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Detection of Epistasis for Yield and its Contributing Traits in Garden Pea under Mountain Himalayan Region

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ABSTRACT: Gene action studies were conducted using Triple Test Cross (TTC) analysis with the objective of determining the nature and magnitude of gene action for various horticultural traits under different environmental conditions. The ultimate goal was to enhance productivity in garden pea through suitable breeding strategies. Seventy-eight TTC progenies were developed by mating 26 lines (individual F_2 plant progenies from the cross between Palam Sumool × Palam Priya) with three testers—namely, the two parents (L_1 and L_2) and their single-cross F_1 hybrid (L_3). These were evaluated to detect epistasis and gene action across variable environments. Epistasis was detected for most traits, with a predominance of j + l type interactions. Traits such as pod length, seeds per pod, plant height, and pod yield per plant showed isodirectional dominance effects with decreasing magnitude, suggesting the potential utility of dominance effects in breeding. The presence of significant additive gene action for several traits, including pod yield per plant, indicates that early-generation selection could be effective for their improvement. However, the simultaneous expression of j + l type epistasis suggests that heterosis breeding may also have value. Despite this, exploiting hybrid vigor in pea is challenging due to its autogamous (self-pollinating) nature and the lack of genetic or cytoplasmic male sterility systems. Hence, alternative breeding strategies such as diallel selective mating, biparental mating, or recurrent selection followed by pedigree breeding are recommended. Additionally, delayed selection for pod yield and related traits in later generations could allow the exploitation of additive × additive epistatic effects more effectively.

Keywords: *Pisum sativum* L., triple test cross, gene action, epistasis, methodology.

INTRODUCTION

Garden pea (*Pisum sativum* L.), a member of the Fabaceae family, is an important vegetable crop cultivated widely in temperate and sub-tropical regions. It is valued for its high protein content (up to 22%) (Burstin *et al*., 2015; Bheri *et al.*, 2016) and is also rich in essential amino acids, notably lysine, which is typically deficient in cereals (Sharma *et al.*, 2014). Garden pea is consumed in multiple forms—fresh, frozen, canned, and dehydrated making it a versatile component of human diets (Ambrose, 2008; Anitha and Hanumantharaya 2022; Kumari *et al.*, 2023).

The North-Western Himalayan region of India provides diverse agroclimatic zones, allowing year-round pea cultivation. It is grown as an off-season cash crop in high hills during summer and in low to mid hills during winter, fetching premium market prices. In Himachal Pradesh alone, garden pea accounts for nearly 30% of the area under vegetable cultivation, covering approximately 26,000 hectares and yielding 328.8 thousand tonnes annually with a productivity of 12.64 metric tonnes per hectare (NHB, 2021-2022).

High yield, long and dark green pods, sweetness and resistant to pests and diseases are the main principles, being taken into consideration by the breeders for its genetic improvement keeping in view the demand of growers and consumers. Despite on-going breeding efforts, the average yield of garden peas in India is very low. This is primarily due to the limited genetic diversity used in developing new varieties (Kumar *et al*., 2004). Farmers tend to prefer cultivars that display specific desirable traits, such as lush green pods, which further constrains the genetic base being utilized. Relying heavily on a limited number of age-old cultivars can cause genetic diversity to decline. This reduction in genetic variability can make crops more vulnerable to evolving pathogens, leading to the emergence of new pathogen races. Consequently, these dynamics can result in decreased crop yields.

As a self-pollinated crop, garden pea relies on recombinant breeding to combine favourable alleles for

traits like pod length, yield, and disease resistance. The efficient breeding programme with an aim of developing varieties with desirable traits warrants recognizing the mode of inheritance of traits in question (Cockerham, 1961; Farshadfar *et al.*, 2008). Quantitative traits like yield are typically polygenic, influenced by many genes each contributing small effects. Biometrical methods help elucidate the genetic architecture of such traits, but the ideal approach makes minimal assumptions and yields reliable estimates.

