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Investigating the Gene Action and Combining Ability Effects on Yield Attributes in Cotton (Gossypium hirsutum L.)

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Abstract

Gossypium hirsutum L. is a major cash crop that supports the textile and edible oil industries. To meet the growing demand, identifying parent plants with superior economic and quality traits is essential. This study aimed to assess the combining ability and vigor performance of four cotton genotypes through a complete diallel mating system. F1 hybrids were grown in a randomized complete block design with three replications. Traits studied included plant height, boll number, branch types, seed per boll, seed cotton yield, and fiber quality, including fiber length, strength, and fineness. The SGA and Cyto-178 cultivars exhibited high general combining ability (GCA), indicating their potential for hybrid breeding programs. Among the crosses, Cyto-178×SLH-8 showed the best fiber length, while VH-369×SLH-8 excelled in fiber strength. The VH-369×SGA cross demonstrated high specific combining ability (SCA) for fiber fineness. The study revealed that SCA variance was more significant than GCA and RCA variance, providing valuable insights for future cotton breeding programs to improve F1 hybrids and benefit both farmers and consumers.

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Introduction

The cultivation of cotton is essential to the South Asian agricultural sector, as it is the leading cash crop (Rana et al., 2020). Known as the "king of natural fibers", cotton has a significant global presence and importance (Shahin et al., 2022). It is a crucial oilseed and fiber crop in tropical regions, playing a vital role in agriculture, employment, and industrial development (Shahrajabian et al., 2020). With cotton accounting for 95% of global fiber production, it is the backbone of the textile industry by supplying raw materials (Atkar et al., 2021). The average productivity of cotton is approximately 695 kg/ha, accounting for about 60% of the country's total exports (Shuli et al., 2018).

It is a significant crop for fiber and oilseeds in tropical regions, and it is also crucial for the country's agriculture, employment, and industrial development. Pakistan is the world's fourth-largest cotton producer, but it often imports cotton to meet its textile needs (Frederick et al., 2019).

To meet the rising demand for cotton, plant breeders need to create cotton varieties that are both productive and consistently high-yielding. Aslam et al. (2020) point out that this can only be done with access to a wide range of genes in cotton germplasm. Because a crop's genetic make-up is the basis for its improvement, breeders must look at all of its genetic traits to improve a cultivar (Begna, 2021c). The existence of variation is the basis for improvement, so breeders need to acquire information about different accession patterns, along with their inheritance, yields, contributing factors, and genetic relationships, to make the best selection of parents and ensure high productivity (Begna, 2021b; Khan et al., 2021).

It is essential to utilize genetic variation and combining ability tools to determine the breeding values of different populations (Begna, 2021a). Combining ability is an appropriate way to choose parental lines when you want to make better genotypes because it tells you which ones have high and low general combining ability. Combining ability also tells us about the effects of both additive and non-additive genes, which are important for controlling fiber and yield traits (Akbar et al., 2020). Numerous studies have utilized parallel analysis to evaluate individuals' ability to integrate information effectively (Yuan et al., 2021). Full diallel mating patterns can also help build a stronger genetic base. It is also possible to determine breeding values and investigate the potential of parental lines by combining their abilities (Max et al., 2021; Muthoni & Shimelis, 2020).

There are various conventional techniques for examining base populations and analyzing genetic differences; the diallel technique is the most reliable, assisting plant breeders in distinguishing differences among different genotypes (Abdel-Aty et al., 2022). This technique has been rapidly used in recent years to analyze variation in plant genotypes which is heritable for different traits. For desirable genotypes, this approach makes adequate stipulation about gene activity-interaction, general combining ability (GCA), and specific combining ability (SCA). Moreover, SCA and GCA analyses help identify and evaluate superior and advantageous segregants (Arifin et al., 2018).

This study was designed to investigate gene interactions of four different cotton genotypes that play a significant role in determining economically important traits in cotton (Khokhar

et al., 2018). It is hypothesized that breeding strategies that consider both general combining ability (GCA) and specific combining ability (SCA) would be effective in developing cotton varieties with superior yield and fiber quality. The research investigates the influence of GCA and SCA on important cotton characteristics through controlled breeding experiments using these genetic strains. The analysis will provide practical knowledge for breeding programs that aim to improve yields and fiber characteristics in cotton plants.

