



RESEARCH ARTICLE

Elucidating combining ability and gene action for some chemo-morphological characters in grasspea (*Lathyrus sativus* L.)

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Abstract

This study aimed at the identification of good general combiners and specific crosses of grass pea (*Lathyrus sativus* L.) based on their combining ability and understanding of the gene action underlying the expression of various characters, including seed ODAP content. Five parents were crossed in half-diallel design and were evaluated with the resultant crosses. Most of the characters showed a broad range of genetic variability. The number of pods per plant, protein content of seed, ODAP content in seed and seed yield per plant exhibited high heritability. The expression of most characters was affected by both additive and non-additive gene action. Dominance variance without significant additive variance was observed only for the seed index. Interestingly, recessive alleles contributed more to ODAP content than dominant alleles. The parents BK-1, Mahateora, Ratan and Nirmal were good general combiners for various desirable traits and may be utilized in the further crossing program. The cross BK-1 x Ratan was the best specific combiner for days to early flowering and maturity, with higher protein content, lower ODAP content and seed yield per plant whereas the crosses BK-1 x Pratik and Mahateora x Pratik were better specific combiners for seed ODAP content and protein content. The selected crosses from this study can be used to raise segregating generations to obtain transgressive segregants for better yield and low ODAP content in seeds for future breeding programs.

Keywords: Combining ability, gene action, good combiner, *Lathyrus*, ODAP

Introduction

Grasspea (*Lathyrus sativus* L.; 2n =14), one of the oldest crops that have been domesticated, is grown throughout the world, including Eurasia, East Africa, temperate South America, and North America. It has become one of the most significant crops in several low-input farming systems (Yegrem et al. 2024) due to its ability to withstand abiotic stress factors and nutrient-dense nature (Fernand et al. 2019). The overconsumption of grass peas has been linked to neurolathyrism, a neurodegenerative disease that affects humans as well as domestic animals due to the presence of the neuroexcitatory β -N-oxalyl-L- α , β -diaminopropionic acid (β -ODAP). There is tremendous potential in the grasspea for introducing multiple abiotic stress-tolerance genes into general crop improvement programs with appropriate breeding strategies (Das et al. 2021). However, a slow breeding process is evident in grasspea (Hao et al. 2017). The importance of grasspea in developing countries has prompted breeding programs aimed at producing a genotype with better seed yield and low ODAP concentration in seeds.

The present study was conducted at AB Block farm of BCKV, Kalyani, West Bengal (21.5°N, 85°E). Five grasspea genotypes viz. Bidhan Khesari 1 (BK-1), Nirmal, Ratan

(Bio-L-212), Prateek and Mahateora were crossed in half-diallel fashion during Rabi 2017-18 yielding 10 resultant F₁ combinations. Parents and F₁s were grown during rabi 2018-19 in 2 m long rows following RCBD with three replications. ODAP analysis was delayed due to the COVID-19 pandemic, affecting the timeline of data analysis and

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publication. Since grasspea is often cross-pollinated (Sharma et al. 2022) and maintenance of purity is difficult in open conditions, all the genotypes were grown under caging continuously for several years to maintain the purity of the materials. Data were recorded for yield and its attributes, protein content (Lowry et al. 1951) and ODAP content (Rao 1978) of the seeds. A total of sixteen characters were taken into consideration.

Analysis of variance (Gomez and Gomez 1983) and combining ability analysis using Griffing's (1956) Method 2 Model 1 were carried out. A numerical approach was used to analyze genetic components of variation following the method given by Jinks and Hayman (1953), Hayman (1954) and Aksel and Johnson (1963). Estimates were also made of genetic variation components.

