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Additive Gene Action and Cross-Specific Heterosis Shape Yield Traits in Pigeonpea: Evidence from NC-III Design

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Abstract

Understanding the relative contribution of additive and non-additive gene effects is essential for designing efficient breeding strategies in pigeonpea (*Cajanus cajan* (L.) Millsp.). The present study employed a North Carolina Design III (NC-III) in biparental populations derived from three crosses (PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881) to simultaneously dissect genetic variance components, heritability, and heterotic responses for ten agronomic traits. Significant variability among progenies indicated effective recombination and generation of exploitable genetic diversity. Additive variance predominated for most traits, particularly number of pods per plant and plant height, suggesting high potential for selection-based improvement, whereas dominance effects were appreciable for seed yield and pod length in specific crosses, indicating the importance of non-additive gene action. Moderate to high narrow-sense heritability coupled with substantial genetic advance further supported the effectiveness of early-generation selection for key traits. Heterosis analysis revealed cross-specific advantages, with PADT-16 × Pusa 992 exhibiting superior performance for yield-related traits, while PADT-16 × PAU 881 was advantageous for earliness and seed attributes. By integrating variance components, heritability, variability, and heterotic responses, this study proposes a trait-specific and cross-specific breeding framework that aligns genetic architecture with optimized selection strategies. The findings provide practical insights for improving yield and adaptability in pigeonpea and demonstrate the utility of NC-III-derived biparental populations for decision-oriented breeding.

Keywords: biparental mating; gene action; heterosis; heritability; pigeonpea; NC-III design

1. Introduction

Pigeonpea (*Cajanus cajan* (L.) Millspaugh) is an important grain legume cultivated in tropical and subtropical regions, particularly in India, where it serves as a major source of dietary protein. It is a diploid species (2n = 2x = 22) with a genome size of approximately 833 Mb organized into 11 linkage groups (**Varshney et al., 2012**). Globally, pigeonpea occupies about 6.66 million hectares with an annual production of 4.85 million tonnes, of which India contributes more than 90% (**Directorate of Economics and Statistics, 2023**). Despite its significance, yield levels remain relatively low due to limited genetic variability and the complex inheritance of yield-related traits.

In plant breeding, the presence of limited variability and unfavourable trait associations often restricts the effectiveness of selection. Biparental mating has been recognized as an effective approach to enhance genetic recombination and break undesirable linkages, thereby generating superior recombinants. Intermating in early segregating generations (F_2 and F_3) increases heterozygosity and facilitates the accumulation of favourable allelic combinations (**Chandrakant et al., 2015**). However, a comprehensive understanding of the underlying gene action governing yield and its components is essential for designing efficient breeding strategies. Biometrical genetic approaches, particularly mating designs, play a crucial role in partitioning genetic variance into its components. Among these, the North Carolina Design III (NC-III) proposed by **Comstock and Robinson (1948, 1952)** is widely used to estimate additive and dominance genetic variances with high efficiency. Compared to other mating designs such as diallel analysis, NC-III requires fewer crosses, minimizes maternal effects, and provides reliable estimates of genetic parameters (**Hallauer and Miranda, 1988**). Despite its advantages, the application of NC-III in pigeonpea, especially using biparental progenies, remains limited.

Understanding the relative importance of additive (σ^2A) and dominance (σ^2D) genetic variances is critical for determining appropriate breeding strategies. Traits governed predominantly by additive effects can be improved through selection, whereas non-additive effects can be exploited through heterosis breeding (**Singh and Vashisht, 2023; Deep et al., 2025**). Therefore, simultaneous estimation of gene action and heterosis provides valuable insights into the genetic architecture of yield and its component traits. Despite the

availability of studies on genetic variability and heterosis in pigeonpea, most investigations have examined these components independently, providing limited guidance for integrated breeding decisions. In addition, the application of North Carolina Design III (NC-III) to biparental populations in pigeonpea remains relatively underexplored, particularly for developing trait-specific selection strategies. The present study addresses this gap by integrating genetic variance components, heritability, phenotypic variability, and heterotic responses within a unified analytical framework. This approach enables the identification of cross-specific and trait-specific breeding strategies, thereby linking quantitative genetic analysis with practical decision-making in crop improvement programs. The findings are expected to provide a scientific basis for selecting appropriate breeding strategies aimed at developing high-yielding pigeonpea genotypes.

2. Materials and Methods

2.1. Experimental Site and Plant Material

The field experiment was conducted at the Norman E. Borlaug Crop Research Centre, GBPUA&T, Pantnagar, located in the Shivalik foothills of the Himalayas. The soil of the experimental site was sandy loam with a pH of 7.2 and a relatively high-water table. Three pigeonpea crosses, namely PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU-881, were used to develop the experimental material. The crosses were initiated during the Kharif 2019–20 season. The F_1 generation was raised in Kharif 2020–21, followed by F_2 in 2021–22 and F_3 in 2022–23 through selfing.

2.2. Development of Biparental Progenies and NC-III Design

Biparental progenies (BIPs) were developed from F_3 plants using the North Carolina Design III (NC-III). Randomly selected F_3 plants were used as males and crossed with inbred female lines to generate progenies. A total of 48 biparental progenies were developed. The experiment was laid out in a randomized complete block design (RCBD) with three replications. Each cross was divided into two sets, and each set was evaluated separately.

2.3. Traits Recorded

Data were recorded on ten agronomic traits: days to 50% flowering (DFF), days to maturity (DM), plant height (PH), number of primary branches per plant (NPB), number of secondary

branches per plant (NSB), number of pods per plant (NPP), pod length (PL), number of seeds per pod (NSP), hundred seed weight (HSW), and seed yield per plant (SYP).

2.4. Statistical Analysis

The following linear model was used for analysis:

$$Y_{(ijklt)} = \mu + s_i + b_{ij} + f_{ik} + m_{il} + (f_m)_{ikl} + e_{(ijklt)}$$

where μ is the overall mean; s_i is the effect of the i^{th} set; b_{ij} is the effect of the j^{th} replication within the i^{th} set; f_{ik} is the effect of the k^{th} female; m_{il} is the effect of the l^{th} male; $(f_m)_{ikl}$ represents the interaction effect; and $e_{(ijklt)}$ is the experimental error.