Materials and Methods

The research was done at the University of Agriculture in Faisalabad, Pakistan, in the Department of Plant Breeding and Genetics. As shown in Table 1, four types of upland cotton-SLH-8, Cyto-178, VH-369, and SGA-were crossed randomly with each other in a diallel pattern in a greenhouse in 2017, and the time of planting the seeds from the greenhouse into the field in May 2017. Combinations were made in a full diallel manner; emasculation was done manually using tweezers and petri plates. Pollens were carefully shredded with the help of a brush on the stigma of emasculated plants, and appropriate care was adopted to avoid foreign pollen contamination. Butter paper bags had to be used to keep emasculated flowers from getting dirty, and craft paper bags were used to cover whole flowers so they could grow seeds on their own. The seeds that were taken from the greenhouse were planted in the field during the next growing season. There were ten plants in each row, with 75 cm between rows and 30 cm between plants. From planting the cotton to picking it, standard agricultural practices were used. Five plants were marked so that data could be collected on them, and their growth and development were carefully tracked. We measured different agronomic traits, like plant height, number of branches, boll weight, and seed yield per plant, on each of the five guarded plants from each line when they were fully grown. A high-volume instrument was used to look at the length, strength, and fineness of fibers in the Department of Fiber Technology at the University of Agriculture in Faisalabad. Following the method explained by Steel et al. in 1997, the collected data were then used to find any genetic differences between the F1 hybrids and their parent plants. Griffing developed a method to test combining ability in 1956. It involved determining the parents' general and specific combining ability, and then using Method 1, Model 1 of Griffing's approach to perform an analysis of variance.
Table 1. Parents and their direct and indirect crosses.

Parents	Crosses	Self
SLH-8	SLH-8× Cyto-178	SLH-8×SLH-8
	SLH-8× VH-369	
	SLH-8× SGA	
Cyto-178	Cyto-178× SLH-8	Cyto-178×Cyto-178
	Cyto-178× VH-369	
	Cyto-178× SGA	
VH-369	VH-369× SLH-8	VH-369×VH-369
	VH-369× Cyto-178	
	VH-369× SGA	
SGA	SGA× SLH-8	SGA×SGA
	SGA× Cyto-178	
	SGA× VH-369	

Morphological traits

The following methodology was adopted to collect and analyze the data for each character. *Plant height (cm)*

A measuring tape was used to measure the height of different plants randomly. Specifically, five plants were selected on a standard basis, and their heights were recorded in centimeters. We kept in mind that height should be measured when the final growth is complete and the plant is mature.

Number of sympodial branches

The direct, clear fruit-producing branches. On a standard basis, five plants were selected in a row, and the number of branches was counted. Care is taken to ensure the plant is completely mature, and data for further analysis is collected.

Monopodial branches

Monopodial branches are those on which indirect fruit is produced; we can say secondary branches. They are usually far less in number than a sympodial number of branches. Manually, five mature plants are selected from a row and counted. The mean value was calculated by averaging several measurements across multiple plants.

Bolls per plant

When the plant matured, the number of bolls from the selected five plants was counted. The mean value was obtained for analysis.

Seeds per boll

The formula for counting the number of seeds per boll is as follows:

Number of seeds per boll = Boll size
$$\frac{100 - lint \%}{Seed index}$$

Seed index

The weight of 100 seeds from each plant was taken and further analyzed by taking the mean values. A random sample of 100 seeds was taken after ginning, and balance weighing was used for weight. Mean was then subjected to further analysis. *Boll weight* (g)

From a random five plants, different bolls, i.e., five from random positions, were picked and subjected to analysis by taking their mean values.