The mean performance for sixteen characters of the parents and their crosses is provided in Supplementary Table S1. It is notable that the ODAP content of seed in parental lines ranged from 0.07 to 0.16%, while that of F_1 crosses ranged from 0.08 to 0.18%. Among the parents, the maximum ODAP content of the seed was recorded for Nirmal (0.16%) followed by Pratik (0.14%) and BK-1 (0.09%). However, the most desirable (least) ODAP content of seed was observed in the parent Ratan (0.08%). Analysis of variance (Supplementary Table S1) showed significant differences for all the 16 characters studied. Gonçalves (2024) and Dutta et al. (2024) also reported high variability in grasspea genotypes. In general, the genotypic coefficient of variation was found to be lower than the corresponding phenotypic coefficient of variation, which indicates the influence of the environment on the expression of the characters (Table 1).

The characters exhibiting high genetic advance were plant height (20.1) and no. of pods per plant (35.1). All other characters exhibited low (<10) genetic advance. Low genetic advance for these traits was also observed by Parihar et al. (2016). These two characteristics (plant height and number of pod per plant) showing high heritability coupled with high genetic advance indicate that they are governed by the additive nature of gene action and selection for these traits in early generation would be rewarding. Similar findings were also obtained by previous workers (Abate et al. 2018; Mekonen et al. 2024). In contrast, traits such as the length and width of the pod exhibit lower genetic control, indicating limited potential for genetic improvement through selection (Table 1).

The analysis of variance revealed significant values for both GCA and SCA for all the sixteen characters studied, indicating the role of both additive and dominant genes in the control of these traits (Supplementary Table S2). The GCA effect estimated of parents for all the sixteen characters was obtained (Table 2). BK-1 proved to be a good combiner for early maturity since it has a high GCA effect for days to 50% flowering and days to maturity. Mahateora was found to be a

Table 1. Analysis of variance (mean squares) and genetic variability parameters for 16 characters

| Source of variation | d.f. | Days to 50% flowering | Plant height (cm) | No. of branches per plant | No. of pods per plant | Length of internode (cm) | Length of pedicel (cm) | Days to maturity | Length of pod (cm) | Width of pod (cm) | No. of seed per pod | Seed Index | Seed length (mm) | Seed width (mm) | Protein content in seed (%) | ODAP content in seed (%) | Yield per plant (g) |
|----------------------------------|------|-----------------------|-------------------|---------------------------|-----------------------|--------------------------|------------------------|------------------|--------------------|-------------------|---------------------|------------|------------------|-----------------|-----------------------------|--------------------------|---------------------|
| Replications | 2 | 69.1 | 54.5 | 0.10 | 24.3 | 0.09 | 0.01 | 32.7 | 0.012 | 0.001 | 0.01 | 0.003 | 0.024 | 0.01 | 0.01 | 0.001 | 0.55 |
| Treatments | 14 | 81.2** | 351.9** | 33.2** | 971.8** | 0.67*** | 0.55** | 121.4** | 0.036** | 0.004** | 0.40** | 1.95** | 1.90** | 0.79** | 20.9** | 0.004** | 41.6** |
| Error | 28 | 12.6 | 18.5 | 0.33 | 26.1 | 0.13 | 0.03 | 25.3 | 0.049 | 0.002 | 0.02 | 0.048 | 0.016 | 0.01 | 0.04 | 0.000 | 0.97 |
| GCV (%) | | 6.76 | 12.4 | 28.4 | 28 | 10.1 | 11.7 | 5.16 | 3.2 | 3.26 | 9.75 | 10.4 | 14.4 | 9.5 | 9.08 | 30.1 | 28.9 |
| PCV (%) | | 8.42 | 13.4 | 28.8 | 29.1 | 13.1 | 12.8 | 6.89 | 7.77 | 5.39 | 10.5 | 10.8 | 14.6 | 9.86 | 9.11 | 30.2 | 29.9 |
| h^2 in the broad sense | | 64.4 | 85.7 | 97 | 92.3 | 58.8 | 84.8 | 55.9 | 16.9 | 36.6 | 85.6 | 92.9 | 97.5 | 92.8 | 99.4 | 99.1 | 93.3 |
| h^2 in a narrow sense | | 0.74 | 0.66 | 0.23 | 0.05 | 0.05 | 0.5 | 0.76 | 0.03 | 0.36 | 0.45 | 0.29 | 0.11 | 0.49 | 0.49 | 0.63 | 0.2 |
| Genetic advance | | 7.9 | 20.1 | 6.72 | 35.15 | 0.67 | 0.79 | 8.72 | 0.08 | 0.04 | 0.68 | 1.58 | 1.62 | 0.98 | 5.41 | 0.07 | 7.32 |
| Genetic advance as % of the mean | | 11.1 | 23.7 | 57.6 | 55.3 | 15.9 | 22.3 | 7.94 | 2.71 | 4.07 | 18.6 | 20.8 | 29.3 | 18.8 | 18.6 | 61.6 | 57.5 |