2.4.1. Genetic variance components

Genetic variance components were estimated following the method of Comstock and Robinson (1952):

$$\sigma^2_m = \frac{(MMS - EMS)}{2r}$$

$$\sigma^2_{mf} = \frac{(FMMS - EMS)}{r}$$

$$\sigma^2_e = EMS$$

Additive and dominance variances were estimated as:

$$\sigma^2_A = 4\,\sigma^2_m$$

$$\sigma^2_D = 2\,\sigma^2_{mf}$$

The phenotypic variance was computed as:

$$\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2_e$$

The average degree of dominance was calculated as:

$$\bar{d} = \sqrt{\sigma^2_D / \sigma^2_A}$$

2.4.2. Estimation of Heterosis

Mid-parent heterosis (MPH) and better-parent heterosis (BPH) were calculated as:

$$Mid\ parent\ heterosis\ (MPH) = \frac{(F_1 - MP)}{MP} \times 100$$

$$Better\ parent\ heterosis\ (BPH) = \frac{(F_1 - BP)}{BP} \times 100$$

The significance of heterosis was tested using t-tests:

$$S.E.of\ MP = \sqrt{\frac{3}{2r}\ EMS}\ ;\ S.E.of\ BP = \sqrt{\frac{2}{r}\ EMS}$$

$$t\ value\ for\ MPH = \frac{(F_1 - MP)}{SE} \times 100\ ;\ t\ value\ for\ BPH = \frac{(F_1 - BP)}{SE} \times 100$$

All statistical assumptions, including normality and homogeneity of variance, were tested and found to be satisfied.

2.5. Software Used

Statistical analyses were performed using the "*agricolae*" package in R (version 4.3.3).

3. Results

3.1. Analysis of Variance

Analysis of variance revealed highly significant ($p \leq 0.05$) differences among biparental progenies for all studied traits across the three crosses, indicating the presence of substantial genetic variability (**Table 1**). Replication effects were largely non-significant, confirming uniform experimental conditions and minimal environmental influence. Mean squares due to males and females within sets were highly significant for all traits, demonstrating considerable genetic variability among the F_3-derived parents and testers. The significance of male × female interaction across traits indicates the involvement of both additive and non-additive gene effects. The magnitude of variance due to females was generally higher than that of males for most traits.

3.2. Components of Genetic Variance

Estimates of genetic variance components revealed that additive variance (σ^2A) exceeded dominance variance (σ^2D) for the majority of traits across all crosses (**Table 2**). The average degree of dominance was less than unity for most traits, indicating partial dominance.

However, relatively higher dominance effects were observed for days to 50% flowering (DFF) and seed yield per plant (SYP) in PADT-16 × Pusa 992; plant height (PH), pod length (PL), and SYP in PADT-16 × UPAS 120; and PL in PADT-16 × PAU 881.

3.3. Heritability and Genetic Advance

Narrow-sense heritability (h^2) estimates ranged from moderate to high across traits and crosses (**Table 3**). In PADT-16 × Pusa 992, all traits except DFF exhibited moderate to high heritability, whereas in PADT-16 × UPAS 120, SYP showed relatively lower heritability. All traits in PADT-16 × PAU 881 exhibited moderate to high heritability. High heritability coupled with high genetic advance as percent of mean was observed for number of pods per plant (NPP) and plant height (PH) across most crosses. In contrast, number of primary branches (NPB) and number of secondary branches (NSB) exhibited high heritability but low genetic advance.

3.4. Mean Performance and Variability of Biparental Progenies

Significant variation ($p \leq 0.05$) among biparental progenies was observed for all traits. The coefficient of variation (CV) revealed distinct patterns of variability across traits and crosses. Higher CV values were consistently recorded for number of seeds per pod (NSP) (8.26–10.42%), NPB (6.62–7.85%), PH (3.73–6.36%), and SYP (5.10–5.36%). In contrast, DFF (0.58–0.99%) and days to maturity (DM) (0.64–0.98%) exhibited low variability across all crosses. The range of variation indicated substantial diversity among progenies. DFF ranged from 76 to 87 days, and DM ranged from 118.67 to 147.67 days. Plant height varied from 123.23 cm to 295.43 cm. Among yield-related traits, NPP reached a maximum of 211, NSP reached 4.70, and SYP ranged from 32.83 g to 52.73 g. Among the crosses, PADT-16 × Pusa 992 exhibited superior mean performance for yield and its component traits, whereas PADT-16 × PAU 881 showed relatively superior performance for earliness and seed weight (**Figure 1b**).

3.5. Variability and Precision Parameters

Estimates of CV, standard error of mean (S.Em.), and critical difference (CD) indicated a satisfactory level of experimental precision and the presence of exploitable variability among progenies (**Table 4a, b**). The magnitude of S.Em. was low for most traits, indicating high precision of estimates. The CD values at both 5% and 1% levels were sufficient to

discriminate among progenies for key traits. Traits such as NPP and SYP exhibited moderate CV along with significant CD values, indicating reliable differentiation among genotypes.

3.6. Relative Heterosis and Heterobeltiosis

Significant heterosis ($p \leq 0.05$) was observed across traits, with magnitude and direction varying among crosses (**Table 5**). All crosses exhibited negative heterosis for DFF (−10.38% to −5.38%) and DM (−14.21% to −4.45%). Positive heterosis was observed for branching traits, with NPB ranging from 11.11% to 45.45% and NSB from 13.68% to 68.88%. Yield-related traits showed substantial positive heterosis, with SYP ranging from 9.35% to 40.95%. NPP and NSP also exhibited positive heterotic responses. Plant height showed negative heterosis (up to −50%). Heterobeltiosis followed similar trends, with negative values for phenological traits and positive values for yield-related traits. However, no single progeny exhibited superiority across all traits. A comparison between mid-parent heterosis and heterobeltiosis was made between the BIPs for seed yield and its contributing traits (**Figure 1a**). Correlation analysis revealed a strong positive association between DFF and DM, while SYP exhibited positive associations with most component traits (**Figure 2**). Negative associations involving hundred seed weight (HSW) were observed in PADT-16 × PAU 881.