Seed cotton yield per plant

To measure the yield of seed cotton on an individual plant basis, the electric balance was used. Out of five guarded plants, seed cotton was picked from the individual plant in a separate bag. The average yield was taken for further analysis. *Uniformity ratio*

The formula for the calculation of uniformity ratio is as follows:

$$Uniformity\ ratio = \frac{50\%\ span\ length}{2.5\%\ span\ length} (100)$$

Lint index

The formula for the estimation of lint index is as follows:

$$Lint index = \frac{Seed index}{Lint \%} (100)$$

Fiber quality traits

A pure lint sample from each experimental plant was used to measure fiber quality. The Department of Fiber Technology at the University of Agriculture, Faisalabad, used the High-Volume Instrument (HVI) method to measure fiber length, strength, and fineness.

Statistical analysis

The information and data collected through the above-mentioned methods are then subjected to statistical analysis for further examination, as described by Veturi and Ritchie (2018) and De Santiago (2020), using a proper approach. Statistical inspection was carried out to estimate distinctions among traits at the genetic level, especially for all mentioned traits, whether they are immensely differentiated or not. Combining ability examination was conducted using the formulas mentioned below, and the investigation was first devised by Li et al. (. Estimates of general and specific combining ability within parents and analysis of variance were assessed using the following Method 1, Model 1 approach. **Results**

Results

Plant height

The SCA variance for plant height was significantly higher than the GCA variance. This suggests that the genetic differences and similarities between these genotypes are primarily caused by non-additive gene action, rather than additive gene action. The parental genotypes VH-369 and Cyto-178 showed better-performing general combiners for plant height. All other parental genotypes showed low general combining ability. The genotype crosses VH-369 × SGA, Cyto-178 × VH-369, and Cyto-178 × SGA showed higher SCA variance for plant height, while the remaining crosses proved to be poor combiners. These hybrids exhibited better plant height than their parents (> 100 cm) (Fig. 1a).



Figure 1. SCA variance And performance of genotype crosses for plant height (a), sympodial branches per plant (b), monopodial branches (c), and overall SCA value (d). The graph displays the SLH-8, Cyto-178, VH-369, and SGA genotypes, as well as their hybrids.

Number of sympodial branches per plant

For the number of sympodial branches, although the General Combining Ability (GCA) mean square was not significant, the Specific Combining Ability (SCA) estimation showed significance (P < 0.05). This suggests that non-additive gene action is responsible for genotype differences. Genotypes VH-369 and Cyto-178 are strong general combiners for plant sympodial branches. SLH-8×SGA, Cyto-178×SLH-8, and VH-369×Cyto-178 genotype crosses showed the highest SCA variance for sympodial branches per plant, while others showed fewer branches (Fig. 1 b).

Number of monopodial branches per plant

SGA and SLH-8 had the highest general combining ability for monopodial branches, while all other parent genotypes had lower GCA values per plant. The SLH-8×VH-369 hybrid had the most monopodial branches and a higher SCA value (Fig. 1c). The VH-369×Cyto-178 hybrid has the lowest performance.

Number of bolls per plant

It was found that the parental genotypes SGA and VH-369 were very good at combining the number of bolls on each plant. The genotype cross of VH-369×SGA had the highest SCA number of bolls per plant (see Fig. 1d). On the other hand, the hybrid of VH-369 and Cyto-178 had the lowest SCA value, as shown in Fig. 1d, which shows a graph of the parents and their hybrids.

Number of seeds per boll

There was non-additive gene action because the SCA variance for seed count was higher than the GCA variance. The parent genotypes VH-369 and Cyto-178 did a good job of combining for the number of seeds per boll. Notably, the VH-369 Cyto-178 hybrid had the highest SCA value of all the hybrids (see Fig. 2 b). On the other hand, the SGA Cyto-178 hybrid had the fewest seeds, and the other hybrids did not produce any noticeable results.

Boll weight (g)

There was more SCA variance for boll weight than GCA variance. For boll weight, nonadditive gene action was seen, which means that genes did not only add up to make one thing. In terms of boll weight, the parental genotypes SGA and Cyto-178 were very good at combining, while the other parental genotypes were not as effective. The crosses between SLH-8 and SGA and SGA and Cyto-178 had the highest SCA variance for boll weight. The cross between Cyto-178 and SLH-8 had the lowest SCA variance (see Fig. 2c).

