

Generation Mean Analysis for Yield and Yield Contributing Characters in Okra (*Abelmoschus esculentus* L.)

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Abstract

The research aims to map genetic factors which determine okra yield and its associated characteristics to develop breeding methods which will produce stable results. The plant breeding community uses generation mean analysis (GMA) as an effective method to analyze quantitative trait genetic makeup because it enables them to calculate genetic effects through analyzing different generation means which result from a breeding cross. The article establishes okra yield and yield contributing character analysis through generation mean analysis principles which researchers tested across various studies from South Asia and other regions. The research discovered that okra yield traits depend on a complex combination of genetic factors which include both additive and non-additive gene effects with dominance and epistasis acting as major elements in addition to basic additive inheritance. The research results show how breeders should select between two methods which involve selection or hybridization for crop improvement. The article presents information about scaling tests and assessment of additive-dominance model effectiveness and common types of epistatic interactions and methods to use generation mean analysis findings in vegetable crop breeding decision-making.

Keywords: okra, additive dominance, quantitative inheritance, generation mean analysis, gene effects, epistasis

I. Introduction

The edible plant okra (*Abelmoschus esculentus* L.) plays a critical role in sustaining the dietary needs and agricultural practices of South Asia and West Africa and various tropical regions. The crop serves three different purposes as a vegetable for consumption and as a medicinal product and as a source of fiber and seed oil which results in greater nutritional value and economic importance than its size would suggest. The development of better okra crop yields has progressed at a slower pace than most similar vegetable crops because breeders lack complete understanding of genetic elements that determine crop performance in their breeding work.

The breeding program selection process requires clarity about which genetic mechanism operates in the target trait because it uses three options of genetic inheritance patterns that include additive gene action and dominance effects and epistatic interactions. Breeders who want to achieve better okra yield results need to follow the process of selecting superior plants from initial generations which will produce stable breeding outcomes. Life, unfortunately, is rarely that simple. Most yield traits in most crops involve some combination of additive and non-additive gene action, and untangling those contributions requires specific experimental designs and analytical tools.

Generation mean analysis is one of those tools. Developed formally by Hayman (1958) and Jinks and Jones (1958), and subsequently refined through decades of application across crops ranging from wheat to tomato, GMA uses the mean performance of a defined series of generations — parents (P_1 and P_2), the first filial generation (F_1), the second filial generation (F_2), and the first backcross generations (BC_1 and BC_2) — to estimate the components of genetic variance and test whether a simple additive-dominance model is sufficient to explain the data, or whether epistatic interactions are also necessary.

The practical value of this approach is hard to overstate. A breeder working with okra who knows that fruit yield in a particular cross is primarily additive can focus on pedigree selection in early segregating generations. One who discovers that dominance effects are large — and specifically, that heterosis is driving F_1 performance — is better served by investing in hybrid seed production systems. When epistasis dominates, the picture becomes more complex, and different types of epistasis (additive \times additive, additive \times dominance, dominance \times dominance) point toward different optimal strategies.

This article traces the application of generation mean analysis to okra, examines what the accumulated research has revealed about the genetic architecture of key traits, and discusses how those findings should inform breeding program design.

II. The Logic of Generation Mean Analysis

2.1 Setting Up the Generations

The classic generation mean analysis requires at least six generations from a cross between two contrasting parental lines: P_1 , P_2 , F_1 , F_2 , BC_1 (the backcross of F_1 to P_1), and BC_2 (the backcross of F_1 to P_2). Each generation has a defined expected genetic composition in terms of gene frequencies and levels of heterozygosity, and this known structure is what makes it possible to use the mean performance of each generation to solve for the underlying genetic parameters.

The simplest model — the additive-dominance model — uses just three parameters: the population mean (m), the additive effect (d), and the dominance effect (h). If this model fits the data adequately, it tells you that gene interactions between loci (epistasis) are either absent or small enough to ignore in that cross. When the model does not fit — when the observed generation means cannot be reconciled with the predictions of a three-parameter model — the researcher must expand to a six-parameter model that adds three epistatic components: additive \times additive (i), additive \times dominance (j), and dominance \times dominance (l).