* , ** significant at 0.05 and 0.01 probability levels, respectively

Table 2. Estimates of GCA and SCA effects of parents and F_1 combinations, respectively for 16 characters

| Parents | Days to 50% flowering | Plant height (cm) | No. of branch per plant | No. of pod per plant | Length of internode (cm) | Length of pedicel | Days to maturity | Length of pod (cm) | Width of pod (cm) | Seed per pod | Seed Index | Seed length (mm) | Seed width (mm) | Protein content in seed (%) | ODAP content in seed (%) | Yield per plant (g) |
|--------------------|-----------------------------|-------------------------|----------------------------------|----------------------------|--------------------------------|-------------------------|---------------------|-----------------------|----------------------|-----------------|---------------|---------------------|-----------------------|-----------------------------------|--------------------------------|------------------------|
| BK-1 | -4.63** | -2.77** | -0.62** | -0.87 | 0.07 | 0 | -5.85** | 0.02 | -0.01 | 0.08* | -0.07 | 0.08** | -0.04 | -0.26** | -0.01** | 0.90** |
| Mahateora | -2.49** | -9.04** | 0.33** | -1.01 | 0.1 | -0.32** | -2.51* | -0.03 | -0.01 | -0.16** | 0.15** | 0.24** | -0.12** | 1.16** | -0.02** | 1.25** |
| Ratan | 2.23** | 7.69** | 1.43** | 3.69** | -0.27** | 0.13** | 2.01 | 0.04 | 0.03** | -0.17** | 0.46** | 0.03 | 0.46** | 1.32** | -0.00** | -0.53* |
| Nirmal | 2.80** | 3.76** | 0.64** | -0.94 | 0.01 | 0.27** | 2.30* | 0.04 | 0.01 | 0.30** | -0.22** | -0.22** | -0.08** | -1.67** | 0.02** | -0.77** |
| Pratik | 2.09** | 0.36 | -1.78** | -0.87 | 0.08 | -0.09* | 4.06** | -0.07 | -0.02** | -0.04 | -0.32** | -0.14** | -0.22** | -0.54** | 0.02** | -0.85** |
| Crosses | | | | | | | | | | | | | | | | |
| BK-1 x Mahateora | 0.38 | 0.47 | -0.05 | -2.63 | -0.28** | -0.06 | -3.46* | 0.01 | 0.02* | 0.15** | 0.03 | -0.55** | -0.22** | -3.62** | 0.02** | -1.46** |
| BK-1 x Ratan | -6.33** | 8.00** | -0.48** | -1.54 | 0.67** | -0.53** | -5.98** | -0.06 | -0.03** | 0.02 | 0.42** | -0.01 | -0.18** | 1.92** | -0.02** | 2.32** |
| BK-1 x Nirmal | -0.9 | -7.53** | 0.98** | 2.43 | -0.53** | -0.33** | -2.27 | -0.02 | -0.03** | -0.27** | 1.31** | 0.24** | 0.08* | -0.09 | 0 | 3.77** |
| BK-1 x Pratik | 1.81 | 0.66 | 3.73** | 9.03** | -0.02 | 0.10* | -0.03 | 0.03 | -0.02 | 0.13** | 0.96** | 0.15** | 0.01 | 1.97** | -0.00* | 5.73** |
| Mahateora x Ratan | -1.48 | 10.68** | 6.57** | 35.47** | 0.31** | -0.07 | -0.32 | 0.20** | 0.04** | 0.23** | 0.06 | 0.51** | 0.28** | 0.60** | 0.01** | -0.1 |
| Mahateora x Nirmal | 0.95 | -9.79** | -0.64** | 0.03 | -0.32** | -0.37** | 2.4 | 0 | -0.04** | -0.32** | -0.20** | 0.51** | 0.97** | -0.70** | -0.03** | 2.50** |
| Mahateora x Pratik | -0.33 | 2.15 | 3.45** | 20.37** | 0.27** | 0.13** | -1.03 | 0.1 | -0.02 | 0.41** | 0.43** | -0.12** | 0.19** | 2.41** | -0.01** | 6.22** |
| Ratan x Nirmal | 1.24 | -0.72 | -0.93** | 11.73** | 0.42** | 0.01 | 0.87 | -0.02 | 0 | 0.24** | 0.61** | -1.67** | 0 | -0.28** | 0.04** | -0.59* |
| Ratan x Pratik | 0.95 | -0.72 | -2.11** | -1.34 | 0.45** | 0.34** | 1.11 | -0.11* | 0.02 | -0.22** | -0.13* | -1.21** | 0.07* | 2.67** | 0.04** | -2.09** |
| Nirmal x Pratik | -0.62 | 6.41** | 0.48** | 20.29** | -0.14 | 0.27** | -0.17 | 0.09 | 0.05** | 0.31** | -0.50** | 1.17** | -0.19** | -1.99** | 0.01** | -2.27** |