4. Discussion

The present investigation provides a comprehensive assessment of the genetic architecture of yield and its component traits in pigeonpea using NC-III-derived biparental populations. The significant variability observed across all traits confirms that biparental mating effectively enhanced recombination and generated a broad spectrum of segregants, thereby increasing the probability of recovering superior genotypes. Such enhancement of variability through intermating has been widely recognized as a key mechanism for breaking undesirable linkages and accumulating favourable alleles (**Comstock and Robinson 1952; Hallauer and Miranda 1988; Rudra et al. 2009**).

A major outcome of this study is the predominance of additive genetic variance for most traits, particularly number of pods per plant and plant height. This suggests that these traits are primarily governed by fixable gene effects and can be effectively improved through direct selection (**Ranjan et al., 2024**). The concurrence of high heritability with substantial

genetic advance further reinforces the role of additive gene action, as these parameters together indicate the expected response to selection (**Falconer and Mackay 1996; Sharma J.R. 2008**). Similar predominance of additive effects for yield components has been reported in pigeonpea and other self-pollinated crops (**Ajay et al. 2012; Singh and Bajpai 2005**). From a breeding standpoint, such traits are ideal targets for early-generation selection, enabling rapid genetic gain.

In contrast, the presence of appreciable dominance variance for traits such as seed yield per plant, pod length, and phenological traits in specific crosses highlights the importance of non-additive gene effects. The cross-dependent expression of dominance suggests that allelic interactions vary with parental combinations, reflecting the complex genetic control of these traits. Similar observations have been reported in quantitative genetic studies using mating designs and test cross approaches (**Hendawy, 2008; Maurya et al. 2019**). These findings imply that exclusive reliance on direct selection may not be sufficient for such traits, and alternative strategies such as delayed selection, recurrent intermating, or exploitation of heterosis may be required.

The combined interpretation of heritability and genetic advance provided additional insight into the underlying gene action. Traits such as number of primary and secondary branches exhibited high heritability but relatively low genetic advance, indicating that non-additive gene effects and environmental influences may limit the effectiveness of selection. This pattern has been frequently reported in quantitative genetic studies, where high heritability alone does not necessarily translate into high selection response (**Falconer and Mackay 1996; Hassan et al. 2013**). This highlights the limitation of relying solely on heritability estimates and underscores the importance of integrating multiple genetic parameters for accurate inference.

The variability analysis further revealed that yield-related traits exhibited relatively higher phenotypic variation compared to phenological traits, suggesting greater scope for selection. In contrast, the low variability observed for days to flowering and maturity indicates phenotypic stability, which is advantageous for developing varieties adapted to specific cropping systems. Similar patterns of variability have been reported in pigeonpea and other legumes (**Yadav et al. 2006; Guddadamath et al. 2011**). The identification of early-maturing progenies within certain crosses further demonstrates the potential for tailoring breeding objectives based on target environments.

Heterosis analysis complemented the variance component results by revealing the practical implications of non-additive gene action. The consistent negative heterosis for flowering and maturity across crosses indicates the feasibility of developing early-maturing genotypes through the exploitation of dominance effects. This is particularly important in pigeonpea-based cropping systems, where earliness contributes to cropping intensity and resource use efficiency (**Saxena et al. 2021**). The substantial positive heterosis observed for yield and its components, especially in the PADT-16 × Pusa 992 cross, reflects favourable allelic complementation and suggests its suitability for yield improvement programs. Similar heterotic responses for yield traits have been reported in pigeonpea and other crops (**Shukla et al. 2016; Kalola and Pandya 2016**).

Importantly, the absence of a single progeny combining superiority across all traits highlights the polygenic and complex nature of yield. The observed trade-offs, particularly involving hundred seed weight and yield components, suggest potential resource allocation constraints that must be considered in breeding programs. Such trade-offs have been widely documented in quantitative genetics and emphasize the need for balanced selection approaches (**Falconer and Mackay 1996**). This reinforces the need for index-based or multi-trait selection approaches rather than single-trait improvement strategies.

A key contribution of this study is the integration of genetic parameters into a decision-oriented breeding framework. By classifying traits based on their underlying gene action and aligning them with appropriate breeding strategies, the study provides a practical guide for trait prioritization and selection (**Figure 3**). Such integrative approaches have been increasingly emphasized in crop improvement programs to bridge the gap between statistical genetic analysis and field-level breeding decisions (**Hallauer and Miranda 1988; Sharma 2008**).

However, it is important to acknowledge certain limitations. The study was conducted under a single environmental condition, which may influence the expression of genetic parameters and limit the generalizability of the results. In addition, the absence of molecular marker-based validation restricts the ability to directly associate observed variation with underlying genomic regions. Previous studies have highlighted the importance of integrating molecular tools with quantitative genetic approaches for improved selection efficiency (**Varshney et al. 2012; Varshney et al. 2017**). Future studies incorporating multi-environment evaluation and genomic approaches would further strengthen breeding outcomes.

Overall, the findings demonstrate that the integration of biparental mating with NC-III analysis provides a robust framework for dissecting gene action and designing efficient breeding strategies in pigeonpea.

5. Conclusion

The present study demonstrates that biparental mating under the NC-III design effectively generates exploitable genetic variability in pigeonpea. The predominance of additive gene action for key traits, along with moderate to high heritability and genetic advance, supports the effectiveness of early-generation selection. However, the presence of dominance effects for traits such as seed yield and pod length highlights the need for complementary strategies, including delayed selection and heterosis exploitation. Cross-specific responses indicate that PADT-16 × Pusa 992 is most suitable for yield improvement, whereas PADT-16 × PAU 881 is advantageous for earliness and seed traits. Overall, the integration of genetic parameters enables a trait-specific and cross-specific breeding approach, providing a practical framework for developing high-yielding and adaptable pigeonpea genotypes.

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Conflict of Interest

All authors declare that there is no conflict of any interest whatsoever among them.

