 1). The variance estimates for the segregating generations of four biparental crosses (Climax × It-96, Climax × No.267, PF-400 × It-96 and PF-400 × No.267) was higher than the non-segregating generations regardless of the cross combinations (Table 1).

The “It-96” had the highest mean values for number of nodes bearing first flower (15.5) and number of pods/plant (49.06). The “No. 267” had highest mean values for total number of nodes (49.7) and number of productive nodes (19.93). The cultivar “PF-400” had maximum mean values for seed traits *viz.*, number of seeds/pod (6.76), 100-seed weight (fresh) (42.8g) and 100-seed weight (dry) (15.3g). The widely grown commercial cultivar “Climax” had higher mean values for four economically important yield related traits, number of productive branches (2.9), pod length (8.3cm), pod width (1.7cm) and weight of pods/plant (78.46g) (Table 1).

Among segregating generations (F_2 , BC_1 , BC_2) of all biparental cross combinations, the BC_1 generation had the highest mean values for all the traits [number of node bearing first flower, total number of nodes, number of pods/ plant, pod length, pod width, number of seeds/ pod, weight of pods/plant, 100-seed weight (fresh) and 100-seed weight (dry)] except number of productive branches in three of four cross combinations (Table 1); F_2 generation had highest mean value for this trait in three cross combinations *viz.*, Climax × It-96, Climax × No.267 and PF-400 × It-96 (Table 1). The BC_2 generation of “PF-400 × It-96” cross combination had highest mean value for pod width (Table 1).

Before the estimation of components of genetic variation, epistasis was tested for all the traits through scaling test. This test determines the presence or absence and type of non-allelic interactions (epistatic effects). Among four biparental crosses, almost all the traits expressed significant values for different scaling tests respectively (Table 2). For cross ‘Climax × It-96’ eight characters (node bearing 1st flower, total number of nodes, number of productive nodes, number of pods per plant, pod length, pod width, weight of pods per plant and 100 seed weight fresh) had significant values for all four scaling tests while number of productive branches, number of seed per pod and 100 seed weight dry showed significant values for three (B, C and D) and two (A, C and B, C) scaling tests, respectively (Table 2). In ‘Climax × No.267’, five yield contributing traits (total number of nodes, number of productive nodes, pod length, weight of pods per plant and 100 seed weight dry) were significant for scaling test A, B, C and D. Whereas, four traits, node bearing 1st flower, number of productive branches, number of pods per plant and 100 seed weight fresh showed significance for three scaling tests *viz.*, (A, B and C), (B, C and D), (A, C and D) and (A, B, C), respectively. The number of seeds per pod and pod width were significant for two tests (A, C) and (C, D), respectively (Table 2).

Table 1. Means and standard deviations for different yield related traits in six generations of four biparental crosses in pea.