*, ** significant at 0.05 and 0.01 probability levels, respectively

Table 3. Estimates of components of variation and their related statistics for 16 characters

| Components of variation and related statistics | Days to 50% flowering | Plant height (cm) | No. of branches per plant | No. of pods per plant | Length of internode (cm) | Length of pedicel (cm) | Days to maturity | Length of pod (mm) | Width of pod (cm) | Seeds per pod | Seed index | Seed length (mm) | Seed width (mm) | Protein content of seed (%) | ODAP content in seeds (%) | Yield per plant (g) |
|--|-----------------------|-------------------|---------------------------|-----------------------|--------------------------|------------------------|------------------|--------------------|-------------------|---------------|------------|------------------|-----------------|-----------------------------|---------------------------|---------------------|
| \hat{D} | 33.33 | 153.99 | 11.54 | 77.28 | 0.50 | 0.34 | 30.21 | 0.005 | 0.0013 | 0.24 | 0.69 | 0.47 | 0.445 | 5.99 | 0.0013 | 3.35 |
| \hat{H}_1 | 13.55 | 202.61 | 41.37 | 1391.15 | 1.04 | 0.52 | 20.19 | 0.0027 | 0.0029 | 0.30 | 2.24 | 3.40 | 0.72 | 23.89 | 0.0027 | 60.03 |
| \hat{H}_2 | 11.19 | 152.72 | 35.57 | 1232.90 | 0.63 | 0.34 | 13.11 | 0.0028 | 0.0027 | 0.27 | 1.84 | 2.78 | 0.54 | 17.27 | 0.0022 | 51.58 |
| \hat{F} | -10.88 | 27.59 | 11.81 | 202.81 | 0.89 | 0.33 | -40.03 | 0.0042 | 0.0002 | 0.16 | 0.72 | 0.925 | 0.36 | 4.39 | -0.0002 | 5.38 |
| \hat{h}^2 | 0.83 | 11.39 | 27.81 | 2023.63 | 0.13 | 0.06 | 12.71 | 0.0008 | -0.0003 | 0.098 | 2.06 | 0.22 | 0.23 | 1.93 | 0.0008 | 45.24 |
| \hat{E} | 5.47 | 6.96 | 0.11 | 8.67 | 0.04 | 0.01 | 8.58 | 0.0155 | 0.0005 | 0.0069 | 0.015 | 0.0056 | 0.005 | 0.013 | 0.0000 | 0.316 |
| $(\hat{H}_1/\hat{D})^{1/2}$ | 0.64 | 1.14 | 1.89 | 4.24 | 1.44 | 1.24 | 0.82 | 0.71 | 1.51 | 1.11 | 1.795 | 2.68 | 1.27 | 1.997 | 1.43 | 4.24 |
| (\hat{H}_2/\hat{H}_1) | 0.21 | 0.19 | 0.21 | 0.22 | 0.15 | 0.16 | 0.16 | 0.26 | 0.23 | 0.22 | 0.205 | 0.204 | 0.18 | 0.18 | 0.21 | 0.214 |
| (KD/KR) | 0.59 | 1.17 | 1.74 | 1.89 | 4.19 | 2.31 | 0.10 | 3.401 | 1.11 | 1.86 | 1.81 | 2.15 | 1.95 | 1.45 | 0.91 | 1.47 |
| (\hat{h}^2/\hat{H}_2) | 0.07 | 0.07 | 0.78 | 1.64 | 0.21 | 0.17 | 0.97 | 0.2747 | -0.126 | 0.37 | 1.12 | 0.08 | 0.43 | 0.11 | 0.36 | 0.877 |