Testing whether the simple model fits is done through scaling tests, most commonly the A, B, C, and D scales proposed by Mather and Jinks (1982). If any of these scales deviates significantly from zero, the additive-dominance model is considered inadequate and epistasis must be included. This is not just a statistical formality — the presence and type of epistasis detected has real biological meaning and real breeding consequences.

2.2 Why Six Generations and Not Fewer

A reasonable question is why breeders need all six generations rather than just, say, the parents and F_2 . The answer is that each generation contributes independent information about different components of the genetic architecture. The F_1 tells you directly about dominance through the degree of heterosis it shows over the parental midpoint. The F_2 gives you a segregating generation where all possible genotypic classes appear, reflecting the full range of additive and dominance effects. The backcross generations BC_1 and BC_2 are particularly informative because they have different gene frequencies from the F_2 — this difference is what allows the scaling tests to detect epistasis that would otherwise be confounded with the other effects.

Researchers sometimes work with fewer generations when resource constraints make a full six-generation design impractical. Three-generation analyses using P_1 , P_2 , and F_1 can estimate m , d , and h if epistasis is assumed absent. Five-generation designs dropping one backcross are also reported. These shortcuts are pragmatically useful but analytically weaker — they reduce the researcher's ability to detect and characterize epistasis, which, as the okra literature consistently demonstrates, is often present for yield traits (Jinks and Jones, 1958; Mather and Jinks, 1982).

III. Applying Generation Mean Analysis to Okra: Key Findings

3.1 Fruit Yield Per Plant

The main focus of okra improvement research studies on fruit yield per plant since it remains the most important trait for scientists to evaluate through generation mean analysis. The accumulated research leads to one conclusion that okra yield operates through multiple factors which combine with each other to create a total yield. All researched studies that evaluated the additive-dominance model for fruit yield found that scaling tests produced significant results which confirmed the existence of epistasis (Amoatey and Klu, 2000; Ariyo *et al.*, 2007; Kumar *et al.*, 2010).

When scientists apply the complete six-parameter model to analyze yield data they discover that dominance effects (h) which show strong statistical significance often surpass the size of additive effects (d). The high yield potential in okra F_1 hybrids shows substantial heterosis which Indian commercial seed companies have effectively used in their operations. Heterozygosity leads to higher yields because it typically creates positive dominance which helps to develop overdominance through the protection of harmful recessive alleles in individuals with heterozygous genotypes.

Epistatic effects, when present, tend to involve dominance \times dominance (l) interactions more frequently than additive \times additive (i) interactions for yield. This type of epistasis is sometimes called duplicate epistasis when the l component has the same sign as h , and complementary epistasis when they have opposite signs. Duplicate epistasis tends to slow genetic advance from selection because the favorable effects of dominance are partially canceled across loci — it suggests that the trait will respond poorly to simple selection but may show strong heterosis in hybrid combinations (Mather and Jinks, 1982; Singh and Chaudhary, 2004).

As illustrated in Figure 1, the relative magnitudes of estimated gene effects — additive, dominance, and various epistatic components — typically differ substantially across traits and across cross combinations in okra, underscoring why it is dangerous to assume a single genetic architecture applies to the species as a whole.