Traits	Cross	P ₁		P ₂		F ₁		F ₂		BC ₁		BC ₂	
		Mean		Mean		Mean		Mean		Mean		Mean	
Node bearing 1st flower	Climax × It-96	15.50 ± 0.94		11.60 ± 0.72		16.20 ± 0.89		13.20 ± 1.98		15.30 ± 1.58		12.90 ± 1.33	
	Climax × No. 267	14.30 ± 0.55		11.70 ± 0.74		15.10 ± 0.91		13.40 ± 2.15		13.80 ± 1.64		12.60 ± 1.45	
	PF-400 × It-96	15.10 ± 0.79		11.80 ± 0.90		15.80 ± 0.99		13.90 ± 2.30		14.80 ± 1.90		13.60 ± 1.45	
	PF-400 × No. 267	14.4 ± 0.57		12.1 ± 0.82		14.9 ± 0.81		13.7 ± 2.60		14.1 ± 2.02		13.3 ± 1.77	
Total number of nodes	Climax × It-96	41.80 ± 1.14		28.80 ± 0.94		41.60 ± 1.30		36.10 ± 2.36		39.20 ± 1.82		35.80 ± 1.55	
	Climax × No. 267	49.70 ± 0.98		28.40 ± 0.73		44.80 ± 1.36		38.70 ± 2.45		47.80 ± 1.98		37.60 ± 1.61	
	PF-400 × It-96	42.50 ± 0.77		25.80 ± 1.29		43.10 ± 1.35		33.20 ± 3.15		40.50 ± 2.37		28.50 ± 2.11	
	PF-400 × No. 267	49.2 ± 1.10		25.6 ± 1.13		37.4 ± 1.68		37.8 ± 3.29		37.9 ± 2.60		37.5 ± 2.03	
No. of productive nodes	Climax × It-96	18.53 ± 0.62		13.86 ± 1.02		21.56 ± 0.90		16.16 ± 2.00		21.36 ± 1.58		18.80 ± 1.36	
	Climax × No. 267	19.56 ± 0.97		14.03 ± 0.93		21.30 ± 1.12		17.22 ± 2.24		21.80 ± 1.77		19.37 ± 1.46	
	PF-400 × It-96	18.30 ± 0.65		11.06 ± 0.52		21.67 ± 1.95		17.85 ± 2.56		20.53 ± 2.08		16.53 ± 1.92	
	PF-400 × No. 267	19.93 ± 1.01		11.33 ± 1.03		13.96 ± 1.07		14.53 ± 2.44		16.46 ± 1.96		12.89 ± 1.69	
No. of productive branches	Climax × It-96	2.83 ± 0.44		2.67 ± 0.49		2.83 ± 0.46		2.90 ± 0.66		2.86 ± 0.45		1.82 ± 0.60	
	Climax × No. 267	2.90 ± 0.30		2.43 ± 0.50		3.03 ± 0.85		3.12 ± 1.32		2.80 ± 1.10		2.42 ± 0.95	
	PF-400 × It-96	1.96 ± 0.32		1.23 ± 0.44		2.10 ± 0.40		2.36 ± 0.72		1.93 ± 0.62		1.37 ± 0.45	
	PF-400 × No. 267	2.3 ± 0.70		1.56 ± 0.68		1.73 ± 0.64		1.76 ± 0.77		1.86 ± 0.64		1.66 ± 0.60	
Number of pods per plant	Climax × It-96	47.56 ± 0.62		31.20 ± 1.13		48.10 ± 0.96		38.87 ± 2.18		46.43 ± 1.73		38.63 ± 1.43	
	Climax × No. 267	49.06 ± 0.74		30.96 ± 0.81		49.33 ± 1.71		39.56 ± 2.81		48.33 ± 2.18		39.86 ± 1.87	
	PF-400 × It-96	47.83 ± 0.59		10.96 ± 0.85		48.63 ± 1.85		37.50 ± 3.17		42.03 ± 2.50		23.06 ± 2.09	
	PF-400 × No. 267	48.93 ± 0.98		11.2 ± 1.22		33.2 ± 1.37		32.15 ± 3.15		32.93 ± 2.50		30.17 ± 1.99	
Pod length (cm)	Climax × It-96	8.29 ± 0.26		6.64 ± 0.66		7.69 ± 0.61		7.07 ± 0.87		7.41 ± 0.57		7.43 ± 0.80	
	Climax × No. 267	7.96 ± 0.33		4.73 ± 0.14		7.55 ± 0.55		6.83 ± 0.94		7.13 ± 0.81		6.83 ± 0.72	
	PF-400 × It-96	7.45 ± 0.61		6.38 ± 0.60		6.23 ± 0.93		6.07 ± 1.06		6.19 ± 1.01		5.83 ± 1.01	
	PF-400 × No. 267	7.5 ± 0.70		4.82 ± 0.69		5.83 ± 0.76		5.69 ± 1.09		5.94 ± 0.79		5.74 ± 0.80	
Pod width (cm)	Climax × It-96	1.69 ± 0.14		1.55 ± 0.10		1.75 ± 0.14		1.56 ± 0.17		1.63 ± 0.14		1.59 ± 0.14	
	Climax × No. 267	1.71 ± 0.10		1.28 ± 0.10		1.68 ± 0.26		1.47 ± 0.32		1.67 ± 0.22		1.50 ± 0.26	
	PF-400 × It-96	1.52 ± 0.10		1.51 ± 0.10		1.55 ± 0.14		1.43 ± 0.24		1.47 ± 0.20		1.49 ± 0.17	
	PF-400 × No. 267	1.55 ± 0.10		1.27 ± 0.10		1.59 ± 0.10		1.35 ± 0.28		1.52 ± 0.24		1.31 ± 0.17	
Number of seeds per pod	Climax × It-96	6.20 ± 0.48		4.20 ± 0.41		6.36 ± 0.67		5.35 ± 1.32		5.66 ± 1.10		5.30 ± 1.01	
	Climax × No. 267	6.16 ± 0.37		3.60 ± 0.57		6.33 ± 1.03		5.17 ± 1.32		5.26 ± 1.11		4.97 ± 1.09	
	PF-400 × It-96	6.13 ± 0.77		4.10 ± 0.40		6.30 ± 0.92		5.86 ± 1.64		6.00 ± 1.32		4.73 ± 1.13	
	PF-400 × No. 267	6.76 ± 0.68		3.83 ± 0.70		4.2 ± 0.99		4.13 ± 1.87		5.13 ± 1.49		4.17 ± 1.22	
Weight of pods per Plant	Climax × It-96	78.29 ± 1.08		27.38 ± 0.80		79.04 ± 1.06		53.26 ± 3.03		68.13 ± 2.28		51.73 ± 2.14	
	Climax × No. 267	78.46 ± 1.14		30.00 ± 0.66		51.88 ± 1.18		53.84 ± 2.91		75.80 ± 2.28		52.06 ± 2.07	
	PF-400 × It-96	45.19 ± 1.17		27.17 ± 0.96		45.70 ± 1.37		35.12 ± 3.03		41.20 ± 2.29		35.57 ± 2.02	
	PF-400 × No. 267	45.63 ± 0.99		30.26 ± 0.92		46.58 ± 1.24		37.52 ± 2.60		42.26 ± 2.02		37.9 ± 1.91	
100 seed weight-fresh (g)	Climax × It-96	37.23 ± 1.05		26.28 ± 0.90		39.28 ± 1.41		35.01 ± 2.80		36.48 ± 2.15		34.60 ± 1.94	
	Climax × No. 267	37.40 ± 0.84		23.46 ± 0.66		39.12 ± 1.28		35.66 ± 3.07		37.13 ± 2.37		34.87 ± 2.01	
	PF-400 × It-96	42.44 ± 0.78		26.18 ± 0.93		43.68 ± 1.08		35.82 ± 3.27		41.07 ± 2.53		29.57 ± 2.08	
	PF-400 × No. 267	42.8 ± 1.01		23.68 ± 0.78		46.71 ± 1.33		35.46 ± 2.44		41.6 ± 1.85		28.52 ± 1.83	
100 seed weight-dry (g)	Climax × It-96	14.29 ± 1.17		12.49 ± 0.73		12.74 ± 1.28		12.80 ± 1.77		13.74 ± 1.34		12.19 ± 1.33	
	Climax × No. 267	14.44 ± 0.81		12.40 ± 0.86		15.13 ± 1.17		18.87 ± 2.62		19.62 ± 2.17		12.86 ± 1.56	
	PF-400 × It-96	15.29 ± 0.83		12.43 ± 0.83		12.36 ± 1.13		13.91 ± 2.57		15.13 ± 2.09		13.46 ± 1.74	
	PF-400 × No. 267	15.15 ± 0.94		12.7 ± 0.72		14.03 ± 1.36		13.96 ± 2.17		15.63 ± 1.57		13.96 ± 1.74	