*, ** significant at 0.05 and 0.01 probability levels, respectively

good combiner for the protein content of the seed and yield per plant. Ratan exhibited a good gca effect for plant height, no. of pod per plant and protein content in seed but proved to be the only poor combiner for a length of the internode. Nirmal showed a good GCA effect for plant height but not for no. of pod per plant. The parent Prateek showed to be a good combiner for ODAP content in seed only.

Among F_1 s, only BK-1 x Ratan was identified as a good general combiner for early flowering as it showed significant negative sca effects for days to 50% flowering while the other crosses had significant positive sca effects for this trait. The F_1 combinations, Mahateora x Ratan, BK-1 x Ratan and Nirmal x Pratik, were identified as good general combiners for plant height as these crosses showed significant positive GCA effects for plant height. However, the crosses, Mahateora x Nirmal and BK-1 x Nirmal were found to exhibit significant negative sca effects (Table 2).

Among the ten F_1 combinations, four combinations had desirable significant negative sca effects for ODAP content in seed. The best general combiner for this trait was Mahateora x Nirmal followed by BK-1 x Ratan, Mahateora x Pratik and BK-1 x Pratik. The crosses Ratan x Nirmal followed by Ratan x Pratik, BK-1 x Mahateora, Mahateora x Ratan and Nirmal x Pratik had significant positive sca effects for this trait. A negative and significant sca effect indicating non-additive gene action was also observed by Tripathy et al. (2015) and Giri (2018). The F_1 combination, Mahateora x Pratik, was identified as the best general combiner for fruit yield per plant followed by BK-1 x Pratik, BK-1 x Nirmal, Mahateora x Nirmal and BK-1 x Ratan since these five crosses had significant positive sca effects.

The sca effect in F_1 combinations was higher for branches per plant, no. of pods per plant, length of internode and seed length indicating that these characters are predominantly governed by dominant gene action. Improvement of these characters through conventional hybridization and selection, therefore, could be misleading if selection is done in early generations. However, in later generations when the alleles are fixed and homozygosity is attained, selection might be effective. The commercial varieties viz. Ratan (Dixit et al. 2016), Mahateora (ICAR 2009), Bari Khesari 3 (Rizwi et al. 2016), Waise (ICARDA 2007), Ceora (Kumar et al. 2021) have been developed through hybridization followed by selection in later generation.