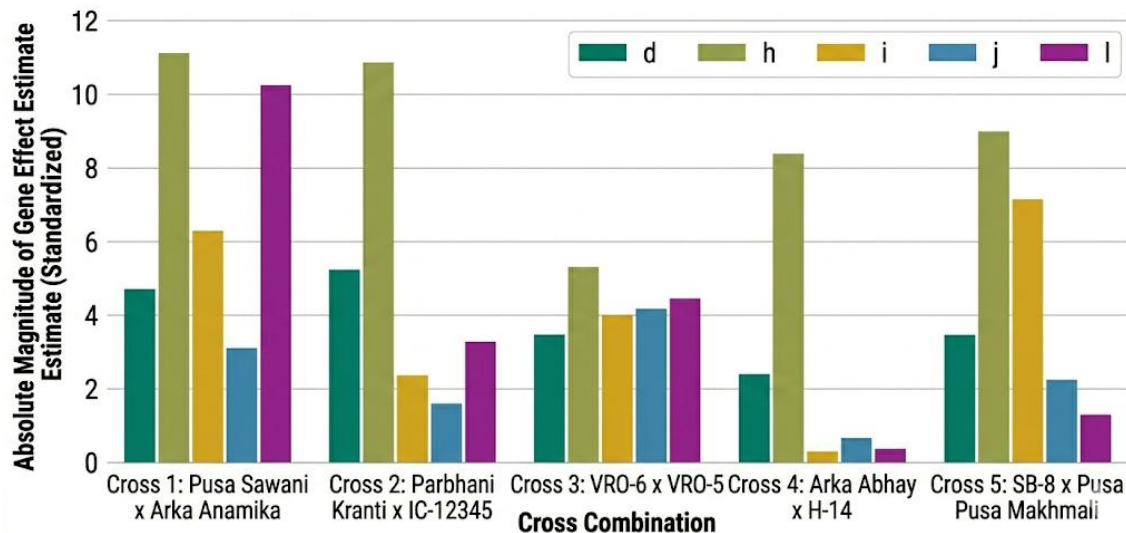


Figure 1: Estimated Gene Effect Magnitudes for Fruit Yield Per Plant Across Multiple Okra Cross Combinations — Additive, Dominance, and Epistatic Components

This grouped bar chart presents the estimated magnitudes of gene effects — additive (d), dominance (h), additive × additive (i), additive × dominance (j), and dominance × dominance (I) — for fruit yield per plant across five representative okra cross combinations drawn from published generation mean analysis studies. The vertical axis represents the absolute magnitude of each effect estimate (standardized to allow comparison across crosses), and each cross combination is represented by a cluster of five bars. Dominance effects are consistently the tallest bars across most crosses, with additive effects moderate in size. The epistatic components show high variability across cross combinations, with some crosses showing large I effect and others showing negligible epistasis. The key insight is that the relative importance of additive versus non-additive gene action varies considerably across specific cross combinations, meaning that genetic architecture cannot be assumed from species-level generalizations alone.

3.2 Number of Fruits Per Plant

The single most important yield component in okra exists through number of fruits which multiple scientists consider as the most vital yield component because this trait shows all three effects from branching pattern and fruiting duration and pod setting efficiency through a single measurable value. The results from generation mean analysis studies show that this particular trait exhibits complex genetic patterns which vary according to different cross combinations between genetic groups. Researchers typically find that high-yielding and low-yielding parental lines produce significant positive dominance effects which increase number of fruits in their offspring. The observation that okra F1 hybrids produce more fruits than their parents indicates that the genetic control of fruit number operates through either overdominance or strong directional dominance. The research by Reddy and his team at Reddy Institute of Technology from 2012 and Solanki and Dhaduk in 2009 found that dominance elements for this trait show strong presence while some crosses exhibit significant additive × additive epistasis which indicates duplicate gene interaction, which creates challenges during selection processes in segregating generations. The practical implication is that breeding for number of fruits per plant through conventional pedigree selection in F₂ and later generations may be less efficient than exploiting dominance through hybrid development. The presence of the additive component allows breeders to achieve better results through selection over multiple generations, but they need more cycles to obtain gains than what they anticipated at first.

3.3 Days to First Flowering

Days to first flowering is a trait with different genetic architecture than yield, and this difference shows up clearly in generation mean analysis results. Several studies have found that this trait fits the simple additive-dominance model adequately — in other words, scaling tests do not reveal significant epistasis for flowering time in many cross combinations (Ariyo *et al.*, 2007; Sharma and Sharma, 2011). When the model is adequate with just three parameters, additive effects for days to flowering are typically significant and often larger relative to dominance than is the case for yield traits.

This genetic architecture — predominantly additive, low epistasis — is actually the most favorable scenario a breeder can encounter. It means that selection for early or late flowering in segregating generations should be effective, that progress should be consistent across environments, and that lines fixed for desired

flowering time can be developed without the complications of heterozygosity-dependent performance. Early flowering is particularly desirable in many South Asian and African growing environments, where shorter crop duration allows double-cropping or escape from end-of-season drought stress. The genetic architecture of this trait, as revealed by generation mean analysis, directly supports selection-based strategies for improving it.

