



RESEARCH ARTICLE

Combining ability and gene action studies for various yield contributing traits in local cucumber (*Cucumis sativus* L.) of Jammu region

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Received: 08 July 2025; Accepted: 12 August 2025; Available online: Version 1.0: 08 January 2026

Cite this article: Raman T, Sanjeev K, Anil B. Combining ability and gene action studies for various yield contributing traits in local cucumber (*Cucumis sativus* L.) of Jammu region. Plant Science Today (Early Access). <https://doi.org/10.14719/pst.10515>

Abstract

The present investigation was conducted at the Vegetable Research Farm, Division of Vegetable Science, FoH & F, Chatha, SKUAST-Jammu (J & K) during 2022-23 and 2023-24 and was aimed at evaluating the general and specific combining abilities among the existing germplasm and assessing the gene action of different quantitative characters in 8 × 8 half-diallel mating design to facilitate the formulation of a sound breeding programme in this crop with the objective of studying combining ability and gene action in cucumber genotypes for various horticultural traits. Combining ability analysis showed that the mean sum of square attributable to General Combining Ability (GCA) among parents were significant for all traits and Specific Combining Ability (SCA) among crosses were significant for all traits. Parents identified as good general combiners included CS-5 (days to first female flowering), CS-4 and CS-7 (node number at which first female flower appears), CS-1 and CS-8 (number of female flowers per plant), CS-4 (fruit length and fruit diameter), CS-1 (average fruit weight), CS-2, CS-1 and CS-5 (number of fruits per vine) and CS-1, CS-5 and CS-3 (fruit yield per vine and fruit yield/ha). Crosses identified as good specific combiners were CS-2 × CS-8 (days to first female flowering), CS-3 × CS-5 (node number at which first female flower appears), CS-6 × CS-8 (number of female flowers per plant), CS-5 × CS-8 (fruit length), CS-5 × CS-6 (fruit diameter), CS-4 × CS-7 (average fruit weight), CS-2 × CS-8 (number of fruits per vine) and CS-2 × CS-8 (fruit yield per vine and fruit yield/ha). Estimates of gene action revealed that for most traits such as days to first female flowering, node number of first female flower, number of female flowers per plant, fruit dimensions, weight, fruit yield per vine and yield per hectare SCA variances (σ^2_s) exceeded GCA (σ^2_g), suggesting that non-additive gene action dominates their inheritance. The GCA/SCA ratio was less than unity for the majority of traits studied, supporting the greater influence of non-additive gene action. This implies that hybridization or heterosis breeding would be effective for exploiting hybrid vigour in cucumber crops in the future.

Keywords: GCA; gene action; local cucumber; SCA

Introduction

Cucumber (*Cucumis sativus* L.), belonging to the Cucurbitaceae family ($x = 7$), is a highly diverse crop with 118 genera and 825 species, of which 34 genera and 108 species are found in India (1,2). It is a popular vegetable cultivated in hills and plains under both open-field and protected conditions (3). In cucumber, besides open pollinated varieties and hybrids, some local yellow skinned cucumbers are also being grown in subtropical plains of Jammu. Cucumber production in the subtropical plains of Jammu faces challenges due to insect pests like red pumpkin beetle (*Alucophora foveicollis*) and fruit fly (*Dacus cucurbitae*) and diseases such as powdery mildew (*Erysiphe cichoracearum*) and downy mildew (*Pseudoperonospora cubensis*). Recently, cucumber production has suffered substantial losses due to these insect pests and diseases during the summer months in the subtropical plains of Jammu and these local cucumber lines are reported to have resistance against both insect pests and diseases (4).

Limited efforts have been made toward crop improvement in local cucumbers. There is therefore a strong need to develop cucumber hybrids with high yield and resistance to diseases and insect pests for direct selection or use as a parent in hybridization programs. F_1 hybrids in cucumber as in many vegetable crops have several well-known advantages over open-pollinated varieties and thus provide opportunities for breeder to identify appropriate combinations to develop superior hybrids.

Combining ability analysis is a crucial tool for identifying superior parents and crosses, aiding in the exploitation of heterosis (5). GCA reveals additive gene action, while SCA indicates non-additive effects, guiding parental selection. Combining ability analysis helps in selecting parents with high GCA effects and identifying superior cross combinations with high SCA, which is essential for exploiting hybrid vigour (heterosis) in breeding programs for deriving elite pure lines from hybrid progeny. Understanding the genetic basis of various traits allows breeders to formulate effective breeding strategies to improve existing germplasm in the future. The assessment of

combining ability helps evaluate the potential of inbred lines when used in hybrid combinations (6). Diallel mating design allows systematic evaluation of parental combinations, helping breeders choose optimal crosses for yield improvement (7,8).