The D , H_1 , and H_2 components tested significant ($p = 0.05$) for days to 50% flowering, plant height, number of branches per plant, number of pods per plant, days to maturity, seed protein content and yield indicating these characteristics were governed by both additive and non-additive type of gene action (Table 3).

$$KD/KR = (4\hat{D}\hat{H}_1)^{1/2} + \hat{F} / (4\hat{D}\hat{H}_1)^{1/2} - \hat{F}$$

Dominance variance was greater than additive variance for

these characters except days to 50% flowering and days to maturity in which case additive variance was greater than dominance variance. Dominant variance without significant additive variance was observed only for the seed index. Excess of dominance alleles in controlling variance was observed for length of internode, length of the pedicel, length of pod, width of a pod, seeds per plant, seed index, seed length, and seed width. Excess of recessive alleles responsible for controlling variance was observed only for ODAP content in seeds. A significant dominance effect resulting from loci in the heterozygous phase was observed for plant height, number of branches per plant, number of pods per plant, days to maturity, and yield per plant. Interestingly, no significant dominance effect was observed for seed protein content and ODAP content in seed indicating the presence of additive effect and hence selection will be rewarding. Presence of overdominance with asymmetrical distribution of positive and negative alleles was observed for plant height, number of branches per plant, number of pods per plant, length of internode, length of pedicel, width of pod, seed per pot, seed index seed length, seed width, seed protein content, yield per plant and ODAP content. The presence of partial dominance with asymmetrical distribution of positive and negative alleles was observed only for days to 50% flowering, days to maturity and length of pod. However, asymmetrical distribution of positive and negative alleles was observed for the character studied including seed protein and ODAP content. The preponderance of dominant alleles was observed for all characters including seed protein content except days to 50% flowering, days to maturity, and ODAP content in seeds. Only the number of pods per plant and seed index were controlled by more than one gene complex with the rest of the characters including seed protein content and ODAP content in seed being controlled by only one gene complex as has been reported earlier (Tripathy et al. 2015; Parihar et al. 2016).

Supplementary materials

Supplementary Tables S1 and S2 are provided which can be accessed at www.isgpb.org

Authors' contribution

Conceptualization of research (RS); Designing of the experiments (RS, APS); Contribution of experimental materials (RS); Execution of field/lab experiments and data collection (APS); Analysis of data and interpretation (DD, SB, APS); Preparation and editing of the manuscript (APS, DD, SS, UCJ).

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Supplementary Table S1. Mean value and range of variations for yield and its attributing traits of parents and their crosses