3.4 Plant Height and Internodal Length

The height of okra plants displays an engaging difference because it shows different growth patterns. Generation mean analysis studies for this trait frequently detect significant dominance and epistatic effects with the dominance direction being toward taller plants in many crosses which shows that tall stature hybrids between lines of different heights will produce hybrid vigor effects (Kumar *et al.*, 2010 and Patel *et al.*, 2014).

The distance between fruiting nodes along the stem depends on internodal length which shows most studies that investigate this trait exhibit non-additive genetic effects. Shorter internodes concentrate fruiting points which enables higher fruit density per unit stem length to develop — a trait that compact varieties which grow in high-density planting areas value. Dominance effects for internodal length show that hybrid varieties will succeed in short-term use of this characteristic (Solanki and Dhaduk, 2009).

IV. Scaling Tests and Model Adequacy

4.1 What Scaling Tests Actually Tell You

The four scaling tests — A, B, C, and D — test different aspects of how well the additive-dominance model fits the observed generation means. Scale A essentially compares BC_1 and F_2 in a way that should give zero if the model is adequate. Scale B does the same using BC_2 and F_2 . Scale C involves all six generation means. Scale D is derived from the others and tests specifically for the presence of additive \times additive epistasis.

When all four scales are non-significant, the researcher can confidently proceed with the three-parameter model. When one or more scales are significant, the researcher needs the six-parameter model — but also gains useful information about which types of epistasis are involved. Scale C significant but A and B non-significant, for instance, points toward dominance \times dominance (I) epistasis specifically. These distinctions matter for breeding because, as discussed, different types of epistasis have different implications for what breeding method will be most effective (Mather and Jinks, 1982).

Figure 2. summarizes the pattern of scaling test outcomes across a range of published okra generation mean analysis studies, illustrating how frequently each scale is found significant and for which traits the additive-dominance model most often breaks down.

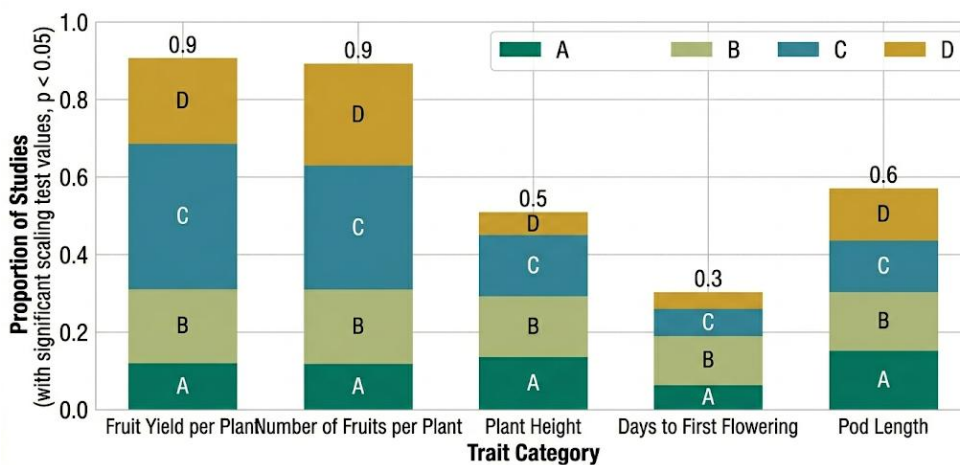


Figure 2: Frequency of Significant Scaling Test Outcomes (A, B, C, D) Across Published Okra Generation Mean Analysis Studies, by Trait Category

This stacked bar chart shows, for five trait categories in okra (fruit yield per plant, number of fruits per plant, plant height, days to first flowering, and pod length), the proportion of published generation mean analysis studies in which each of the four scaling tests — A, B, C, and D — was found statistically significant at $p < 0.05$. The horizontal axis lists trait categories; the vertical axis represents the proportion of studies (0 to 1.0) showing significant scaling test values. For fruit yield per plant and number of fruits per plant, scales C and D show the highest proportion of significant outcomes, indicating frequent dominance \times dominance and additive \times additive epistasis for these traits. Days to first flowering shows the lowest overall proportion of significant scales, consistent with its predominantly additive genetic architecture. The key insight is that model adequacy in okra varies systematically by trait, with yield traits far more frequently showing epistasis than developmental traits like flowering time.