Genetic variance can be partitioned into phenotypic, genotypic, and environmental components, with genotypic variance further divided into additive, dominance, and epistatic components. The most complex is epistatic for trait inheritance studies (Fisher, 1984) and is important in quantitative trait inheritance (Rebetzke *et al.,* 2006; Sood *et al.,* 2007). Bernardo (2002) defines epistasis as situations where the combined effect of loci differs from the sum of individual effects; in its absence, an additive–dominance model suffices. In the absence of epistasis, additive-dominance models are adequate. However, when epistasis is present, ignoring it can lead to biased estimates of heritability and response to selection (Barona *et al.,* 2012). Most traditional biometrical analyses rely on second-order statistics that assume no epistasis, which can limit their validity (Kempthorne and Curnow 1961; Sharma *et al.,* 2008).

Epistasis affects virtually all complex traits in crops, ignoring it leads to biased results and missed insights. (Mather and Jinks 1982). In literature, emphasis has been made repeatedly for its importance in quantitative traits inheritance without consistent results. Presently, interest in epistasis is increasing because it influences both heterosis and inbreeding depression (Primomo *et al.,* 2005). In self-pollinated crop like pea, additive × additive epistasis is particularly significant, as it can be harnessed during the development of pure lines.

Among various methods to detect epistasis, the Triple Test Cross (TTC) analysis proposed by Kearsey and Jinks (1968) is one of the most powerful. It not only detects epistasis but provides detailed estimates of the genetic architecture, including inbreeding level, linkage disequilibrium, and gene distribution (Barona *et al.,* 2012). Its advantages include command to detect epistasis, accommodates large number of samples from the population (Pooni *et al.,* 1994; Kearsey and Jinks 1968; Kearsey and Pooni 1996). It not only identifies epistasis but also provides accurate estimates of additive and dominance variance components in the absence of epistasis (Viana, 2005). Its flexibility allows it to be applied across a range of populations and mating systems—including segregating (F_2, backcross) and non-segregating generations (Chahal & Jinks 1978). In light of this, the present study aimed to detect non-allelic gene interactions and to estimate additive and dominance components of variance for pod yield and related horticultural traits in garden pea. The insights gained from this study will inform breeding strategies aimed at isolating transgressive segregants with superior pod quality traits in advanced generations.

MATERIALS AND METHODS

The present investigation was conducted at two distinct locations in Himachal Pradesh, India: the Experimental Farm of the Department of Vegetable Science and Floriculture at Himachal Pradesh Agricultural University, Palampur (E1), and the Highland Agricultural Research and Extension Centre, Kukumseri (E2).

Demographic features of experimental locations.

Feature	Palampur (E_1)	Kukumseri (E_2)
Altitude	1290.8 m	2,672 m
Latitude and longitude	32°8' N and 76°3' E	31˚44'N and 76˚41'E
Climate	Humid and temperate	Dry temperate
Annual rainfall	2500 mm	125 mm
Soil	Clay acidic soils with pH 5.6	Sandy loam soils with near neutral pH 6.8

EXPERIMENTAL MATERIAL

Two genetically diverse homozygous parents namely, Palam Sumool (very long, bright green pods, powdery mildew resistant) and Palam Priya (yellowish green, medium sized pods, slow mildewing) were crossed to develop F_1. The F_1 seed was raised to produce F_2 seed by selfing. Parents along with F_1 were used as testers 'L_1', 'L_2' and 'L_3', respectively. Twenty six plants were randomly chosen from F_2 population and were backcrossed with the three testers i.e. parents and their F_1 at Palampur as per mating design proposed by Kearsey and Jinks (1968). Thus, the experiment material consisted of '3n' families *i.e.* 78 triple test cross progenies.

Experimental Design and Layout. The experimental material thus, comprising of 78 triple test cross progenies along with 26 F_3 lines and three testers was raised in randomized complete block design with three replications at two diverse environments *viz.*, Kukumseri (E_1) and Palampur (E_2) during summer and winter, respectively. Each cross and parent was sown in single row of 2.7 m length with inter and intra-row spacing of 45 cm and 10 cm, respectively. The experimental fields were disked and the recommended rate of N:P:K fertilizer (50N:60P_2O_5:60K_2O kg per hectare) were applied in the rows at the time of sowing. Seed treatment with Bavistin @ 3g/ kg of seed was done. Irrigation was given prior to sowing and as needed thereafter. The weedicide Pendimethalin @ 1.5 kg/ha was applied immediately after sowing followed by two hand weedings during entire crop duration to keep the field weed free.