Table 2. A, B, C and D scaling test using six generations of four biparental pea crosses for different yield related traits.

Traits	Cross	A	B	C	D
Node bearing 1st flower	Climax × It-96	-3.14*	-6.63**	15.82**	-6.34**
	Climax × No. 267	-5.45**	-5.00*	20.11**	1.31 ^{ns}
	PF-400 × It-96	-3.36*	-1.17 ^{ns}	19.00**	-1.82 ^{ns}
	PF-400 × No. 267	-2.92*	-1.12 ^{ns}	19.34**	0.00 ^{ns}
Total number of nodes	Climax × It-96	-11.54**	3.10*	41.73**	-8.35**
	Climax × No. 267	2.47*	5.20**	40.71**	-22.80**
	PF-400 × It-96	-9.59**	-24.54**	23.26**	-5.82**
	PF-400 × No. 267	-19.25**	24.18**	38.34**	0.43 ^{ns}
Number of productive nodes	Climax × It-96	8.05**	6.54**	17.57**	-27.27**
	Climax × No. 267	6.92**	9.55**	19.88**	-21.03**
	PF-400 × It-96	2.16*	0.68 ^{ns}	21.74**	-3.63*
	PF-400 × No. 267	-2.32*	1.27 ^{ns}	17.58**	-0.82 ^{ns}
Number of productive branches	Climax × It-96	0.44 ^{ns}	-11.86**	12.80**	11.51**
	Climax × No. 267	-1.36 ^{ns}	-2.61*	9.21**	5.29**
	PF-400 × It-96	-1.45 ^{ns}	-4.53*	17.12**	13.62**
	PF-400 × No. 267	-1.53 ^{ns}	0.15 ^{ns}	4.22*	0.00 ^{ns}
Number of pods per plant	Climax × It-96	-7.98**	-5.72**	43.55**	-23.51**
	Climax × No. 267	-3.52*	-1.24 ^{ns}	31.33**	-22.67**
	PF-400 × It-96	-22.97**	-26.73**	42.02**	21.90**
	PF-400 × No. 267	-31.81**	34.14**	37.96**	2.68*
Pod length (cm)	Climax × It-96	-7.57**	2.52*	17.31**	-5.43**
	Climax × No. 267	-7.10**	8.81**	23.44**	-2.15*
	PF-400 × It-96	-4.98*	-3.65*	9.45**	0.71 ^{ns}
	PF-400 × No. 267	-6.35**	3.64*	11.09**	-1.93 ^{ns}
Pod width (cm)	Climax × It-96	-4.17*	-3.06*	17.22**	-3.87*
	Climax × No. 267	-0.79 ^{ns}	0.59 ^{ns}	9.77**	-4.98*
	PF-400 × It-96	-2.86*	-1.89 ^{ns}	14.10**	-2.81*
	PF-400 × No. 267	-2.10*	-6.27**	12.51**	-3.18*
Number of seeds per pod	Climax × It-96	-5.30**	0.18 ^{ns}	11.37**	-1.33 ^{ns}
	Climax × No. 267	-7.30**	0.04 ^{ns}	9.20**	0.56 ^{ns}
	PF-400 × It-96	-1.40 ^{ns}	-3.62*	13.03**	4.18*
	PF-400 × No. 267	-2.13*	1.04 ^{ns}	2.92*	-3.89*
Weight of pods per Plant	Climax × It-96	-45.44**	-6.94**	33.82**	-30.76**
	Climax × No. 267	44.51**	53.09**	65.96**	-48.12**
	PF-400 × It-96	-17.03**	-3.85*	24.82**	-15.19**
	PF-400 × No. 267	-17.50**	-2.47*	34.88**	-13.61**
100 seed weight-fresh (g)	Climax × It-96	-7.46**	8.27**	43.11**	-2.64*
	Climax × No. 267	-4.74*	17.03**	48.96**	-1.56 ^{ns}
	PF-400 × It-96	-8.30**	-25.03**	35.21**	2.16*
	PF-400 × No. 267	-14.69**	-32.48**	36.73**	2.27*
100 seed weight-dry (g)	Climax × It-96	1.17 ^{ns}	-2.45*	17.41**	-1.29 ^{ns}
	Climax × No. 267	22.01**	-4.92*	43.44**	14.11**
	PF-400 × It-96	6.11**	5.57**	20.61**	-2.08*
	PF-400 × No. 267	5.24**	2.97*	18.93**	-5.30**

The four scaling tests were significant in the cross 'PF-400 × It-96' for the total number of nodes, number of pods per plant, weight of pods per plant, 100 seed weight fresh and 100 seed weight dry. While the traits including number of productive branches (B, C and D), number of seeds per pod (B, C and D), number of productive nodes (A, C and D), pod width (A, C and D) and pod length (A, B and C) were significant for three scaling tests. Only node bearing 1st flower expressed significance for two scaling tests (A, C) (Table 2).