Author Contributions

All authors contributed to the conception, design, and execution of the study. All authors read and approved the final version of the manuscript for submission.

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Table 1. Analysis of variance (mean squares) for North Carolina Design III in biparental F_1 populations derived from three pigeonpea crosses (PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881) for ten quantitative traits.

Source of variation	Crosses	df	MS									
			DFF	DM	NPB	NSB	NPP	NSP	PH	PL	HSW	SYP
Set	1 × 2	1	13.02**	31.69**	3.00**	7.52**	616.33**	0.99**	1407.25**	1.48**	4.51**	40.15**
	1 × 3	1	3.52**	6.75**	1.69**	5.33**	247.52**	1.65**	938.99**	0.64**	1.47**	32.67**
	1 × 4	1	33.33**	16.33**	3.00**	6.75**	652.69**	0.68**	370.74**	1.61**	1.02**	32.84**
Replication (within set)	1 × 2	4	2.29**	0.98	0.29	0.83	20.08	0.18	74.45	0.26	0.20	24.47**
	1 × 3	4	0.27	1.60	0.00	0.42	29.52	0.05	35.09	0.05	0.46*	31.67**
	1 × 4	4	0.83	10.08**	0.10	0.17	116.23	0.26*	78.72	0.10	0.03	20.70**
Female (within set)	1 × 2	2	225.60**	709.69**	18.75**	232.52**	11706.42**	8.37**	60383.33**	9.43**	2.41**	568.84**
	1 × 3	2	429.52**	1650.08**	3.85**	221.04**	5971.60**	10.06**	35164.25**	12.88**	0.92**	464.91**
	1 × 4	2	204.17**	1785.75**	17.71**	241.33**	2720.10**	9.61**	33397.19**	4.52**	1.92**	546.44**
Male (within set)	1 × 2	6	1.24*	4.16**	6.44**	36.74**	4318.33**	0.55**	5519.61**	0.45**	0.40**	24.35**
	1 × 3	6	0.94*	36.64**	4.80**	36.26**	2370.02**	0.67**	807.64**	0.33**	0.47**	15.23**
	1 × 4	6	2.39**	79.00**	3.76**	14.03**	1027.77**	0.46**	1727.25**	0.33*	0.50**	23.31**
Female x Male	1 × 2	6	1.83**	4.08**	0.86**	6.02**	417.19**	0.46**	1119.09**	0.44**	0.35**	26.42**
	1 × 3	6	0.58**	2.86**	0.80**	6.93**	266.49**	0.40**	1259.41**	0.35**	0.45**	28.52**
	1 × 4	6	2.39**	6.36**	1.15**	4.17**	241.10**	0.33**	774.10**	0.37*	0.18**	21.87**
Residuals	1 × 2	28	0.41	1.15	0.22	0.86	78.68	0.12	174.53	0.12	0.09	4.68
	1 × 3	28	0.22	0.70	0.19	0.61	31.31	0.11	110.62	0.06	0.12	3.81
	1 × 4	28	0.64	1.80	0.27	0.74	51.09	0.09	46.56	0.13	0.04	3.88

Abbreviations: DFF, days to 50% flowering; DM, days to maturity; NPB, number of primary branches per plant; NSB, number of secondary branches per plant; NPP, number of pods per plant; NSP, number of seeds per pod; PH, plant height; PL, pod length; HSW, hundred-seed weight; SYP, seed yield per plant. *, ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively; 1 × 2, 1 × 3, and 1 × 4 represent the crosses PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881, respectively.

Table 2. Estimates of genetic variance components and related parameters for ten quantitative traits in biparental F_1 populations of pigeonpea derived from three crosses under North Carolina Design III.

Parameters	Crosses	DFF	DM	NPB	NSB	NPP	NSP	PH	PL	HSW	SYP
Additive variance (σ^2_A)	**1 × 2**	0.55	2.01	4.15	23.92	2826.44	0.29	3563.39	0.22	0.2	13.11
	1 × 3	0.48	23.96	3.07	23.77	1559.14	0.38	464.68	0.18	0.23	7.62
	1 × 4	1.16	51.47	2.33	8.86	651.12	0.25	1120.46	0.13	0.31	12.96
Dominance variance (σ^2_D)	**1 × 2**	0.94	1.95	0.43	3.44	225.68	0.22	629.71	0.22	0.17	14.49
	1 × 3	0.24	1.44	0.41	4.22	156.79	0.2	765.86	0.2	0.22	16.48
	1 × 4	1.16	3.04	0.59	2.29	126.68	0.16	485.03	0.17	0.09	11.99
Phenotypic variance (σ^2_P)	**1 × 2**	1.91	5.11	4.8	28.22	3130.79	0.63	4367.62	0.56	0.47	32.28
	1 × 3	0.93	26.1	3.67	28.59	1747.24	0.68	1341.16	0.43	0.57	27.9
	1 × 4	2.97	56.31	3.19	11.88	828.89	0.5	1652.05	0.42	0.44	28.83
Genotypic variance (σ^2_G)	**1 × 2**	1.5	3.96	4.58	27.37	3052.11	0.51	4193.09	0.44	0.38	27.6
	1 × 3	0.71	25.4	3.48	27.99	1715.93	0.57	1230.53	0.38	0.45	24.09
	1 × 4	2.33	54.51	2.92	11.15	777.8	0.41	1605.49	0.3	0.4	24.95
Degree of Dominance ($\sqrt{(\sigma^2D/\sigma^2A)}$)	**1 × 2**	1.7	0.97	0.1	0.14	0.08	0.77	0.18	0.98	0.85	1.11
	1 × 3	0.49	0.06	0.13	0.18	0.1	0.53	1.65	1.09	0.95	2.16
	1 × 4	1	0.06	0.25	0.26	0.19	0.66	0.43	1.24	0.3	0.93
Mean	**1 × 2**	81.81	136.23	6.92	18.10	147.08	3.44	203.14	5.34	8.43	43.73
	1 × 3	81.65	134.79	6.31	17.88	139.77	3.46	196.79	4.95	8.72	40.95
	1 × 4	80.58	132.67	6.46	18.21	136.27	3.71	191.67	4.99	8.95	43.81

Abbreviations: DFF, days to 50% flowering; DM, days to maturity; NPB, number of primary branches per plant; NSB, number of secondary branches per plant; NPP, number of pods per plant; NSP, number of seeds per pod; PH, plant height; PL, pod length; HSW, hundred-seed weight; SYP, seed yield per plant; 1 × 2, 1 × 3, and 1 × 4 represent the crosses PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881, respectively.