| Genotypes | Days to 50% flowering | Plant height (cm) | No. of branch per plant | No. of pod per plant | Length of internode (cm) | Length of pedicel (cm) | Days to maturity | Length of pod (cm) | Width of pod (cm) | Seed per pod | Seed Index | Seed length (mm) | Seed width (mm) | Protein content of seed (%) | ODAP content in seed (%) | Yield per plant (g) |
|-----------------------------------|-----------------------|-------------------|-------------------------|----------------------|--------------------------|------------------------|------------------|--------------------|-------------------|--------------|--------------|------------------|-----------------|-----------------------------|--------------------------|---------------------|
| Parents | | | | | | | | | | | | | | | | |
| BK-1 | 64.0 | 79.0 | 8.3 | 58.1 | 4.4 | 3.96 | 104.0 | 3.18 | 0.96 | 3.78 | 6.10 | 5.76 | 5.28 | 28.4 | 0.09 | 9.34 |
| Mahateora | 66.0 | 64.8 | 7.67 | 34.8 | 4.4 | 3.09 | 106.0 | 2.91 | 0.92 | 3.08 | 7.75 | 5.83 | 4.37 | 32.0 | 0.07 | 11.64 |
| Ratan | 78.0 | 91.4 | 13.0 | 48.7 | 2.7 | 3.93 | 116.0 | 3.20 | 0.98 | 3.16 | 8.05 | 6.77 | 6.05 | 29.2 | 0.08 | 11.90 |
| Nirmal | 76.0 | 98.0 | 13.0 | 44.4 | 4.5 | 4.30 | 114.0 | 3.18 | 0.97 | 4.25 | 6.56 | 4.96 | 4.61 | 27.2 | 0.16 | 9.48 |
| Pratik | 74.0 | 81.8 | 5.33 | 37.6 | 4.1 | 2.95 | 118.0 | 2.93 | 0.88 | 3.24 | 6.59 | 5.25 | 4.73 | 25.4 | 0.14 | 7.23 |
| Mean | 71.6 | 83.0 | 9.46 | 44.7 | 4.07 | 3.65 | 111.6 | 3.08 | 0.94 | 3.50 | 7.00 | 5.71 | 5.00 | 28.4 | 0.108 | 9.92 |
| Range | 64.0 to 78.0 | 64.8 to 98.0 | 5.3 to 13.0 | 34.8 to 58.1 | 2.7 to 4.5 | 2.95 to 3.96 | 104.0 to 118.0 | 2.93 to 3.20 | 0.92 to 0.98 | 3.08 to 4.25 | 6.10 to 8.05 | 4.96 to 6.77 | 4.37 to 6.05 | 25.40 to 32.00 | 0.07 to 0.16 | 9.34 to 11.90 |
| F₁ Combinations | | | | | | | | | | | | | | | | |
| BK-1 x Mahateora | 64.0 | 73.3 | 11.3 | 59.0 | 4.13 | 3.17 | 98.0 | 3.12 | 0.95 | 3.70 | 7.72 | 5.29 | 4.84 | 26.3 | 0.10 | 13.4 |
| BK-1 x Ratan | 62.0 | 97.6 | 12.0 | 64.8 | 4.72 | 3.14 | 100.0 | 3.13 | 0.93 | 3.56 | 8.42 | 5.62 | 5.45 | 32.0 | 0.08 | 15.4 |
| BK-1 x Nirmal | 68.0 | 78.1 | 12.6 | 64.1 | 3.79 | 3.49 | 104.0 | 3.16 | 0.92 | 3.73 | 8.63 | 5.62 | 5.16 | 27.0 | 0.13 | 16.6 |
| BK-1 x Pratik | 70.0 | 81.6 | 13.0 | 70.8 | 4.37 | 3.56 | 108.0 | 3.10 | 0.90 | 3.80 | 8.18 | 5.61 | 4.96 | 30.1 | 0.12 | 18.5 |
| Mahateora x Ratan | 69.0 | 94.0 | 20.0 | 101.6 | 4.38 | 3.28 | 109.0 | 3.34 | 1.00 | 3.54 | 8.28 | 6.30 | 5.83 | 32.1 | 0.10 | 13.3 |
| Mahateora x Nirmal | 72.0 | 69.6 | 12.0 | 61.6 | 4.02 | 3.12 | 112.0 | 3.14 | 0.90 | 3.45 | 7.33 | 6.05 | 5.97 | 27.8 | 0.09 | 15.7 |
| Mahateora x Pratik | 70.0 | 78.1 | 13.1 | 82.0 | 4.69 | 3.27 | 110.3 | 3.13 | 0.89 | 3.84 | 7.87 | 5.50 | 5.07 | 32.0 | 0.11 | 19.3 |
| Ratan x Nirmal | 77.0 | 95.4 | 12.80 | 78.0 | 4.39 | 3.95 | 115.0 | 3.19 | 0.98 | 4.00 | 8.46 | 3.67 | 5.58 | 28.3 | 0.18 | 10.8 |
| Ratan x Pratik | 76.0 | 92.0 | 9.20 | 65.0 | 4.51 | 3.92 | 117.0 | 2.98 | 0.96 | 3.21 | 7.62 | 4.20 | 5.52 | 32.4 | 0.17 | 9.26 |
| Nirmal x Pratik | 75.0 | 95.2 | 11.0 | 82.0 | 4.18 | 4.00 | 116.0 | 3.18 | 0.98 | 4.20 | 6.56 | 6.33 | 4.72 | 24.8 | 0.17 | 8.84 |
| Mean | 70.3 | 85.5 | 12.7 | 72.9 | 4.31 | 3.49 | 108.9 | 3.146 | 0.94 | 3.70 | 7.90 | 5.41 | 5.30 | 29.3 | 0.126 | 14.1 |
| Range | 62.0 to 77.0 | 69.6 to 97.6 | 9.20 to 13.6 | 59.0 to 101.6 | 4.02 to 4.72 | 3.17 to 3.95 | 98.0 to 117.0 | 2.98 to 3.34 | 0.89 to 1.00 | 3.21 to 4.20 | 6.56 to 8.63 | 4.20 to 6.33 | 4.72 to 5.97 | 24.8 to 32.4 | 0.08 to 0.18 | 8.84 to 19.3 |
| C.V. (%) | 5.03 | 5.08 | 4.95 | 8.05 | 8.44 | 4.99 | 4.58 | 7.08 | 4.29 | 3.99 | 2.89 | 2.30 | 2.33 | 0.69 | 2.77 | 7.76 |
| S.E.m ± | 2.05 | 2.48 | 0.33 | 2.95 | 0.21 | 0.10 | 2.90 | 0.12 | 0.02 | 0.08 | 0.13 | 0.07 | 0.07 | 0.11 | 0.01 | 0.57 |
| C.D. at 5% | 5.95 | 7.20 | 0.97 | 8.56 | 0.60 | 0.29 | 8.41 | 0.37 | 0.06 | 0.24 | 0.37 | 0.21 | 0.20 | 0.33 | 0.01 | 1.65 |
| C.D. at 1% | 8.01 | 9.69 | 1.30 | 11.51 | 0.80 | 0.39 | 11.3 | 0.49 | 0.09 | 0.32 | 0.49 | 0.28 | 0.27 | 0.45 | 0.01 | 2.22 |