In fourth cross (PF-400 × No.267) five out of 11 traits (number of pods per plant, pod width, weight of pods per

plant, 100 seed weight fresh and 100 seed weight dry) revealed significance for all scaling tests, while three traits (total number of nodes, pod length and number of seeds per pod) have shown significance for three scaling tests. Two traits viz., node bearing 1st flower and number of productive nodes, were significant for two scaling tests. There was only one trait (number of productive branches) which showed significance for one scaling test (Table 2).

To determine the best genetic model fit for all the variables, the generation mean analysis was done for 11 yield-related traits. Generation means parameters, mean (m), additive [d], dominance [h], additive × additive [i],

additive \times dominance [j] and dominance \times dominance [l] for various plant traits in four biparental cross combinations along with the chi-squared (χ^2) (Table 3).

The estimates obtained in the four crosses validated the significance of additive-dominance genetic effects and their digenic interactions in the inheritance of yield contributing traits. Of 44 cross combinations the epistasis genetic effect was involved in the inheritance of yield related traits in maximum cross combinations (43) followed by additive (42) and dominance genetic effects (32) respectively involving four biparental cross combinations for eleven yield related traits. Among epistasis genetic effects, [i] additive \times additive, influenced the inheritance of yield related traits in more number of cross combinations (28) followed by [l] dominance \times dominance (25) and [j] additive \times dominance (21), respectively. In fourteen of 44 estimates only one of three above mentioned non allelic digenic interactions influenced the inheritance of yield related traits in pea while the combination of two out of three non-allelic digenic interactions influenced the inheritance of 27 traits while only for two traits all the three forms of non-allelic digenic interactions (i, j and l) were involved (Table 3).

The generation means analysis performed for node bearing first flower revealed that three parameter model (m, d and l) was best fit for cross combinations Climax \times No.267, PF-400 \times It-96 and PF-400 \times No.267, while for cross Climax \times It-96 five parameter model (m, d, h, i and j) was adequate. The genetic estimates recorded for total number of nodes indicated that five parameter model was fit for the cross combinations PF-400 \times It-96 (m, d, i, j and l), Climax \times It-96 (m, d, h, i and j) and Climax \times No.267 (m, d, h, i and l) while for the cross PF-400 \times No.267 three parameter model (m, d and j) has shown adequate results. In case of number of productive nodes five parameter model (m, d, h, i and l) was adequate for three cross combinations PF-400 \times It-96, Climax \times It-96 and Climax \times No.267 while four parameter model (m, d, h and j) was best fit for the cross PF-400 \times No.267. (Table 3).

The generation means estimates for number of productive branches suggested that five parameter model is best fit for the crosses PF-400 \times It-96 (m, d, h, i and l), Climax \times It-96 (m, h, i, j and l) and Climax \times No.267 (m, d, h, i and l). For the cross PF-400 \times No.267 two parameter model (m and d) was adequate for the number of productive branches. Five parameter model involving m, d, h, i and l components was adequate for number of pods/plant in three cross combinations viz., PF-400 \times It-96, Climax \times It-96 and Climax \times No.267 while four parameter model (m, d, h and j) was best fit for the cross combination PF-400 \times No.267. In case of pod length, four parameter model was best fit for the cross combinations PF-400 \times It-96 (m, d, h and l), PF-400 \times No.267 (m, d, i and j) and Climax \times No. 267 (m, d, h and j). A five-parameter model involving m, d, h, i and j was adequate for the cross Climax \times It-96. (Table 3).

The genetic estimates for pod width have indicated that four parameter model involving m, d, h and i genetic components was best fit for two crosses (Climax \times It-96 and Climax \times No.267). Similarly, four parameter model (m, d, i and l) was adequate for the cross PF-400 \times No.267,

while three parameter model (m, h and i) was adequate for the cross PF-400 \times It-96. For number of seeds per pod, the four-parameter model was adequate for three cross combinations viz., PF-400 \times No.267 (m, d, i and j), Climax \times It-96 and Climax \times No.267 (m, d, j and l) but for cross combination PF-400 \times It-96 a five-parameter model (m, d, h, i and l) was best fit. A five-parameter model involving m, d, h, i and j was adequate for weight of pods/plant in three crosses viz., PF-400 \times It-96, PF-400 \times No.267 and Climax \times It-96 while for the cross Climax \times No.267 five parameter model involving m, d, h, i and l was best fit (Table 3).