Table 3. Estimates of narrow-sense heritability (h^2) and genetic advance as percent of mean (GA%) for ten quantitative traits in biparental F_1 populations of pigeonpea under North Carolina Design III.

Traits	PADT-16 x Pusa 992		PADT-16 x UPAS 120		PADT-16 x PAU 881	
	h^2_{NS}	GA%	h^2_{NS}	GA%	h^2_{NS}	GA%
DFF	78.49	0.83	76.12	1.01	78.36	1.39
DM	77.57	1.83	97.32	9.66	96.81	14.13
NPB	95.41	3.9	94.81	3.3	91.5	2.69
NSB	96.96	9.28	97.88	9.16	93.79	5.29
NPP	97.49	104.06	98.21	76.84	93.84	46.59
NSP	80.75	0.75	84.3	0.94	82.83	0.72
PH	96	111.07	91.75	26.14	97.18	56.79
PL	79.24	0.61	87.19	0.57	70.32	0.42
HSW	80	0.61	78.38	0.63	91.41	0.96
SYP	85.51	4.75	86.35	2.97	86.55	4.97

Abbreviations: DFF- Days to 50% flowering, DM- Days to maturity, NPB- Number of primary branches per plant, NSB- Number of secondary branches per plant, NPP- Number of pods per plant, NSP- Number of seeds per pod, PH- Plant height, PL- Pod length, HSW- Hundred seed weight, SYP- Seed yield per plant; Genetic advance (GA) was estimated at 5% selection intensity and expressed as percent of mean.

Table 4a. Mean Values of Biparental Progenies (BIPs) Derived from Three Crosses: PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881, Based on the NCD-III Base Population for five Morphological Traits (DFF, DM, NPB, NSB, NPP) in Pigeonpea

Set	Biparental Progenies (BIPs)	Days to 50% Flowering			Days to Maturity			Number of Primary Branches per plant			Number of Secondary branches per plant			Number of pods per plant		
		PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881
I	**P1xM1**	86.00	85.67	81.67	141.00	139.33	140.00	7.00	6.00	6.33	21.00	16.67	21.33	166.33	153.00	142.67
	P1xM2	85.00	85.67	83.33	140.67	143.67	135.67	7.33	6.67	6.33	17.33	21.00	21.33	178.67	158.67	131.67
	P1xM3	84.67	85.67	84.00	141.00	144.33	142.00	7.67	7.00	8.00	23.67	23.67	24.33	195.00	186.67	156.33
	P1xM4	85.33	85.00	81.67	141.00	143.33	145.67	8.67	6.67	8.33	25.33	25.33	19.33	138.00	131.67	142.00
	P2xM1	78.33	77.00	77.33	127.67	123.00	124.00	4.00	4.00	4.00	15.33	12.67	14.67	127.67	127.67	121.00
	P2xM2	80.33	77.00	76.00	129.00	127.67	119.00	5.33	5.33	5.33	13.33	14.33	14.33	145.33	125.33	118.00
	P2xM3	79.33	78.00	77.00	131.67	128.67	124.67	6.33	6.33	5.67	16.00	16.00	17.33	150.00	141.33	134.33
	P2xM4	79.67	77.00	77.00	131.33	125.33	125.67	7.00	7.00	5.67	16.00	16.00	16.00	104.33	112.00	114.67
II	**P1xM1**	85.00	86.67	83.67	143.00	139.67	139.67	7.00	6.00	6.67	19.33	17.33	22.33	168.67	142.00	142.33
	P1xM2	84.33	86.00	84.00	143.00	144.33	137.67	7.67	6.33	7.67	16.67	18.67	18.67	182.33	152.00	139.33
	P1xM3	83.33	85.33	86.00	142.67	147.67	144.00	8.33	7.00	7.00	22.33	23.67	23.67	211.00	195.00	186.67
	P1xM4	85.33	87.00	83.67	141.00	142.33	145.67	8.67	8.00	8.00	24.00	20.67	20.00	111.67	125.33	134.33
	P2xM1	78.67	78.00	78.67	132.33	124.33	126.00	5.00	5.00	5.00	13.00	12.33	14.33	114.67	114.67	124.33
	P2xM2	78.33	77.67	78.00	130.33	127.67	118.67	5.67	5.67	5.33	13.33	14.67	13.33	120.00	123.33	121.00
	P2xM3	77.67	77.33	79.00	132.33	128.67	126.67	6.67	6.67	7.00	15.67	15.67	15.67	144.33	141.00	141.67
	P2xM4	77.67	77.33	78.33	131.67	126.67	127.67	8.33	7.33	7.00	17.33	17.33	14.67	95.33	106.67	130.00
	Mean	81.81	81.65	80.58	136.23	134.79	132.67	6.92	6.31	6.46	18.1	17.88	18.21	147.08	139.77	136.27
	C.V.	0.85	0.58	0.99	0.80	0.64	0.98	6.62	6.68	7.85	5.02	4.40	4.57	5.86	3.89	5.26
	S.Em.	0.57	0.39	0.65	0.89	0.70	1.06	0.37	0.34	0.41	0.74	0.64	0.68	7.04	4.44	5.85
	CD 5%	1.16	0.79	1.33	1.81	1.43	2.16	0.76	0.70	0.85	1.52	1.31	1.39	14.37	9.07	11.95
	CD 1%	1.56	1.07	1.79	2.44	1.93	2.91	1.03	0.95	1.14	2.04	1.77	1.87	19.36	12.22	16.10

Table 4b. Mean Values of Biparental Progenies (BIPs) Derived from Three Crosses: PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881, Based on the NCD-III Base Population for five Morphological Traits (NSP, PH, PL, HSW, SYP) in Pigeonpea