To address the current challenges, it is essential to focus on creating region-specific hybrids with high yield and quality traits and ensuring that these seeds are supplied to farmers at a reasonable cost. By leveraging combining ability studies and diallel analysis, breeders can develop superior cucumber varieties, ensuring sustainable production in diverse agro-climatic conditions. The study aimed to identify superior parental combinations for yield and horticultural traits, facilitating cucumber breeding programs in subtropical regions.

Materials and Methods

The present study was conducted at Vegetable Research Farm-I, SKUAST-Jammu, during 2022-23 and 2023-24 under subtropical conditions. Eight diverse cucumber genotypes, selected based on D² clustering, were used for developing cross combinations in half diallel mating design (4). Seeds were sown in January 2023 under protected conditions and healthy seedlings were transplanted on 1 March 2023 for raising the crossing block, generating 28 F₁ hybrids. In 2024, the 28 hybrids and eight parents were sown on 30 January under protected structures and transplanted on 19 March in a Randomized Complete Block Design (RCBD) with three replications at a spacing of 1 m × 1 m. Standard agronomic practices were followed to raise a healthy crop (9). Griffing's diallel analysis, Method-2 Model-I (fixed effects), was employed for combining ability analysis, as only parents and F₁'s (without reciprocals) were available (7). This approach estimates GCA and SCA and helps in assessing genetic components. The analysis was based on the following statistical model:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + 1/bc \sum \sum e_{ijkl}$$

Where,

μ = population mean

g_i & g_j = GCA effects of i^{th} and j^{th} parents, respectively

s_{ij} = SCA effect of the hybrid between i^{th} and j^{th} parent

e_{ijkl} = error effect associated with the $ijkl^{\text{th}}$ observation

Results and Discussion

Analysis of variance for combining ability

The analysis of variance revealed significant GCA mean squares for all traits, indicating substantial parental contributions to GCA variance (Table 1). Similarly, SCA mean squares were significant for all traits, highlighting the major role of hybrids in SCA variance. Similar results were reported by earlier findings in cucumber (10).

Estimates of GCA and SCA effects

The GCA and SCA effects for the traits studied (Table 2 & 3). Estimates of combining ability for days to first female flowering showed that parent CS-5 (-0.71) was the best general combiner for the trait, making it suitable for hybridization to develop superior hybrids. Among the 28 crosses, CS-2 × CS-8 and CS-2 × CS-6 with -3.24 and -2.04 SCA values respectively, were identified as good specific combiners for days to first female flowering despite involving poor (low) × poor (low) and poor (low) × average (moderate) general combiners. Similar results were reported by earlier workers in cucumber and noting that F₁ crosses exhibiting high SCA effects did not always involve parents with high GCA effects, indicating that the inter-allelic interactions are important for the number of fruits per vine trait (11,12). These crosses resulted from the parents having average (moderate) × poor (low) GCA effects. This suggests the presence of additive × additive and additive × dominance gene interactions, with early flowering being dominant and primarily influenced by non-additive gene action.

For the node number at which first female flower appears, parents CS-4 (-0.43) and CS-7 (-0.16) were found as good general combiners. Crosses CS-3 × CS-5 (-0.74), CS-3 × CS-4 (-0.68), CS-3 × CS-6 (-0.52) and CS-2 × CS-7 (-0.49) were found to be good specific combiners for the trait. These crosses involved poor (low) × poor (low), poor (low) × good (high), poor (low) × poor (low) and poor (low) × good (high) general combiners, suggesting both additive and non-additive gene action. These results are in accordance with the findings of in cucumber and such combinations are ideal for heterosis breeding, indicating that while early flowering is dominant, non-additive gene effects play a more significant role (13–15).

Parents CS-1 (1.25) and CS-8 (0.91) were found to be good general combiners for number of female flowers per plant. Among 28 crosses, CS-6 × CS-8 (2.32) and CS-4 × CS-5 (1.70) exhibited good SCA for the trait despite involving poor (low) × good (high) and poor (low) × poor (low) parental combinations. These findings are well supported by a previous work and these crosses could be utilized as hybrids after multi-location trials or for generating transgressive segregants in advanced generations (16).