Seed cotton yield

For SCA, the range for boll weight was wider than for GCA. It seems that non-additive gene action, not additive gene action, was more important in deciding the weight of the boll. The parental genotypes SGA and Cyto-178 were generally good at combining for boll weight, while the other genotypes were not as effective. The SCA variance for boll weight was highest for the genotype crosses SLH-8 × SGA and SGA × Cyto-178. The SCA variance for boll weight was lowest for the hybrid Cyto-178×SLH-8 (Fig. 2a). The self-cross of SGA, which had the best GCA value, showed SCY the most. The cross between Cyto-178 and SGA, on the other hand, had the lowest SCA values. *Fiber length (mm)*

The study's results showed that non-additive gene action changed the length of fibers. The parental genotypes with the best general combining ability were Cyto-178 and SLH-8. The

cross between Cyto-178 and SLH-8 had good specific combining ability. The hybrid made from SLH-8 and Cyto-178 had the lowest values for these genetic components (Fig. 3a). The other genotypes examined did not show any significant differences.



Figure 2. (a) shows that hybridization significantly affects seed cotton yield, with the selfcross of SGA having the highest GCA and the Cyto-178-SGA cross having the lowest SCA variance, (b) shows that VH-369 Cyto-178 had the highest SCA value of all hybrids, while SLH-8 and SGA and SGA and Cyto-178 had the most significant boll weight SCA variance, and (c) shows the Cyto-178-SLH-8 cross's lowest boll weight SCA variance. *Fiber Strength (g/tex)*

The study's findings showed that non-additive gene action could change the strength of fiber. When compared to the other parental genotypes, genotype SGA had better general combining ability (GCA). The cross between VH-369 and SLH-8 had the best specific combining ability (SCA), while the cross between VH-369 and SGA had the worst. (Fig. 3b) represents the parents and their hybrids.

Fiber fineness (µg/inch)

The genotypes VH-369 and SGA exhibited better general combining ability (GCA) for fiber fineness than the other parental genotypes. For specific combining ability (SCA), the cross between VH-369 and SGA had the best results. However, the parents exhibited higher fiber fineness (>5.0) in comparison to their hybrids. The cross between SGA and Cyto-178 showed the least fiber fineness (4.0). Fig. 3c represents the fiber fineness of all the genotypes and their hybrids.



Figure 3. (a) shows the low genetic parts of the SLH-8-Cyto-178 hybrid, while (b) shows the superior specific combining ability (SCA) of the VH-369-SLH-8 cross. (c) shows how the general and specific combining ability affect fiber fineness.



Figure 4. Principal component analysis of multitraits in cotton across various accessions

Biomterical analyses of economical traits of cotton

Principal component analysis (PCA)

Principal component analysis was performed on yield and fiber traits of selected cotton cultivars and their offspring hybrids. The biplot grouped the genotypes based on their performance. Biplot explained 31.5% variance in PC1 and 21.9% in PC2. PCA separated hybrids VH-369 × Cyto-178, SLH-8 × SGA, and Cyto-178 × VH-369 together; however, parents SGA, VH-369, and Cyto-178 grouped separately and were placed in the negative quadrant (Fig. 4). Overall, PCA showed that hybrids were performing better than parental genotypes. Dendrogram clustering and heat map of all parental and hybrid cotton genotypes are shown (Fig. 5).



Figure 5. Dendrogram Heat map of all the cotton genotypes for their yield and fiber traits.

Discussion

This study investigated the genetic basis of several key cotton breeding traits in various genotypes and their hybrids. The primary focus was on the role of non-additive gene action, which influences trait expression through complex interactions between alleles inherited from different parental lines.

Study revealed that non-additive gene action played a dominant role in determining fiber length, highlighting the importance of complementary interactions between alleles for this trait (Abdel-Aty et al., 2023; Fatima et al., 2022). Parental genotypes Cyto-178 and SLH-

8 exhibited high general combining ability (GCA) for fiber length. This suggests they possess favorable alleles that contribute to the development of longer fibers in their offspring (El-Mowafi et al., 2021). The superior performance of the Cyto-178 x SLH-8 hybrid further strengthens this notion, highlighting the positive impact of specific combining ability (SCA) on fiber length (Muthoni & Shimelis, 2020). Conversely, the short fiber length observed in the SLH-8 x Cyto-178 cross suggests potential incompatibility between these genotypes, resulting in adverse SCA effects (Van Eeuwijk et al., 2019).