In case of 100-seed weight (fresh), five parameter model involving m, d, h, j and l was best fit in three cross combinations (PF-400 \times It-96, PF-400 \times No.267 and Climax \times No.267) while four parameter model (m, d, h and j) had adequate estimates for the cross Climax \times It-96. The generation means estimates for 100-seed weight (dry) revealed the adequacy of five parameter model for two cross combinations viz., PF-400 \times No.267 (m, d, h, i and l) and Climax \times No.267 (m, d, h, i and j). The estimates for the cross PF-400 \times It-96 have indicated the fitness of four parameter model (m, d, h and l) while for the cross-combination Climax \times It-96, three parameter model involving m, d and i was best fit (Table 3).

Among all biparental crosses most of the traits indicated the prevalence of significant and positive value of heterosis with few exceptions. In case of cross combinations 'Climax \times It-96' and 'Climax \times No. 267' only one trait each (100 seed weight dry (g) and weight of pods per plant respectively) has shown negative and non-significant value of heterosis. Likewise, in cross combinations 'PF-400 \times It-96', two traits (pod length and 100 seed weight dry) have shown negative values of heterosis, while for cross combination 'PF-400 \times No.267', four traits including number of productive nodes, number of productive branches, pod length and number of seed per pod have shown the similar trend (Table 4).

Of the 11, nine traits of the cross 'Climax \times It-96' and 'PF-400 \times It-96' and eight traits of cross 'Climax \times No. 267' and 'PF-400 \times No. 267' respectively expressed significant positive values of inbreeding depression while negative values were observed for the remaining traits. 100 seed weight (dry) in cross 'Climax \times No. 267' and 'PF-400 \times It-96' expressed significant negative values of inbreeding depression, while number of productive branches in cross 'PF-400 \times It-96' have also shown significant negative values for this parameter (Table 4).

Medium to high values of broad sense heritability (0.30 to 0.90) were observed for all the traits among four biparental crosses except pod length (0.24) in cross 'PF-400 \times It-96'. Similarly, higher estimates of narrow sense heritability (0.60 to 0.99) were also seen in almost all the traits except pod length (0.19) in cross 'PF-400 \times It-96' (Table 4). Degree of dominance was less than unity for all traits in two cross combinations ('Climax \times It-96' and 'Climax \times No.267'). Likewise, for the crosses 'PF-400 \times It-96' and 'PF-400 \times No.267' average dominance ratio was also less than unity for most of the traits except for pod length and number of productive branches (Table 4).

Table 3. Components of generation means i.e., mean (m), additive [d], dominance [h], additive \times additive [i], additive \times dominance [j] and dominance \times dominance [l] for different yield related traits in four biparental pea crosses.