For days to first harvest, parents CS-8 (-1.18) and CS-1 (-1.08) were the best general combiners and only one cross, CS-5 × CS-6 (-3.51), exhibited good SCA, involving average (moderate) × poor (low) general combiners. These results are in accordance with the findings and implying that progeny selection will be effective as influenced by additive gene effects (17,18).

Parent CS-4 (0.17) was good general combiner for fruit length and four crosses namely, CS-5 × CS-8 (1.72), CS-4 × CS-5 (1.67), CS-2 × CS-7 (1.47) and CS-1 × CS-4 (1.08) demonstrated significant positive SCA effects, involving poor (low) × poor (low), good (high) × poor (low), average (moderate) × average (moderate), average (moderate) × good (high) combining parents. These findings are well supported by previous work and these crosses, with their high SCA effects, hold potential for hybrid

Table 1. Analysis of variance for combining ability of parents and F₁'s for various traits in cucumber

| | DF | Days to first female flowering | Node number at which first female flower appears | Number of female flowers per plant | Days to first harvest | Fruit length (cm) | Fruit diameter (cm) | Average fruit weight (g) | Number of fruits per vine | Fruit yield per vine (kg) | Fruit yield/ha (q/ha) |
|-------|----|--------------------------------|--|------------------------------------|-----------------------|-------------------|---------------------|--------------------------|---------------------------|---------------------------|-----------------------|
| GCA | 7 | 2.28* | 0.59** | 6.57** | 15.44** | 0.54* | 0.20** | 187.32* | 1.47** | 0.22** | 2209.91** |
| SCA | 28 | 1.58* | 0.20** | 1.33** | 3.22 | 1.22** | 0.10** | 286.55** | 0.78** | 0.04** | 397.48** |
| Error | 70 | 0.88 | 0.05 | 0.43 | 2.81 | 0.34 | 0.04 | 78.94 | 0.20 | 0.01 | 111.99 |

Table 2. Estimation of GCA effects for various traits in cucumber

| | Days to first female flowering | Node number at which first female flower appears | Number of female flowers per plant | Days to first harvest | Fruit length (cm) | Fruit diameter (cm) | Average fruit weight (g) | Number of fruits per vine | Fruit yield per vine (kg) | Fruit yield/ha (q/ha) |
|----------------|--------------------------------|--|------------------------------------|-----------------------|-------------------|---------------------|--------------------------|---------------------------|---------------------------|-----------------------|
| CS1 | 0.39 | -0.12 | 1.25** | -1.08* | 0.13 | 0.10 | 5.30* | 0.39** | 0.20** | 20.32** |
| CS2 | 0.53 | 0.07 | 0.28 | 0.52 | 0.10 | -0.08 | 3.60 | 0.53** | 0.08** | 8.43** |
| CS3 | 0.12 | 0.06 | 0.33 | -0.98 | 0.08 | -0.02 | 1.10 | 0.07 | 0.10** | 10.41** |
| CS4 | -0.48 | -0.42** | -0.68** | 2.32** | 0.17* | 0.24** | -6.76* | -0.52** | -0.19** | -19.27** |
| CS5 | -0.71* | 0.03 | -0.74** | -0.22 | -0.54** | -0.09 | 2.47 | 0.31* | 0.10** | 10.43** |
| CS6 | -0.31 | 0.15* | -0.89** | 1.15* | 0.09 | 0.05 | -5.61* | -0.18 | -0.10** | -9.71** |
| CS7 | -0.11 | -0.16* | -0.45* | -0.52 | 0.09 | -0.22** | -1.71 | -0.39** | -0.20** | -19.47** |
| CS8 | 0.56* | 0.40** | 0.91** | -1.18* | -0.12 | 0.02 | 1.60 | -0.20 | -0.01 | -1.16 |
| Gi < 0 at 95% | 0.66** | 0.16** | 0.46** | 1.17** | 0.40** | 0.13** | 6.21** | 0.31** | 0.07** | 7.40** |
| Gi < 0 at 99% | 0.97** | 0.23** | 0.68** | 1.73** | 0.60** | 0.20** | 9.20** | 0.47** | 0.11** | 10.95** |
| Gi--Gj at 95 % | 0.99** | 0.24** | 0.69** | 1.77** | 0.61** | 0.20** | 9.40** | 0.48** | 0.11** | 11.19** |
| Gi--Gj at 99 % | 1.47** | 0.35** | 1.02** | 2.62** | 0.90** | 0.30** | 13.90** | 0.70** | 0.16** | 16.56** |