Recording of the data. The data were recorded on 10 randomly selected competitive plants in each of 26 lines, 3 testers (L_1, L_2 and L_3) and 78 triple test cross progenies in each of three replications for days to flowering, days to first picking, pod length (cm), seeds per pod, shelling percentage, average pod weight (g), plant height (cm), pods per plant and pod yield per plant (g).

Statistical analysis. The mean values of all observations for each location were analysed individually and then their combined data were analysed. Analysis of variance for randomized complete block design was done using the model suggested by Panse and Sukhatme (1984). The triple test cross analysis was carried out as suggested by Kearsey and Jinks (1968). Jinks and Perkins (1970) analysis was applied to detect epistasis along with testing and estimating additive and dominance components of genetic variation. The statistical analysis was done using WINDOW SPAR software.

RESULTS

The mean squares due to epistasis (Tables 1 & 2) were significant for the majority of traits across both environments (E1 and E2) as well as the pooled environment (E3), indicating the presence of epistatic interactions for these traits. However, epistasis was non-significant for days to first picking in E1, E2, and E3, and for average pod weight in E2, suggesting the absence of non-allelic interactions in these specific cases.

Further partitioning of epistasis into additive × additive ('i') and additive/dominance × dominance ('j+l') components revealed that 'j+l' interactions significantly contributed to most traits across both individual and pooled environments (Table 1 and 2), except for days to flowering in E1 and days to first picking in all environments. Conversely, the additive × additive ('i') type of epistasis was absent for all traits in E1, and similarly absent in E2 and E3 for most traits, with the exception of plant height and pod yield per plant at E2, and plant height in E3.

The significance of mean squares for sums (D) and differences (H) helped directly detect additive and dominance genetic components in the presence of epistasis. Both D and H were significant for all traits in both environments and the pooled environment (Table 3), except for days to first picking at E2, where dominance variance was non-significant. This underlines the importance of both additive and dominance components in trait control, with additive effects being relatively more prominent.

The average degree of dominance (H/D) mostly indicated partial dominance (Table 4), underscoring the prevalence of additive gene action. However, complete dominance was observed for pods per plant and pod yield per plant at E1, pod length and shelling percentage at E2, and for shelling percentage and pods per plant at E3.

The directional dominance component 'F' was generally positive but non-significant, suggesting ambidirectional dominance for days to flowering, days to first picking, shelling percentage in E1 and E3, and average pod weight in E1, indicating a balanced distribution of dominant and recessive alleles. In contrast, a significant negative 'F' was observed for pod length, seeds per pod, plant height, and pod yield per plant across all environments, as well as for shelling percentage in E2 and average pod weight in E2 and E3. This suggests an isodirectional dominance trend, where recessive alleles were more prevalent. Additionally, pods per plant showed a significant positive 'F' value, indicating the presence of increasing alleles. Correlation coefficients between sums and differences were non-significant (Table 4), further supporting the ambidirectional nature of dominance.

DISCUSSION

The genetic characterization of germplasm using morphological, physiological, and particularly molecular markers is essential prior to executing a breeding program. This ensures the broadening of the genetic base in breeding populations. In the present study, molecular characterization of two parental lines, Palam Sumool and Palam Priya, using 18 genomic SSRs revealed polymorphism in 17 markers (Fig. 1), indicating substantial genetic divergence. This satisfies the fundamental requirement for conducting a triple test cross (TTC) analysis.

The presence of epistasis for the majority of traits (Tables 1 & 2) suggests that estimates of additive and dominance variance would have been biased had a model assuming no epistasis been used (Kumar *et al*., 2011; Patial *et al*., 2022). Epistatic interactions complicate selection due to the involvement of multiple interacting loci. However, a reduction in such interactions can facilitate more efficient selection, which then relies primarily on dominance and environmental variances (Farshadfar *et al.*, 2008). The significant contribution of additive × dominance (j) and dominance × dominance (l) epistatic interactions across environments (Tables 1 & 2) emphasizes the importance of accounting for epistasis in breeding strategies aimed at improving commercially important traits.