Traits	Cross	M	[d]	[h]	[i]	[j]	[l]	Df	χ^2
Node bearing 1st flower	Climax \times It-96	10.39 \pm 0.327	1.97 \pm 0.108	5.85 \pm 0.448	3.19 \pm 0.35	0.92 \pm 0.374	--	1	0.58
	Climax \times No. 267	12.91 \pm 0.068	1.33 \pm 0.075	--	--	--	2.09 \pm 0.185	3	7.38
	PF-400 \times It-96	13.54 \pm 0.086	1.57 \pm 0.098	--	--	--	2.27 \pm 0.212	3	4.04
	PF-400 \times No. 267	13.32 \pm 0.076	1.12 \pm 0.083	--	--	--	1.65 \pm 0.173	3	1.69
Total number of nodes	Climax \times It-96	30.89 \pm 0.461	6.51 \pm 0.134	10.87 \pm 0.645	4.51 \pm 0.493	-6.26 \pm 0.466	--	1	2.54
	Climax \times No. 267	23.15 \pm 0.934	10.57 \pm 0.101	40.66 \pm 2.191	15.90 \pm 0.926	--	-18.96 \pm 1.367	1	2.31
	PF-400 \times It-96	30.18 \pm 0.237	8.33 \pm 0.137	--	3.99 \pm 0.293	7.31 \pm 0.588	12.94 \pm 0.410	1	1.17
	PF-400 \times No. 267	37.60 \pm 0.089	11.81 \pm 0.144	--	--	-22.78 \pm 0.63	--	3	3.92
No. of productive nodes	Climax \times It-96	0.57 \pm 0.818	2.39 \pm 0.093	41.35 \pm 1.83	15.59 \pm 0.809	--	-20.37 \pm 1.087	1	1.16
	Climax \times No. 267	3.33 \pm 0.847	2.69 \pm 0.109	37.58 \pm 2.03	13.45 \pm 0.838	--	-19.61 \pm 1.27	1	1.55
	PF-400 \times It-96	11.88 \pm 0.864	3.66 \pm 0.071	14.68 \pm 1.98	2.80 \pm 0.860	--	-5.50 \pm 1.32	1	3.15
	PF-400 \times No. 267	15.57 \pm 0.119	4.30 \pm 0.132	-1.73 \pm 0.225	--	-1.46 \pm 0.536	--	2	1.44
No. of productive branches	Climax \times It-96	4.97 \pm 0.268	--	-6.15 \pm 0.679	-2.24 \pm 0.261	2.08 \pm 0.172	4.01 \pm 0.447	1	2.02
	Climax \times No. 267	4.66 \pm 0.342	0.278 \pm 0.048	-4.60 \pm 0.864	-2.03 \pm 0.337	--	2.93 \pm 0.606	1	1.49
	PF-400 \times It-96	4.67 \pm 0.282	0.42 \pm 0.042	-6.67 \pm 0.699	-3.09 \pm 0.276	--	4.10 \pm 0.447	1	6.6
	PF-400 \times No. 267	1.78 \pm 0.033	0.29 \pm 0.067	--	--	--	--	4	4.72
Number of pods per plant	Climax \times It-96	24.77 \pm 0.889	8.08 \pm 0.102	33.04 \pm 2.036	14.64 \pm 0.882	--	-9.72 \pm 1.218	1	2.48
	Climax \times No. 267	21.83 \pm 1.090	8.99 \pm 0.095	43.39 \pm 2.614	18.17 \pm 1.085	--	-15.90 \pm 1.664	1	3.15
	PF-400 \times It-96	49.17 \pm 1.30	18.48 \pm 0.090	-46.16 \pm 2.95	-19.80 \pm 1.30	--	45.61 \pm 1.80	1	2.95
	PF-400 \times No. 267	30.08 \pm 0.132	18.86 \pm 0.142	3.17 \pm 0.266	--	-32.18 \pm 0.642	--	2	4.21
Pod length (cm)	Climax \times It-96	6.47 \pm 0.170	0.811 \pm 0.064	1.27 \pm 0.256	1.01 \pm 0.183	-1.58 \pm 0.250	--	1	1.74
	Climax \times No. 267	6.34 \pm 0.031	1.61 \pm 0.031	1.18 \pm 0.081	--	-2.59 \pm 0.225	--	2	2.99
	PF-400 \times It-96	6.91 \pm 0.078	0.503 \pm 0.071	-2.80 \pm 0.369	--	--	2.12 \pm 0.438	2	1.19
	PF-400 \times No. 267	5.71 \pm 0.055	1.34 \pm 0.089	--	0.431 \pm 0.112	-2.30 \pm 0.314	--	2	0.52
Pod width (cm)	Climax \times It-96	1.36 \pm 0.033	0.06 \pm 0.012	0.37 \pm 0.051	0.24 \pm 0.036	--	--	2	1.69
	Climax \times No. 267	1.25 \pm 0.067	0.21 \pm 0.01	0.47 \pm 0.104	0.24 \pm 0.068	--	--	2	5.41
	PF-400 \times It-96	1.31 \pm 0.037	--	0.23 \pm 0.055	0.20 \pm 0.039	--	--	3	0.69
	PF-400 \times No. 267	1.28 \pm 0.021	0.15 \pm 0.011	--	0.12 \pm 0.026	--	0.30 \pm 0.034	2	5.71
Number of seeds per pod	Climax \times It-96	5.17 \pm 0.048	0.99 \pm 0.057	--	--	-1.27 \pm 0.307	1.14 \pm 0.134	2	1.61
	Climax \times No. 267	4.84 \pm 0.053	1.29 \pm 0.061	--	--	-2.0 \pm 0.379	1.38 \pm 0.187	2	1.37
	PF-400 \times It-96	7.09 \pm 0.612	1.05 \pm 0.072	-4.14 \pm 1.48	-1.95 \pm 0.606	--	3.34 \pm 0.944	1	1.68
	PF-400 \times No. 267	4.27 \pm 0.083	1.46 \pm 0.088	--	1.04 \pm 0.129	-0.99 \pm 0.406	--	2	2.87
Weight of pods per Plant	Climax \times It-96	27.84 \pm 0.479	25.46 \pm 0.122	51.26 \pm 0.601	25.01 \pm 0.502	-18.08 \pm 0.728	--	1	2.27
	Climax \times No. 267	13.69 \pm 1.116	24.16 \pm 0.112	122.4 \pm 2.65	40.50 \pm 1.111	--	-84.21 \pm 1.62	1	2.27
	PF-400 \times It-96	24.97 \pm 0.509	9.01 \pm 0.138	20.87 \pm 0.69	11.25 \pm 0.538	-6.67 \pm 0.644	--	1	3.53
	PF-400 \times No. 267	28.68 \pm 0.458	7.68 \pm 0.123	17.93 \pm 0.621	9.27 \pm 0.482	-6.68 \pm 0.604	--	1	1.08
100 seed weight-fresh (g)	Climax \times It-96	31.73 \pm 0.118	5.47 \pm 0.126	7.45 \pm 0.25	--	-7.24 \pm 0.541	--	2	4.28
	Climax \times No. 267	30.43 \pm 0.097	6.97 \pm 0.097	13.25 \pm 0.627	--	-9.36 \pm 0.610	-4.56 \pm 0.714	1	1.36
	PF-400 \times It-96	34.31 \pm 0.111	8.13 \pm 0.111	-4.98 \pm 0.6	--	6.74 \pm 0.551	14.35 \pm 0.643	1	2.71
	PF-400 \times No. 267	33.24 \pm 0.117	9.56 \pm 0.117	-5.6 \pm 0.614	--	7.14 \pm 0.599	19.07 \pm 0.697	1	3.05
100 seed weight-dry (g)	Climax \times It-96	12.79 \pm 0.091	1.08 \pm 0.108	--	0.64 \pm 0.162	--	--	3	6.23
	Climax \times No. 267	22.31 \pm 0.417	1.02 \pm 0.108	-7.31 \pm 0.572	-8.92 \pm 0.437	11.51 \pm 0.566	--	1	3.65
	PF-400 \times It-96	13.86 \pm 0.107	1.45 \pm 0.099	2.68 \pm 0.576	--	--	-4.18 \pm 0.635	2	3.08
	PF-400 \times No. 267	10.43 \pm 0.850	1.29 \pm 0.1	10.49 \pm 2.116	3.50 \pm 0.842	--	-6.90 \pm 1.373	1	2.75

Table 4. Estimates for heterosis, inbreeding depression, degree of dominance, broad sense and narrow sense heritability for yield related traits in four biparental pea crosses.