Table 3. Estimation of SCA effects of F₁S for various traits in cucumber

| | Days to first female flowering | Node number at which first female flower appears | Number of female flowers per plant | Days to first harvest | Fruit length (cm) | Fruit diameter (cm) | Average fruit weight (g) | Number of fruits per vine | Fruit yield per vine (kg) | Fruit yield/ha (q/ha) |
|------------------|--------------------------------|--|------------------------------------|-----------------------|-------------------|---------------------|--------------------------|---------------------------|---------------------------|-----------------------|
| CS1 x CS2 | -0.08 | -0.13 | -0.40 | -1.01 | 0.67 | 0.05 | 12.37 | 0.14 | 0.06 | 6.04 |
| CS1 x CS3 | -0.34 | 0.68** | 0.79 | -0.17 | 0.89 | 0.28 | -26.13** | 0.32 | 0.10 | 10.08 |
| CS1 x CS4 | -0.75 | 0.04 | -0.13 | -2.47 | 1.08* | 0.17 | -2.26 | 0.12 | 0.03 | 2.58 |
| CS1 x CS5 | -1.17 | 0.64** | 0.53 | -0.28 | -0.65 | -0.35 | -9.50 | 0.12 | 0.06 | 5.66 |
| CS1 x CS6 | -0.24 | 0.39 | 0.28 | 0.69 | 1.05 | 0.04 | 12.58 | 0.03 | 0.02 | 1.65 |
| CS1 x CS7 | -0.78 | -0.03 | -0.22 | 3.36* | -0.63 | 0.11 | -10.32 | 0.02 | 0.01 | 0.54 |
| CS1 x CS8 | -0.11 | -0.12 | -1.32* | 0.03 | 0.74 | 0.03 | 3.37 | 0.00 | 0.02 | 1.86 |
| CS2 x CS3 | 1.20 | -0.18 | -0.24 | -1.77 | 0.75 | 0.01 | 6.57 | -1.00* | -0.17 | -17.40 |
| CS2 x CS4 | -1.21 | -0.09 | -0.82 | 1.93 | -0.74 | 0.08 | 20.44* | -0.20 | -0.03 | -2.72 |
| CS2 x CS5 | 0.36 | 0.05 | -0.97 | -0.54 | -0.50 | -0.43* | -14.80 | 0.80 | 0.19 | 18.83 |
| CS2 x CS6 | -2.04* | -0.07 | 1.09 | 3.76* | -0.68 | -0.20 | 14.28 | 0.66 | 0.14 | 13.75 |
| CS2 x CS7 | 0.09 | -0.49* | 0.51 | -1.58 | 1.47** | -0.18 | -8.62 | 0.70 | 0.14 | 13.34 |
| CS2 x CS8 | -3.24** | -0.32 | -0.46 | -1.58 | 0.60 | 0.01 | 4.07 | 0.91* | 0.20* | 20.40* |
| CS3 x CS4 | -0.48 | -0.68** | 0.89 | -1.91 | 0.29 | 0.05 | 6.94 | 0.80 | 0.16 | 16.58 |
| CS3 x CS5 | -1.24 | -0.74** | -0.69 | 0.63 | -0.42 | -0.01 | -19.39* | -0.20 | -0.01 | -1.26 |
| CS3 x CS6 | 1.03 | -0.52* | 1.19 | 2.59 | -1.49** | -0.29 | -13.22 | 0.71 | 0.16 | 15.71 |
| CS3 x CS7 | -0.51 | -0.34 | -1.07 | -0.74 | -0.35 | -0.16 | 24.89** | 0.70 | 0.15 | 14.41 |
| CS3 x CS8 | -1.51 | -0.04 | -0.81 | 0.59 | -0.39 | 0.66** | -3.42 | 0.68 | 0.16 | 16.29 |
| CS4 x CS5 | -0.30 | -0.05 | 1.70** | 0.99 | 1.67** | 0.43* | -1.43 | 0.60 | 0.12 | 12.29 |
| CS4 x CS6 | 0.62 | 0.43* | 0.78 | -0.71 | -1.44* | 0.11 | -3.35 | 0.51 | 0.11 | 10.27 |
| CS4 x CS7 | 0.10 | -0.19 | 0.17 | -1.04 | 0.88 | -0.02 | 26.75** | 0.50 | 0.10 | 10.01 |
| CS4 x CS8 | 0.43 | 0.25 | 0.61 | 2.96 | -0.57 | -0.77** | -15.56 | 0.48 | 0.10 | 10.14 |
| CS5 x CS6 | 1.19 | -0.10 | -1.39* | -3.51* | 0.68 | 0.67** | 25.41** | 0.50 | 0.12 | 11.30 |
| CS5 x CS7 | -0.01 | 0.02 | 0.27 | 0.83 | 0.93 | 0.02 | 7.51 | 0.50 | 0.11 | 10.10 |
| CS5 x CS8 | -0.01 | -0.14 | 0.04 | -0.51 | 1.72** | 0.26 | 15.20 | 0.48 | 0.12 | 11.98 |
| CS6 x CS7 | -0.74 | -0.37 | -1.78** | 0.46 | 0.32 | -0.11 | 2.59 | 0.41 | 0.08 | 8.21 |
| CS6 x CS8 | -0.08 | 0.01 | 2.32** | -2.21 | -1.30* | 0.01 | -17.72* | 0.38 | 0.09 | 8.87 |
| CS7 x CS8 | 0.40 | 0.05 | -1.75** | -0.88 | -0.33 | 0.10 | 21.38* | 0.38 | 0.08 | 8.15 |
| Sij < 0 at 95 % | 1.75 | 0.42 | 1.22 | 3.12 | 1.08 | 0.36 | 16.53 | 0.84 | 0.19 | 19.69 |
| Sij < 0 at 99 % | 2.36 | 0.57 | 1.65 | 4.21 | 1.45 | 0.48 | 22.32 | 1.13 | 0.26 | 26.59 |
| Sij--Sik at 95 % | 2.58 | 0.62 | 1.80 | 4.61 | 1.59 | 0.53 | 24.46 | 1.24 | 0.28 | 29.13 |
| Sij--Sik at 99 % | 3.49 | 0.84 | 2.43 | 6.23 | 2.15 | 0.71 | 33.03 | 1.67 | 0.38 | 39.34 |
| Sij--Skl at 95 % | 2.44 | 0.59 | 1.70 | 4.35 | 1.50 | 0.50 | 23.06 | 1.17 | 0.27 | 27.47 |
| Sij--Skl at 99 % | 3.29 | 0.79 | 2.29 | 5.87 | 2.03 | 0.67 | 31.14 | 1.58 | 0.36 | 37.09 |