Set	Biparental Progenies (BIPs)	Number of seeds per plant			Plant Height (cm)			Pod Length (cm)			Hundred Seed Weight (g)			Seed yield per plant (g)		
		PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881	PADT-16 × Pusa 992	PADT-16 × UPAS 120	PADT-16 × PAU 881
I	**P1xM1**	3.6	3.73	4.17	231.80	238.47	228.47	6.12	5.40	5.42	8.41	8.75	8.80	43.63	41.13	43.63
	P1xM2	4.2	4.07	4.07	295.43	255.43	258.77	5.90	5.96	5.30	8.49	8.76	8.02	47.43	44.93	47.40
	P1xM3	4.4	4.10	4.43	205.50	212.17	232.17	5.52	5.52	5.42	8.42	9.32	8.08	51.90	47.20	51.73
	P1xM4	4.63	4.63	4.70	294.77	223.17	203.17	5.80	6.13	5.28	8.88	8.41	9.11	51.97	46.8	51.77
	P2xM1	2.77	3.07	2.73	162.67	147.43	157.43	4.48	4.15	4.15	7.33	8.54	9.04	38.03	36.93	37.47
	P2xM2	2.73	3.13	3.13	175.93	169.27	172.60	4.42	3.59	4.42	8.05	8.12	9.00	36.67	36.23	38.10
	P2xM3	3.00	2.57	3.53	131.33	158.00	158.00	4.01	3.68	4.01	7.64	7.99	9.09	37.87	34.97	38.23
	P2xM4	3.37	3.87	3.87	170.97	134.97	144.97	5.09	4.21	4.43	7.80	8.46	9.33	35.03	32.83	35.50
II	**P1xM1**	3.33	3.47	4.27	255.77	262.43	252.43	6.30	5.3	5.52	8.88	9.21	8.54	43.70	41.20	44.67
	P1xM2	4.17	4.23	4.43	258.23	252.23	256.90	6.16	5.53	5.46	8.05	8.38	8.75	46.97	44.47	46.93
	P1xM3	4.00	4.40	4.53	193.97	202.63	202.63	6.08	5.58	5.41	9.38	9.39	8.99	52.73	50.13	52.53
	P1xM4	3.93	4.10	4.07	290.63	233.67	197.10	5.87	5.71	5.37	9.25	8.92	9.09	49.27	46.73	49.13
	P2xM1	2.83	2.57	2.93	158.23	154.90	148.23	5.11	4.97	5.31	8.54	8.34	9.14	41.07	39.60	41.13
	P2xM2	2.00	2.17	2.73	139.07	159.07	155.73	4.77	4.24	4.44	8.63	8.63	9.16	40.87	37.07	40.60
	P2xM3	3.13	2.30	2.40	123.23	179.90	149.90	4.28	4.18	4.28	8.62	9.42	9.75	42.70	39.57	42.73
	P2xM4	3.00	2.97	3.37	162.63	164.83	148.17	5.59	4.99	5.59	8.58	8.87	9.38	39.87	35.47	39.33
	Mean	3.44	3.46	3.71	203.14	196.79	191.67	5.34	4.95	4.99	8.43	8.72	8.95	43.73	40.95	43.81
	C.V.	10.42	9.25	8.26	6.36	5.17	3.73	6.21	4.83	6.91	3.72	4.34	2.14	5.36	5.10	4.57
	S.Em.	0.29	0.26	0.25	10.55	8.31	5.84	0.27	0.19	0.28	0.26	0.31	0.16	1.91	1.70	1.64
	CD 5%	0.60	0.53	0.51	21.54	16.97	11.92	0.55	0.40	0.58	0.52	0.63	0.32	3.91	3.48	3.34
	CD 1%	0.81	0.72	0.69	29.01	22.85	16.05	0.74	0.54	0.77	0.70	0.85	0.43	5.26	4.69	4.50