Traits	Cross	Heterosis	Inbreeding depression	H ² _{BS}	h ² _{NS}	Degree of dominance
Node bearing 1st flower	Climax × It-96	19.56	18.52	0.80	0.91	-0.21
	Climax × No. 267	16.15	11.26	0.82	0.97	-0.18
	PF-400 × It-96	17.47	12.03	0.81	0.92	-0.15
	PF-400 × No. 267	12.45	8.05	0.90	0.93	-0.03
Total number of nodes	Climax × It-96	17.85	13.22	0.70	0.97	-0.42
	Climax × No. 267	14.72	13.62	0.69	0.91	-0.22
	PF-400 × It-96	26.21	22.97	0.82	0.98	-0.25
	PF-400 × No. 267	0.00	-1.07	0.74	0.99	-0.32
Number of productive nodes	Climax × It-96	33.13	25.05	0.80	0.92	-0.22
	Climax × No. 267	26.82	19.15	0.75	0.95	-0.32
	PF-400 × It-96	47.62	17.63	0.42	0.78	-0.02
	PF-400 × No. 267	-10.68	-4.08	0.81	0.88	-0.13
Number of productive branches	Climax × It-96	2.91	-2.47	0.51	0.70	-0.56
	Climax × No. 267	13.70	-2.97	0.59	0.79	0.01
	PF-400 × It-96	31.66	-12.38	0.69	0.87	-0.36
	PF-400 × No. 267	-10.36	-1.73	0.32	0.72	-1.32
Number of pods per plant	Climax × It-96	22.14	19.19	0.81	0.95	-0.27
	Climax × No. 267	23.29	19.81	0.63	0.96	-0.27
	PF-400 × It-96	65.44	22.89	0.66	0.95	-0.20
	PF-400 × No. 267	10.43	3.16	0.81	0.97	-0.24
Pod length (cm)	Climax × It-96	3.01	8.06	0.51	0.72	-0.30
	Climax × No. 267	18.99	9.54	0.66	0.67	0.50
	PF-400 × It-96	-9.91	2.57	0.24	0.19	3.45
	PF-400 × No. 267	-5.36	2.40	0.51	0.94	-0.79
Pod width (cm)	Climax × It-96	8.02	10.86	0.33	0.67	-0.67
	Climax × No. 267	12.37	12.50	0.30	0.80	-0.25
	PF-400 × It-96	2.31	7.74	0.67	0.83	-0.13
	PF-400 × No. 267	12.77	15.09	0.88	0.88	0.00
Number of seeds per pod	Climax × It-96	22.31	15.88	0.74	0.73	0.29
	Climax × No. 267	29.71	18.33	0.39	0.60	0.35
	PF-400 × It-96	23.17	6.98	0.69	0.88	-0.18
	PF-400 × No. 267	-20.68	1.67	0.72	0.94	-0.27
Weight of pods per Plant	Climax × It-96	49.60	32.62	0.88	0.94	-0.09
	Climax × No. 267	-4.33	-3.78	0.83	0.88	-0.01
	PF-400 × It-96	26.31	23.15	0.80	0.98	-0.28
	PF-400 × No. 267	22.76	19.45	0.77	0.86	-0.05
100 seed weight-fresh (g)	Climax × It-96	23.70	10.87	0.75	0.93	-0.21
	Climax × No. 267	28.56	8.84	0.83	0.98	-0.15
	PF-400 × It-96	27.31	17.99	0.89	0.99	-0.15
	PF-400 × No. 267	40.52	24.08	0.70	0.86	-0.12
100 seed weight-dry (g)	Climax × It-96	-4.85	-0.47	0.47	0.87	-0.56
	Climax × No. 267	12.74	-24.72	0.80	0.96	-0.20
	PF-400 × It-96	-10.82	-12.54	0.81	0.88	-0.04
	PF-400 × No. 267	0.75	0.50	0.61	0.82	-0.13

Discussion

The green pod and seed yield in pea is an outcome of interaction of many genes with each other and with the environment (Lal *et al.*, 2018; Annicchiarico *et al.*, 2019). The selection of yield contributing traits is one of the recommended solutions to increase the yield (Azmat *et al.*, 2011; El-Nahas & El-Gabry, 2021). The breeding process for yield enhancement initiatives would be more effective if there was information available on the nature and scope

of the genetic factors influencing the inheritance of yield-contributing characteristics. The pattern of expression of quantitative traits is extremely complex because of the little contributions made by individual genes. Generation means analysis is the most preferred method for getting reliable estimates for different genetic components governing quantitatively inherited traits (Wannows *et al.*, 2015).

Since the presence of epistatic effects is confirmed by the significance of any scaling test (Latha *et al.*, 2018), it has been discovered that there are several types of epistatic

gene action in the context of our investigation. Significance of A and B scaling tests for majority of traits pointed towards the presence of all three types of non-allelic interactions. While significant value of C scaling test indicated the prevalence of dominance \times dominance interaction, likewise, the significance of D scaling test pointed the preponderance of additive \times additive type of gene action in controlling the inheritance of a few yields related traits in pea (Table 2).