breeding programs targeting fruit length improvement (19,20). Parent CS-4 (0.24), was good general combiner for fruit diameter, indicating strong additive effects. Among crosses, CS-5 × CS-6 (0.67), CS-3 × CS-8 (0.66) and CS-4 × CS-5 (0.43) were found to be good specific combiners for the trait. These crosses involved poor (low) × average (moderate), poor (low) × average (moderate) and good (high) × poor (low) general combiners. These findings are in accordance with the earlier work in cucumber with significant positive and desirable SCA effects, these hybrids are promising for further breeding programs (19,20).

For the average fruit weight, parent CS-1 (5.30) was observed as good general combiner due to additive genetic effects, while five crosses viz., CS-4 × CS-7 (26.75), CS-5 × CS-6 (25.41), CS-3 × CS-7 (24.89), CS-7 × CS-8 (21.38) and CS-2 × CS-4 (20.44) exhibited the highest significant positive SCA effects, despite involving poor (low) × poor (low), average (moderate) × poor (low), average (moderate) × poor (low), poor (low) × average (moderate) and average (moderate) × poor (low) general combiners. These results suggest non-additive gene action governs the inheritance of this trait. These results agree with the earlier findings, suggesting that non-additive effects in cucumber (19,21). For the number of fruits per vine, parents CS-2, CS-1 and CS-5 were good general combiners with GCA values of 0.53, 0.39 and 0.31, respectively, indicating they possess favourable genes for improving yield components in hybrids. Among crosses, CS-2 × CS-8 (0.91) had the highest significant positive SCA value, demonstrating good SCA, involving good (high) × poor (low) combining ability. Crosses with high × low GCA effects suggested additive × non-additive gene action. These results are in line with the early findings in cucumber with high SCA effects in F_1 crosses did not always correlate with high GCA effects in parents, highlighting the importance of inter-allelic interactions for this trait (22,23).