According to Bernardo (2002), epistatic variation is typically of smaller magnitude and associated with higher estimation error compared to additive and dominance variances, making it difficult to separate these components. The significance of mean squares due to sums (D) and differences (H) for most traits across environments (Tables 3 & 4) underscores the importance of both additive and dominance components (Alam *et al.,* 2023). Notably, additive variance was more pronounced, although estimates were biased to varying degrees due to the presence of epistasis except for traits like days to first picking (E1 and E2) and average pod weight (E2), where epistatic influence appeared minimal.

The relatively high magnitude of additive variance suggests the predominance of fixable gene action in the inheritance of most traits, implying that early generation selection could be effective. However, additive estimates (D) were influenced by additive ×

additive and additive × dominance interactions at some loci (Pooni *et al.*, 1994). Reports supporting additive gene action for several traits using TTC designs have been documented (Singh and Sharma 2006; Singh *et al.*, 2006; Sharma *et al.*, 2008; Nassef and El-Rawy 2013: Patial *et al.*, 2022). Conversely, other studies using line × tester or diallel designs reported a preponderance of non-additive gene action for pod yield and its components (Sharma *et al.*, 2012; Thiyam *et al.*, 2013), highlighting the utility of TTC in precisely delineating gene action.

The isodirectional nature of dominance observed for traits like pod length, seeds per pod, plant height, and pod yield across all environments as well as shelling percentage and average pod weight in some environments suggests decreasing effects of negative alleles. Sharma *et al*. (2008) similarly reported this for seeds per pod, while Singh *et al.* (1997) found a positive and significant F component for pod length in field pea. Non-significant correlation coefficients between sums and differences indicate a nearly equal distribution of increasing and decreasing alleles among the parental lines (Kumar *et al.*, 2011).

In conclusion, excluding epistasis from biometric models may lead to biased estimates of additive and dominance variances. To date, no robust evidence exists quantifying the extent of this bias or the precise impact of epistasis on quantitative trait expression (Sofi *et al.*, 2006). Given that epistatic effects are more environmentally sensitive than additive or dominance effects (Perkins and Jinks 1971), and that environmental interactions increase with the number of genes involved (Gamble, 1962), the observed epistasis × environment interaction in this study is understandable.

Since additive gene action predominated for most traits, early-generation selection may be an effective breeding strategy. Furthermore, the significance of j and l types of epistasis in the inheritance of pod yield and related traits, along with the importance of both D and H components for traits like pods per plant, suggests that non-fixable gene effects could be exploited through heterosis breeding. However, the autogamous nature and cleistogamous flowers of garden pea limit the commercial feasibility of hybrid development. An alternative strategy could involve intermating selected individuals in early segregating generations to form populations with desirable levels of homozygosity and heterozygosity, with delayed selection in later generations.

Exploitation of both additive and non-additive variation—including epistasis—could yield transgressive segregants with enhanced yield potential. This can be achieved through diallel selective mating, biparental mating, or recurrent selection followed by the pedigree method (Sood *et al*., 2007; Sharma *et al*., 2012). In addition, given the focus in pea breeding on disease resistance along with yield, involving multiple parents and promoting random intermating in segregating generations (Doerksen *et al.*, 2003) may effectively pool favorable alleles, maintaining genetic variation within the breeding population.

Table 1: Analysis of variance for the detection of epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) for pod yield per plant and related horticultural traits at Palampur (E_1) and Kukumseri (E_2).

Source of variation		Epistasis		i type interaction		j+l type interaction		Epistasis × Rep.		i type × Rep.		j+l type × Rep.	
Trait	Env.	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2
	d.f.	26	26	1	1	25	25	52	52	2	2	50	50
Days to flowering		33.13*	26.06*	29.54	8.01	33.27	26.79*	19.09	9.72	14.00	33.94*	19.29	8.75
Days to first picking		80.31	5.37	55.85	0.01	81.29	5.59	57.92	5.18	72.83	6.40	57.33	5.13
Pod length (cm)		4.14*	5.79*	0.46	5.35	4.29*	5.81*	0.28	2.00	0.05	0.87	0.27	2.05
Seeds/pod		2.43*	1.68*	1.99	0.41	2.44*	1.73*	0.28	0.71	0.52	1.59	0.27	0.68
Shelling percentage		64.86*	159.73*	49.33	3.39	65.48*	165.99*	17.05	48.14	5.17	48.11	17.53	48.14
Average pod weight (g)		4.68*	2.03	0.64	0.13	4.85*	2.11*	1.15	1.28	0.22	4.00	1.18	1.20
Plant height (cm)		374.23*	401.16*	48.89	764.03*	387.24*	386.65*	13.09	16.66	3.90	1.82	13.45	17.25
Pods/plant		171.34*	19.31*	7.24	0.35	177.90*	20.07*	16.74	1.27	17.46	1.20	16.71	1.27
Pod yield/plant (g)		6712.96*	925.49*	234.73	132.34*	6972.09*	957.21*	70.80	36.28	72.21	0.92	70.74	37.69