Additive, dominance and epistatic genetic effects are the descriptor of quantitatively inherited traits. The average effect of genes that influence a particular trait is termed as additive genetic effect while the allelic and non-allelic interaction of genes are defined as dominance and epistatic genetic effects, respectively. The generation mean estimates for different yield related traits calculated in this study has confirmed the influence of additive and non-additive types of genetic effects in governing the inheritance of different yield related traits in pea.

The estimates for different genetic components have revealed the prevalence of additive genetic effect [d] in governing the inheritance of majority of traits studied in this research. It is also worth mentioning that the additive component [d] was lesser than the corresponding dominance component [h] whenever, it was present for majority of yield related traits with few exceptions. Excluding some traits, the additive [d] component in most of the traits was found less than the additive \times additive [i] component where both the components were present. With few exceptions of some yield related traits the similar trend was observed for the dominance \times dominance [l] and additive \times dominance [j] component (Table 3).

The comparatively low magnitude of additive component [d] in the above-mentioned instances suggested the role of additive and non-additive genes in governing the inheritance of different yield related traits in pea. The traits involving additive \times additive [i] interaction can be fixed in advanced generations (segregating) by simple selection (Said, 2014). For most of the traits the positive values of additive \times additive [i] genetic component indicates the accumulation of favorable alleles in the coming generations. There were very few traits for which the dominance [h] component was comparatively less than the additive component [d], which suggested the preponderance of the additive effects [d] over the dominance effect [h]. The positive value of [d] indicates the involvement of additive genes in the inheritance of that particular trait. Thus, selection in the next coming generations could be helpful in the improvement of the trait under consideration. The absence of epistatic interactions is the indication of simple inheritance and the traits lacking these interactions can be improved through selection even from early generations while the reverse is true if epistatic interactions are involved in the inheritance of traits (as in this study), which delays the selection procedure till later generations (Gunasekar *et al.*, 2018).

In our study, significant positive value of mid-parent heterosis and inbreeding depression for most of the traits were observed once again confirming the presence of both additive as well as non-additive type of gene action in controlling their expression. These results are also in

accordance with the heritability estimates. Similarly, the presence of negative and less than unity degree of dominance expressed the presence of partial dominance in controlling the expression of traits under study.

Since the cultivar Climax had highest mean value for most of the yield related traits among powdery mildew susceptible cultivars followed by the cultivar PF-400. The cv. Climax had shown good performance in pod related traits like pod length, pod width, weight of pods/ plant and number of productive branches and similarly cv. PF-400 was found to be good in seed related traits such as number of seeds/pods, 100-seed weight (fresh) and 100-seed weight (dry). Among powdery mildew resistant genotypes, It-96 has shown better performance in terms of yield related traits like number of pods/plants, while other powdery mildew resistant genotype (No.267) has its own significance with reference to having more number of productive branches. Keeping in view the individual characteristics of each parental genotype, all the four cross combinations have converged the characteristic of corresponding parents with the possibility to have high yielding genetic combination with powdery mildew resistant background. The powdery mildew resistance in It-96 and No.267 has been found to be governed by a single recessive gene (Azmat & Khan, 2013), and the BC₁ of the crosses had the highest mean value for all the economically important yield related traits (Table 1). Therefore, the back cross breeding method is suggested for the incorporation of powdery mildew resistance and the improvement of different yield related traits in pea.

Conclusion

This study focused on the genetic analysis of 11 yield traits in pea using four biparental crosses involving powdery mildew resistant and susceptible parents. The research employed scaling assays to identify the presence of non-allelic interactions (i, j, and l) for most yield-contributing traits. The findings revealed that a simple additive dominance model was not sufficient to explain the inheritance patterns of these traits. Generation mean analysis provided further insights, confirming the influence of both additive and non-additive genetic effects on the inheritance of all traits. The results indicated that additive genetic effects [d] played a significant role in controlling the majority of traits, although some exceptions were noted. The magnitude of additive genetic effects [d] was generally smaller than the corresponding dominant genetic effects [h]. Furthermore, the study demonstrated that, in most traits, the additive genetic component [d] was smaller than the non-allelic genetic components [i], [j], and [l], indicating the involvement of both additive and non-additive genes in controlling their inheritance. The presence of partial dominance was suggested by the values of the degree of dominance, which were smaller than unity. Significant positive mid-parent heterosis, inbreeding depression, and high heritability estimates were observed for most yield-related traits. These findings highlight the potential for exploiting heterosis and heritability to develop high-yielding genotypes with a powdery mildew resistant background in pea.

Considering the interplay of different genetic components involved in controlling the inheritance of yield-related traits and powdery mildew resistance in pea, the study recommends the utilization of the backcross breeding method to obtain genotypes with both high yield potential and resistance to powdery mildew. This approach would facilitate the development of improved pea varieties with enhanced agronomic performance and disease resistance.

Acknowledgements

Authors are thankful to the staff and scientists of Vegetable Research Institute, AARI (Ayyub Agricultural Research Institute), Faisalabad for the provision of experimental land and technical support.

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(Received for publication 14 July 2022)