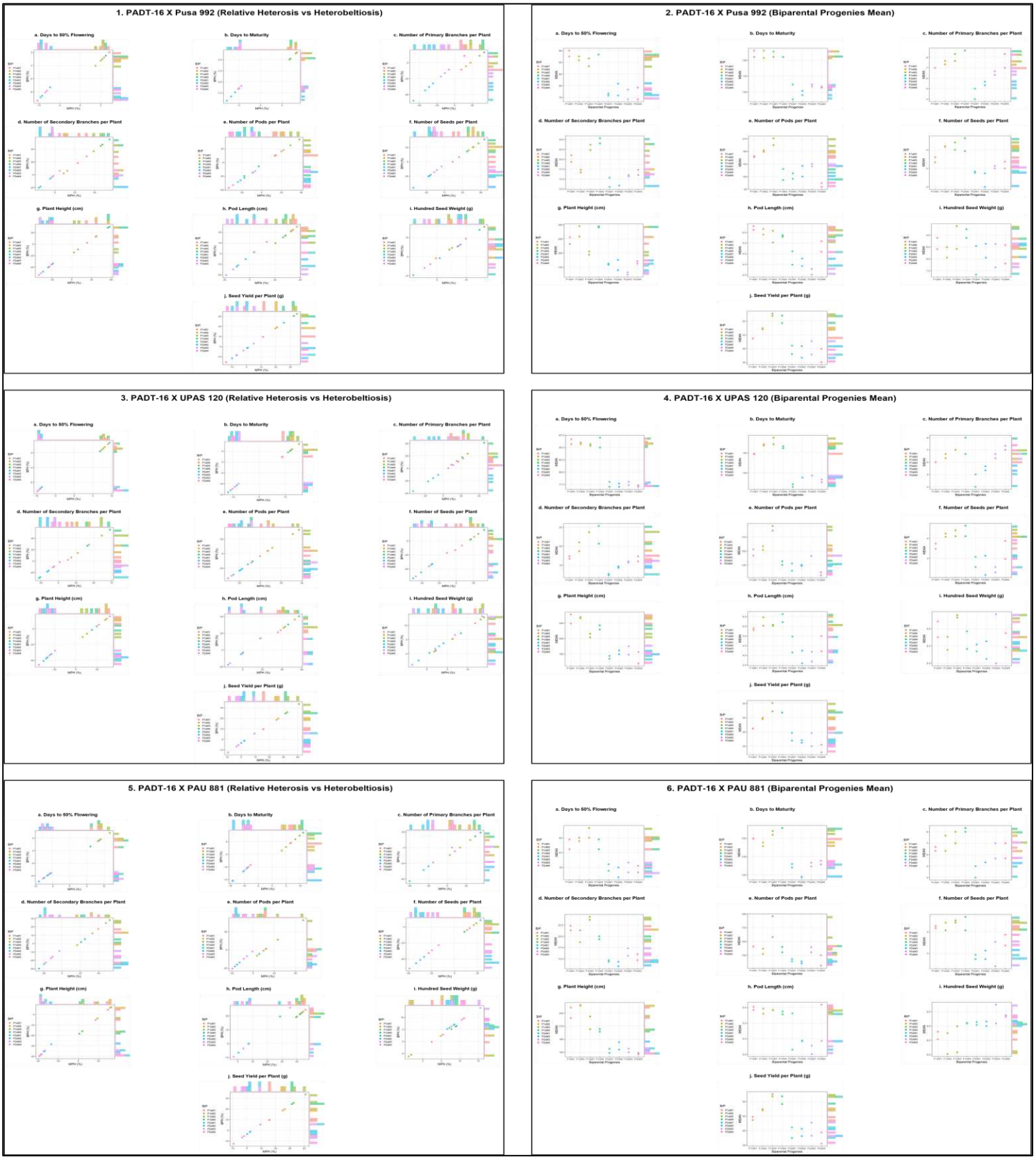


Figure 1. Comparative analysis of yield and yield-contributing traits across three crosses (PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881). (a) Relative heterosis and heterobeltiosis of biparental progenies across generations (S_1, S_3, S_5). (b) Mean performance of biparental progenies for yield and component traits across generations (S_2, S_4, S_6).

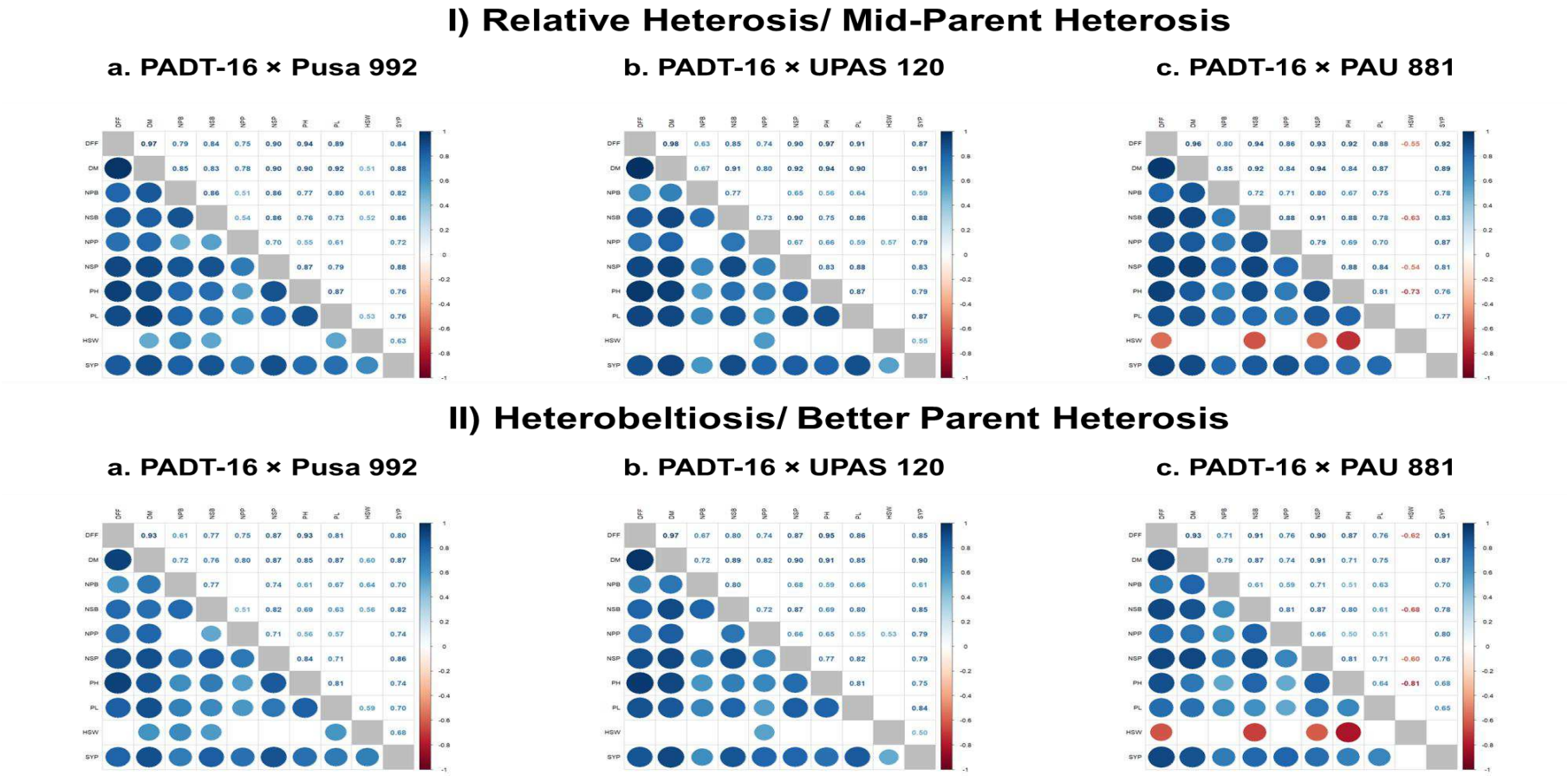


Figure 2. Pearson correlation coefficients between trait means of biparental progenies and heterosis (%) for ten yield-contributing traits across three crosses (PADT-16 × Pusa 992, PADT-16 × UPAS 120, and PADT-16 × PAU 881). (I) Correlation with mid-parent heterosis (a–c). (II) Correlation with better-parent heterosis (d–f). Circle size and color intensity represent the magnitude of correlation; blue and red indicate positive and negative correlations, respectively

Table 5. Trait-wise breeding strategy derived from integrated analysis of variance components, heritability, CV, and heterosis across NC-III biparental populations.