Supplementary Table S2. Analysis of variance (mean squares) for combining ability and predictability ratio for 16 characters

| Source of variation | d.f. | Days to 50% flowering | Plant height (cm) | No. of branch per plant | No. of pod per plant | Length of internode (cm) | Length of pedicel (cm) | Days to maturity | Length of pod (cm) | Width of pod (cm) | Seed per pod | Seed Index | Seed length (mm) | Seed width (mm) | Protein content in seed (%) | ODAP content in seed (%) | Yield per plant (g) |
|--|------|-----------------------|-------------------|-------------------------|----------------------|--------------------------|------------------------|------------------|--------------------|-------------------|--------------|------------|------------------|-----------------|-----------------------------|--------------------------|---------------------|
| GCA | 4 | 78.33** | 285.0** | 10.7** | 29.8** | 0.16** | 0.35** | 116.0** | 0.02** | 0.01** | 0.26** | 0.69** | 0.23** | 0.49** | 10.9** | 0.0029** | 6.92** |
| SCA | 10 | 6.56** | 50.2** | 11.2** | 441.5** | 0.25** | 0.12** | 10.2** | 0.01** | 0.001** | 0.08** | 0.63** | 0.80** | 0.18** | 5.37** | 0.0007** | 16.6** |
| Error | 28 | 4.21 | 6.16 | 0.11 | 8.71 | 0.04 | 0.01 | 8.42 | 0.01 | 0.0005 | 0.007 | 0.02 | 0.01 | 0.01 | 0.01 | 0 | 0.32 |
| σ^2_{gca} | | 10.6 | 39.8 | 1.51 | 3.02 | 0.01 | 0.05 | 15.3 | -0.0000 | 0.0003 | 0.04 | 0.09 | 0.03 | 0.07 | 0.001 | 0.0004 | 0.94 |
| σ^2_{sca} | | 2.35 | 44.05 | 11.1 | 432.8 | 0.21 | 0.11 | 1.84 | -0.006 | 0.0005 | 0.07 | 0.62 | 0.79 | 0.17 | 0.01 | 0.0007 | 16.3 |
| $2\sigma^2_{gca}/(2\sigma^2_{gca} + \sigma^2_{sca})$ | | 0.90 | 0.64 | 0.21 | 0.01 | 0.09 | 0.48 | 0.94 | 0.00 | 0.00 | 0.53 | 0.23 | 0.67 | 0.67 | 0.67 | 0.17 | 0.67 |

* , ** significant at 0.05 and 0.01 probability level, respectively.