These findings emphasize the importance of a two-pronged approach for breeding cotton varieties with longer fibers. Breeders can utilize GCA analysis to identify parents with a high potential to pass on desirable fiber length traits to their offspring. Subsequently, SCA analysis can be employed to assess the specific compatibility between chosen parents, thereby maximizing the likelihood of producing hybrids with even better fiber length through heterosis (the exploitation of favorable allele interactions).

Similar to fiber length, non-additive gene action played a significant role in determining fiber strength and fineness (El Hanafi et al., 2022; Latha et al., 2018). Parental genotype SGA exhibited high GCA for both fiber fineness and strength traits, suggesting it serves as a valuable donor of desirable alleles for breeding programs focused on improving fiber strength and fineness (Gul et al., 2019; Yu et al., 2020). However, the negative SCA of the VH-369 x SGA hybrid for fiber strength demonstrates the complex interplay of parental genotype interactions (Gaballah et al., 2022; Nyaga et al., 2020).

This suggests that it is needed to consider both GCA and SCA when selecting parents for breeding programs focused on fiber strength. Although SGA possesses favorable alleles for fiber strength based on GCA analysis, its negative SCA with VH-369 indicates that these alleles may not interact well with those from VH-369, resulting in offspring with weaker fiber quality traits. For fiber fineness, the positive SCA of the VH-369 x SGA hybrid suggests strong genetic complementarity between these genotypes, leading to offspring with finer fibers (Wahid, 2024; Wahid and Idrees, 2024).

This study underscores the importance of analyzing both GCA and SCA to identify compatible parental lines for breeding cotton with enhanced fiber strength and fineness. Breeders can leverage GCA analysis to identify parents with high potential for desirable fiber strength and fineness traits, followed by SCA analysis to assess compatibility and maximize the likelihood of producing offspring with these enhanced qualities.

Non-additive gene action also significantly influenced plant height and sympodial branch number (Fatima et al., 2022). SCA variance analysis revealed the significant impact of specific parental combinations on these traits (El-Mowafi et al., 2021). While parental genotypes VH-369 and Cyto-178 exhibited high GCA for plant height, the significantly higher SCA observed in particular crosses suggests specific allele interactions can further enhance this trait (Van Eeuwijk et al., 2019). For instance, crosses like SLH-8 x SGA and Cyto-178 x SLH-8 displayed higher SCA for sympodial branches, suggesting these combinations may produce offspring with a desirable increase in this trait (Begna, 2021a). While GCA analysis can be used to identify parents with a high potential for desirable plant height, a more nuanced approach is needed for sympodial branches. SCA analysis remains crucial for assessing compatibility and maximizing the likelihood of producing offspring with an increased number of sympodial branches. However, some crosses, such as those reported by Begna (2021a), showed a decrease in sympodial branches, indicating the potential involvement of specific genes that suppress this trait. Further research is needed to elucidate the underlying genetic mechanisms for these observations. Breeders may need to explore additional selection criteria beyond GCA and SCA, potentially including specific gene markers or physiological assessments, to optimize sympodial branch number in cotton breeding programs. This additional investigation could involve identifying and selecting parents with favorable alleles for genes known to promote sympodial branch development.

The analysis of boll number per plant, seed index, and boll weight revealed non-additive gene action as the primary driver of variation in these traits (El Hanafi et al., 2022; Latha et al., 2018). This indicates that the interactions between alleles inherited from different parental lines play a significant role in determining the number of bolls produced per plant, the number of seeds within each boll, and the overall weight of the bolls.

Parental genotypes SGA and VH-369 exhibited strong SCA for boll count, suggesting their potential value in breeding programs aiming to increase boll production (Nyaga et al., 2020). The positive SCA effect indicates that the specific combination of alleles from these parents leads to offspring with a higher number of bolls compared to the average of their performances. Conversely, the poor performance of the VH-369 x Cyto-178 hybrid emphasizes the importance of parental genotype compatibility for this trait. The adverse SCA effect suggests that the alleles from these parents may not interact well, resulting in offspring with lower boll production than expected.