Trait	Variance Pattern (σ^2A vs σ^2D)	h^2 + GA Interpretation	CV (Variability)	Heterosis Pattern	Cross-Specific Insight	Optimized Breeding Strategy	Priority Level
DFF	$\sigma^2D \geq \sigma^2A$ (in some crosses)	Moderate h^2, moderate GA	Low	Consistently negative	Stable across all crosses	Select in later generations; exploit heterosis for earliness	Medium
DM	$\sigma^2A \approx \sigma^2D$	Moderate–high h^2	Low	Negative	Uniform expression	Recombination + selection for early maturity	Medium
PH	$\sigma^2A >> \sigma^2D$	High h^2 + high GA	Moderate	Negative	Strong additive control	Direct early-generation selection (F2–F4)	High
NPB	$\sigma^2D > \sigma^2A$	High h^2 but low GA	Moderate–high	Variable	Cross-dependent	Recurrent selection / intermating cycles	Medium
NSB	$\sigma^2D > \sigma^2A$	Moderate h^2 + low GA	Moderate	Positive	Unstable across crosses	Population improvement, avoid early fixation	Medium
NPP	$\sigma^2A >> \sigma^2D$	High h^2 + high GA	High	Strong positive	Best in PADT-16 × Pusa 992	Primary selection trait in early generations	Very High
PL	$\sigma^2D \geq \sigma^2A$	Moderate h^2	Moderate	Positive	Cross-specific	Late-generation selection or hybrid-based improvement	Medium
NSP	$\sigma^2A > \sigma^2D$	Moderate–high h^2 + GA	High	Positive	Stable additive effect	Reliable early selection trait	High
HSW	$\sigma^2A > \sigma^2D$ (with trade-off)	Moderate h^2	Moderate	Positive but negatively correlated with yield traits	Trade-off observed	Index-based selection (avoid single-trait selection)	High
SYP	$\sigma^2A + \sigma^2D$ (both important)	Moderate h^2	High	Strong positive	Highest in PADT-16 × Pusa 992	Integrated strategy: early selection + recombination + heterosis exploitation	Very High

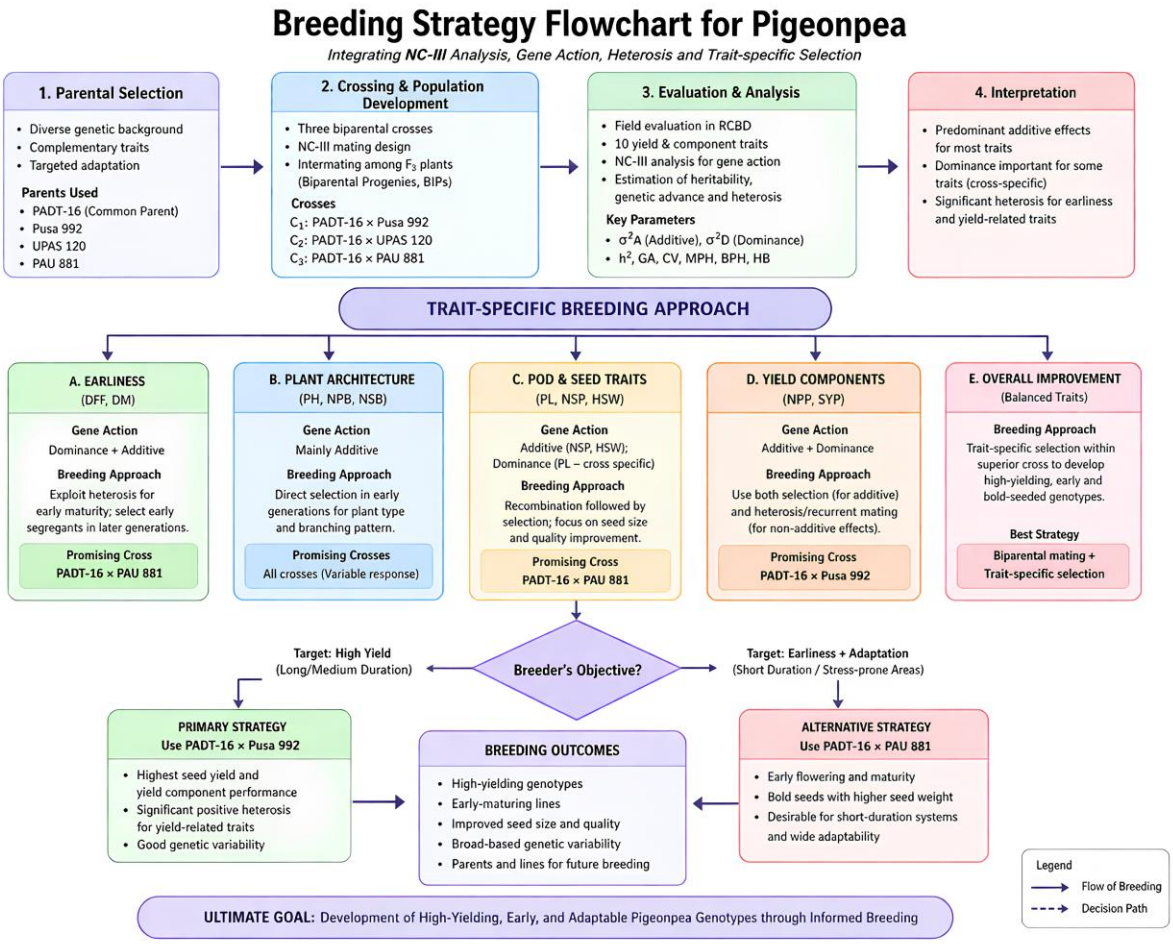


Figure 3. Trait-specific and cross-specific breeding strategy for yield improvement in pigeonpea based on NC-III analysis of biparental progenies.