Data on combining ability for the fruit yield per vine showed that four parents namely CS-1 (0.20), CS-5 (0.10), CS-3 (0.10) and CS-2 (0.08) were good general combiners, as showed significant positive GCA values reflects additive gene effects and breeding value and among 28 crosses, only CS-2 × CS-8 (0.20) exhibited significant positive SCA effects, making it a good specific combiner, despite involving a good (high) × poor (low) general combiner. Similar results had been also reported in previous studies (19–26). For the fruit yield/ha, parents CS-1 (20.32), CS-5 (10.43), CS-3 (10.41) and CS-2 (8.43) were good general combiners and among crosses, only CS-2 × CS-8 (20.40) exhibited the highest significant positive SCA value involving good (high) × poor (low) general combiners. The results are in accordance with earlier findings, indicating the highest significant positive GCA values (19–26). It was attributed to additive and additive × additive gene effects and highest SCA, likely due to complementary gene action or non-allelic interactions and crosses with good SCA effects is desirable for genetic improvement of any crop through hybrid breeding programme (7,27–29).

Gene action

Estimates of gene action showed that GCA variances (σ^2_g) were lower than SCA variances (σ^2_s) for traits like days to first harvest, indicating that non-additive rather than the additive gene action predominates in their inheritance (Table 4). For most traits such as days to first female flowering, node number of first female flower, number of female flowers per plant, fruit dimensions, weight, yield per vine and yield per hectare SCA variances (σ^2_s) exceeded GCA (σ^2_g), suggesting that non-additive gene action dominates their inheritance. This implies that hybridization would be effective for exploiting hybrid vigour in cucumber. The GCA/SCA ratio was less than unity for the majority of traits studied, further confirming the greater influence of non-additive gene action. These results are in consonance with earlier findings of in cucumber and consequently, these traits can be improved through recurrent selection for SCA or heterosis breeding (22,30,31).

Conclusion

From the present studies, top promising parents like CS-5 for days to first female flowering; CS-4 and CS-7 for node number at which first female flower appears; CS-1 and CS-8 for number of female flowers per plant and days to first harvest; CS-4 for fruit length and fruit diameter; CS-1 for average fruit weight; CS-2, CS-1 and CS-5 for number of fruits per vine; CS-1, CS-5 and CS-3 for fruit yield per vine and fruit yield/ha, were identified as potential parents as they exhibited significant desirable GCA effects and may be highly suitable for further breeding programmes.

Top performing cross combinations namely CS-2 × CS-8 and CS-2 × CS-6 for days to first female flowering; CS-3 × CS-5, CS-3 × CS-4 and CS-3 × CS-6 for node number at which first female flower appears; CS-6 × CS-8 and CS-4 × CS-5 for number of female flowers per plant; CS-5 × CS-6 for days to first harvest; CS-5 × CS-8, CS-4 × CS-5 and CS-2 × CS-7 for fruit length; CS-5 × CS-6, CS-3 × CS-8 and CS-4 × CS-5 for fruit diameter; CS-4 × CS-7, CS-5 × CS-6 and CS-3 × CS-7 for average fruit weight; CS-2 × CS-8 for number of fruits per vine, fruit yield per vine and fruit yield/ha, demonstrated significant desirable SCA effects, indicating non-additive gene interactions.

Variance due to SCA was higher in magnitude than variance due to GCA for most traits, also suggesting the importance of non-additive gene action. These findings highlight that heterosis breeding or hybridization can be an effective approach for selecting superior genotypes in future generations, ultimately enhancing yield and its related traits in cucumber. The identified cross combinations may be exploited as hybrid after multilocation trial testing or used to produce transgressive segregants in subsequent generations.

Table 4. Estimation of components of heritable variation and their ratios for various traits in cucumber

| | Days to first female flowering | Node number at which first female flower appears | Number of female flowers per plant | Days to first harvest | Fruit length (cm) | Fruit diameter (cm) | Average fruit weight (g) | Number of fruits per vine | Fruit yield per vine (kg) | Fruit yield/ha (q/ha) |
|---------------|--------------------------------|--|------------------------------------|-----------------------|-------------------|---------------------|--------------------------|---------------------------|---------------------------|-----------------------|
| σ^2_g | 0.14 | 0.05 | 0.61 | 1.26 | 0.02 | 0.02 | 10.84 | 0.13 | 0.02 | 209.79 |
| σ^2_s | 0.70 | 0.15 | 0.90 | 0.41 | 0.88 | 0.06 | 207.62 | 0.58 | 0.03 | 285.49 |
| GCA/SCA Ratio | 0.20 | 0.37 | 0.68 | 3.11 | 0.02 | 0.26 | 0.05 | 0.22 | 0.72 | 0.74 |

Authors' contributions

RT carried out the combining ability and gene action studies, participated in the sequence alignment and drafted the manuscript. SK and AB conceived of the study and participated in its design and coordination. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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Peerreview: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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