Similar to boll count, SCA variance analysis highlighted the influence of parental interactions on seed index (El Hanafi et al., 2022). The VH-369 x Cyto-178 hybrid displayed the highest SCA value for seed index, indicating that this specific combination leads to offspring with a significantly higher number of seeds per boll compared to the average of their parents. This finding suggests the potential exploitation of heterosis (the increased expression of favorable traits in offspring) for seed count through strategic parental selection.

Boll weight also exhibited higher SCA variance compared to GCA variance, suggesting a strong role for parental genotype combinations in determining this trait (Latha et al., 2018). Interestingly, SGA and Cyto-178 displayed high SCA for boll weight. This indicates that the interaction between their alleles leads to offspring with heavier bolls compared to the average of their performances. These findings suggest that these genotypes can be valuable breeding resources for programs focused on increasing boll weight.

The findings of this study highlight the crucial role of considering both general combining ability (GCA) and specific combining ability (SCA) for practical breeding of cotton varieties with enhanced boll count, seed count, and boll weight (El Hanafi et al., 2022; Latha et al., 2018). Breeders can leverage a two-step approach to achieve this goal (Nyaga et al., 2020).

The initial step involves employing GCA analysis to identify parental lines that exhibit high GCA for the desired traits. These parental lines are likely to possess favorable alleles that can be transmitted to their offspring (El-Mowafi et al., 2021; Gul et al., 2019; Yu et al., 2020). For instance, genotypes SGA and VH-369 displayed strong GCA for boll count, suggesting their potential value in breeding programs aiming to increase boll production (Nyaga et al., 2020). Similarly, SGA emerged as a valuable donor for improving fiber strength and fineness based on its high GCA for these traits (Yu et al., 2020).

Following the identification of promising parental lines through GCA analysis, the next step involves evaluating their specific compatibility using SCA analysis. This analysis helps identify combinations that exhibit positive SCA effects, thereby maximizing the likelihood of producing offspring with superior boll count, seed count, and boll weight through heterosis —a phenomenon where offspring exhibit improved traits compared to the average of their parents (Wahid, 2024; Wahid & Idrees, 2024). The positive SCA effect observed in the SGA x VH-369 hybrid for boll count exemplifies this concept, indicating that the specific combination of alleles from these parents leads to offspring with a higher number of bolls compared to the average of their performances (Nyaga et al., 2020). Conversely, the adverse SCA effect observed in the VH-369 x Cyto-178 hybrid for boll count emphasizes the importance of parental genotype compatibility. This adverse effect suggests that the alleles from these parents may not interact well, resulting in offspring with lower boll production than expected (Van Eeuwijk et al., 2019).

This study underscores the critical role of non-additive gene action in determining key cotton breeding traits like fiber traits, boll count, seed count, and boll weight. This highlights the importance of considering both GCA and SCA for effective breeding programs. Breeders can leverage a two-step approach utilizing GCA analysis to identify parents with favorable alleles and SCA analysis to assess specific compatibility for maximizing heterosis. Implementing this strategy has the potential to develop cotton varieties with significantly improved yield through enhanced boll and seed production, as well as heavier bolls. However, further research is necessary to (1) identify the specific genes and quantitative trait loci (QTLs) underlying the observed non-additive gene action for these yield components. (2) Develop molecular markers linked to these genes and QTLs. These markers can then be used for marker-assisted selection in breeding programs, facilitating more efficient selection of desirable traits. (3) Investigate the potential for combining conventional breeding approaches with new technologies like genetic engineering. This could lead to the creation of cotton varieties with even greater improvements in yield-related traits, ultimately contributing to a more sustainable and productive cotton industry. By addressing these, plant breeders can utilize both conventional and advanced breeding techniques to create superior cotton varieties with enhanced yield potential and fiber quality.

Competing Interests

The authors declare that the research was conducted without any commercial or financial relationships that could be perceived as a potential conflict of interest.

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