* Significant at $P \leq 0.05$

Table 2: Analysis of variance for the detection of epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) for pod yield and related horticultural traits over pooled environments (E_3).

Source of variation		Epistasis	i type epistasis	j+l type epistasis	Epistasis × Replication	i type × Replication	(j+l) type × replication
Trait	d.f.	26	1	25	52	2	50
Days to flowering		17.02*	17.08	17.02*	6.18	1.54	6.36
Days to first picking		23.47	14.39	23.83	16.71	30.39	16.16
Pod length (cm)		3.34*	0.67	3.45*	0.56	0.13	0.57
Seeds/pod		1.17*	0.15	1.21*	0.23	0.26	0.22
Shelling percentage		45.29*	6.71	46.83*	15.76	5.67	16.17
Average pod weight (g)		2.19*	0.03	2.28*	0.31	0.99	0.29
Plant height (cm)		180.72*	299.86*	175.95*	6.64	1.62	6.84
Pods/plant		45.71*	2.70	47.43*	4.82	5.97	4.77
Pod yield/plant (g)		2020.85*	179.89	2094.49*	29.77	14.92	30.36

* Significant at $P \leq 0.05$

Table 3: Analysis of variance for sums ($\overline{L}_{1i} + \overline{L}_{2i} + \overline{L}_{3i}$) and differences ($\overline{L}_{1i} - \overline{L}_{2i}$) for pod yield per plant and related horticultural traits at Palampur (E_1), Kukumseri (E_2) and over pooled environment (E_3).

Source of variation		Mean squares due to											
		Additive variance						Dominance variance					
		Sums			Sums × replication			Difference			Difference × replication		
Trait	Env.	E_1	E_2	E3	E_1	E_2	E3	E_1	E_2	E3	E_1	E_2	E3
	d.f.	25	25	25	50	50	50	25	25	25	50	50	50
Days to flowering		57.06*	14.94*	19.81*	8.51	5.86	2.80	13.20*	10.91*	7.41*	4.06	3.70	2.30
Days to first picking		65.80*	2.81*	18.35*	25.24	1.41	6.52	14.75*	2.80	5.35*	6.92	1.72	2.37
Pod length (cm)		4.14*	3.32*	2.48*	0.17	0.70	0.23	1.12*	3.92*	1.11*	0.18	0.83	0.27
Seeds/pod		2.49*	0.91*	1.00*	0.13	0.26	0.11	1.11*	0.60*	0.38*	0.08	0.15	0.06
Shelling percentage		37.58*	78.31*	33.70*	10.65	11.67	5.97	25.65*	72.97*	31.62*	6.69	10.69	3.90
Average pod weight (g)		3.60*	1.25*	1.08*	0.43	0.40	1.10	1.54*	0.74*	0.29*	0.39	0.41	0.12
Plant height (cm)		820.51*	194.61*	300.56*	11.36	4.46	4.19	65.35*	142.13*	46.08*	4.43	3.80	1.96
Pods/plant		190.02*	14.70*	57.13*	3.08	0.49	0.92	187.29*	8.10*	53.77*	6.70	0.36	1.67
Pod yield/plant (g)		7732.36*	895.33*	2734.79*	34.68	16.45	15.38	7382.97*	627.22*	2063.60*	41.39	17.46	14.13

Table 4: Estimates of genetic components of variation for various traits in garden pea at Palampur (E_1), Kukumseri (E_2) and in pooled over environments (E_3).