4.2 The Six-Parameter Model: Estimation and Interpretation

When scaling tests indicate that epistasis is present, researchers move to the six-parameter model. Estimation typically uses weighted least squares regression, fitting the observed generation means to their expected values as functions of the six parameters (m, d, h, i, j, l), with weights inversely proportional to the variance of each generation mean. The resulting estimates — with their standard errors and significance tests — tell the breeder how large each component of the genetic architecture is and whether it is statistically reliable.

Interpreting the six-parameter model output requires some care. The j parameter (additive \times dominance epistasis) is relatively rarely significant in okra studies because it requires asymmetry between the two backcross generations — its detection depends on the specific allele frequencies in the parental lines and is therefore more cross-dependent than the other parameters. The l parameter (dominance \times dominance) is the most commonly significant epistatic component for yield traits, and its sign relative to h is particularly informative. When l and h have the same sign — both positive, pushing in the same direction — this is complementary epistasis, and it amplifies heterosis. When l and h have opposite signs — duplicate epistasis — they partially cancel, tempering the advantage of heterozygosity (Jinks and Jones, 1958).

V. Breeding Strategy Implications

5.1 When Additive Effects Dominate

Several okra traits, including days to first flowering, fruit length, and some quality characters, show predominantly additive genetic control in many cross combinations. For these traits, the breeding strategy is relatively straightforward. Early-generation pedigree selection, bulk selection, or single seed descent are all effective methods because additive variance is fixed progressively as lines are inbred. The gains from selection accumulate across generations and are retained in the homozygous lines that result.

A practical example: if a breeder wants to develop an okra variety that flowers five days earlier than current popular varieties in Bihar's short-season kharif window, and generation mean analysis confirms that days to flowering is primarily additive in relevant crosses, that breeder can confidently select early-flowering plants in F_2 and F_3 generations and expect to develop fixed lines that retain that earliness. The genetic architecture supports the strategy.

5.2 When Dominance and Epistasis Are Large

Yield traits, number of fruits per plant, and plant height in okra frequently show large dominance effects and significant epistasis. When this is the case, pure-line variety development through conventional selection faces real limitations — particularly if l effects are large and of opposite sign to h , creating that duplicate epistasis situation where the heterozygous advantage cannot be easily fixed in homozygous lines.

Under these circumstances, two alternative strategies gain appeal. Hybrid variety development is the more direct response to large dominance effects: if heterozygosity is what drives high performance, then the solution is to keep plants heterozygous through hybrid production, exploiting F_1 vigor in every generation rather than trying to fix it in inbred lines. India's okra hybrid seed market has grown substantially on exactly this biological foundation (Reddy *et al.*, 2012). The other option, reciprocal recurrent selection, aims to improve both parental populations simultaneously for combining ability — gradually shifting the allele frequencies in both lines toward combinations that produce stronger hybrids when crossed.

VI. Conclusion

Generation mean analysis has contributed substantially to our understanding of how yield and yield contributing traits are inherited in okra. The core finding — that these traits are governed by a mixture of additive, dominance, and epistatic gene effects, with dominance and epistasis often playing leading roles for yield per se — has direct and practical consequences for breeding program design.

Breeders working on okra improvement cannot assume that conventional selection in segregating generations will deliver rapid yield gains when the genetic architecture points so persistently toward non-additive control. Hybrid variety development, already commercially successful in India, has strong biological justification rooted in exactly the genetic findings that generation mean analysis has produced. At the same time, the additive components detected for many traits mean that population improvement and pedigree selection retain genuine value, particularly when the goal is to raise the overall mean performance of breeding populations rather than to exploit maximum heterosis in a specific cross.

What this field needs now is more systematic multi-cross studies, integration with modern genomic tools, and more attention to traits beyond yield — quality, nutrition, and stress tolerance among them. The analytical framework is robust and well-validated. The biological questions waiting to be answered through it are, if anything, growing more important as breeders face the dual challenge of increasing production and adapting to a more variable and difficult climate.

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