Source of variation	D			H			$(H/D)^{1/2}$			R			F		
Trait / Env.	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3	E_1	E_2	E_3
Days to flowering	64.74*	12.11*	22.69*	12.19*	8.66*	6.81*	0.43	0.85	0.55	-0.24	-0.21	-0.16	3.36	1.08	1.00
Days to first picking	54.08*	1.87*	15.78*	10.43*	1.44	3.98*	0.44	0.88	0.50	-0.28	-0.03	-0.29	3.32	0.2	0.80
Pod length (cm)	5.29*	3.49*	3.00*	1.25*	4.12*	1.11*	0.49	1.09	0.61	0.15*	0.44*	0.16*	-0.20*	-0.84*	-0.16*
Seeds/pod	3.13*	0.87*	1.19*	1.37*	0.60*	0.04*	0.66	0.83	0.61	0.31*	0.10*	0.25*	-0.32*	-0.12*	-0.08*
Shelling percentage	35.91*	88.86*	36.98*	25.29*	83.05*	36.97*	0.84	0.97	1.00	-0.41	0.03*	-0.03	6.20	-1.28*	0.56
Average pod weight (g)	4.23*	1.13*	1.30*	1.54*	0.44	0.23*	0.60	0.62	0.42	-0.36	0.27*	0.16*	0.48	-0.08*	-0.04*
Plant height (cm)	1078.86*	253.54*	395.16*	81.22*	184.44*	58.83*	0.27	0.85	0.39	0.09*	0.08*	0.09*	-13.32*	-8.64*	-6.84*
Pods/plant	249.2*	18.95*	74.95*	240.79*	10.32*	69.46*	1.00	0.74	0.96	-0.07*	-0.07*	0.02*	8.56*	0.48*	0.10*
Pod yield/plant (g)	10263.58*	1171.84*	3625.87*	9788.79*	813.01*	2732.63*	1.00	0.83	0.87	0.17*	0.23*	0.26*	-852.04*	-112.24*	-409.20*

*** Significant at P ≤ 0.05**

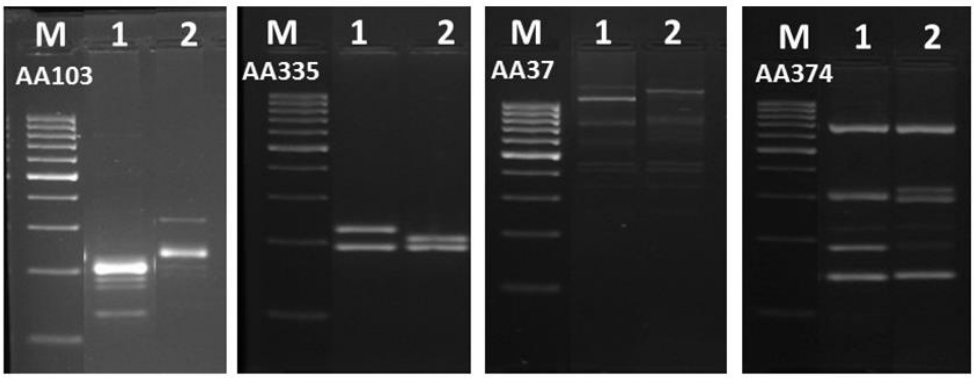

Fig. 1. Genetic diversity between parents Palam Sumool (1) and Palam Priya (2) observed using SSR primers (M, molecular weight marker).

CONCLUSIONS

In pea breeding, the primary objective is to develop pure lines that can fix additive × additive (i-type) epistasis, which contributes to the superiority of elite lines (Goldringer *et al.*, 1997). To achieve this, diallel selective mating, biparental mating, or recurrent selection followed by the pedigree method of selection is recommended. Alternatively, delaying selection until later generations of inbreeding (F5 or F_6) for traits such as pod yield is advised, as it allows the beneficial effects of additive × additive epistasis to be fully exploited once homozygosity is established (Farshadfar *et al.*, 2008).

FUTURE SCOPE

The present investigation indicates that epistasis plays a significant role and should not be ignored, as disregarding it can lead to biased estimates of additive and dominance components, ultimately resulting in misleading conclusions and loss of critical information regarding gene interactions. Hence, insights gained from this study would be utilized to formulate breeding strategy to isolate transgressive segregants with higher pod yield and good quality traits in the advanced generations.

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