



Polygenic Variation-Components of Variance: Phenotypic, Genotypic, Environmental Variance, Heritability and Genetic Advance

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Quantitative genetics forms the cornerstone of modern plant and animal breeding, providing the theoretical and mathematical framework for understanding how complex traits are inherited and improved across generations. Central to this discipline is the concept of polygenic variation — the phenomenon whereby multiple genes, each of small individual effect, collectively govern the expression of continuously variable traits such as yield, height, seed weight, and disease resistance. This review provides a comprehensive analysis of the components of phenotypic variance, dissecting the total observed variation into its genotypic and environmental constituents. Within genotypic variance, the review elaborates upon additive, dominance, and epistatic variance components and their differential contributions to heritable variation. Particular emphasis is placed on heritability — both in the broad and narrow sense — as the pivotal parameter linking parental selection to offspring performance. The concept of genetic advance under selection is examined in relation to heritability, selection intensity, and genetic standard deviation, collectively forming the cornerstone of effective breeding programme design. This article synthesizes foundational theory with applied breeding perspectives and concludes with a discussion on contemporary molecular tools that complement classical variance component analyses. Understanding these components is indispensable for breeders aiming to maximize genetic gain per unit time and resource investment.

Keywords: Polygenic Inheritance, Phenotypic Variance, Genotypic Variance, Environmental Variance, Heritability, Genetic Advance, Additive Variance, Quantitative Traits, Plant Breeding.

Introduction

The inheritance of quantitative traits, those that show continuous variation in a population and are governed by multiple genes acting in concert with the environment, represents one of the most intellectually rich and practically consequential areas of genetics and plant breeding. Unlike qualitative traits, which are controlled by one or a few genes with large, discrete effects and follow simple Mendelian ratios, quantitative traits exhibit a bell-shaped normal distribution within populations, reflecting the additive action of numerous loci with individually small effects — a phenomenon formally described as polygenic inheritance. The theoretical framework for understanding polygenic variation was laid down in the early twentieth century through the pioneering contributions of Fisher (1918), who demonstrated mathematically that Mendelian genetics could account for the continuous inheritance of quantitative traits when multiple loci were considered simultaneously. This seminal work established the biometrical basis of quantitative genetics and introduced the foundational concept of variance partitioning — decomposing the total phenotypic variance observed in a population into genetic and non-genetic components. This review systematically examines the components of phenotypic variance, the concept and estimation of heritability, the

calculation and interpretation of genetic advance, and the interrelationships among these parameters in the context of quantitative plant breeding.

Polygenic Variation and Its Significance

Polygenic variation arises from the cumulative, and often interactive, effects of alleles at multiple loci distributed across the genome. The key characteristics of polygenic traits include continuous phenotypic variation, high sensitivity to environmental modification, and the absence of distinct phenotypic classes in segregating populations. Classic examples include kernel row number in maize, tillering ability in rice, boll weight in cotton, and oil content in groundnut. The genetic architecture underlying polygenic variation encompasses two broad categories of gene action: additive effects, in which each allele contributes an independent, predictable increment to the phenotype; and non-additive effects, which include dominance (interaction between alleles at the same locus) and epistasis (interaction between alleles at different loci). The relative importance of these gene action types profoundly influences the heritability of a trait and the choice of appropriate breeding methodology.

Components of Phenotypic Variance

The fundamental equation of quantitative genetics partitions total phenotypic variance (VP) into its constituent components. The basic partition is expressed as: $VP = VG + VE$, where VG represents genotypic variance — variation attributable to differences in genotype among individuals — and VE represents environmental variance — variation arising from differences in the environmental conditions experienced by individuals with identical or different genotypes. Genotypic variance is further resolved into three components. Additive genetic variance (VA) is the variance due to the average effects of individual alleles, representing the heritable component most directly exploited by selection. Dominance variance (VD) arises from interactions between alleles at the same locus, reflecting the departure from additivity due to dominance relationships. Epistatic variance (VI) encompasses all interaction effects between alleles at different loci and is subdivided into additive $\times$ additive (VAA), additive $\times$ dominance (VAD), and dominance $\times$ dominance (VDD) components. Thus the complete partition becomes: $VP = VA + VD + VI + VE$. Additionally, in some populations, genotype $\times$ environment interaction variance (VGE) is recognized as a significant component, reflecting differential genotypic responses across environments. This interaction is particularly critical in multi-environment trials and is central to the concept of phenotypic stability in plant breeding.

Estimation of Variance Components

Variance components are estimated from the mean squares obtained in analyses of variance (ANOVA) of appropriate genetic designs. The most commonly employed designs include the parent-offspring regression, half-sib and full-sib family analyses, North Carolina Designs I, II, and III, and the diallel cross analysis. In each design, specific combinations of variance components can be estimated by equating observed mean squares to their expected values expressed in terms of VA, VD, and VI. For practical plant breeding purposes, the generation mean analysis, developed by Hayman and Jinks, allows the estimation of additive (d), dominance (h), and epistatic (i, j, l) parameters from the means of parental, F1, F2, and backcross generations. This approach is widely used for initial assessment of gene action before embarking on more elaborate biometrical designs. In the era of molecular markers, genomic tools such as genome-wide association studies (GWAS) and genomic selection further enable the dissection of polygenic variance at the level of individual marker loci.

Heritability — Concept, Types, and Estimation

Heritability is arguably the most important single parameter in quantitative genetics, as it quantifies the proportion of phenotypic variation that is attributable to genetic differences among individuals in a specific population under defined environmental conditions. Two forms of heritability are recognized: broad-sense heritability (H^2 or h^2_B) and narrow-sense heritability (h^2 or h^2_N).

Broad-sense heritability (H^2) is defined as the ratio of total genotypic variance to total phenotypic variance: $H^2 = VG / VP = (VA + VD + VI) / VP$. It represents the degree to which phenotype reflects genotype in its entirety and is relevant for vegetatively propagated crops and inbred lines, where the entire genotypic variance is fixed and transmitted intact to progeny.

Narrow-sense heritability (h^2) is defined as the ratio of additive genetic variance to total phenotypic variance: $h^2 = VA / VP$. It is the more relevant measure for cross-pollinated crops and segregating populations undergoing pedigree or mass selection, as it reflects only the portion of genetic variance that responds predictably to selection — the breeding value component. Narrow-sense heritability ranges from 0 (no additive genetic basis) to 1 (all phenotypic variation is additive genetic), and its magnitude determines the efficiency of selection-based improvement.

Heritability estimates are influenced by population structure, the range of environments sampled, and the trait under study. Traits closely associated with fitness, such as reproductive output, tend to show lower heritability than morphological or compositional traits, reflecting greater evolutionary pressure on the former. In applied breeding, heritability values above 0.50 are generally interpreted as high and indicative of effective selection response; values between 0.20 and 0.50 are considered moderate; and values below 0.20 suggest that environmental effects predominate and that progeny testing or recurrent selection may be more appropriate than individual plant selection.

Genetic Advance — Theory and Application

Genetic advance (GA) refers to the improvement in mean phenotypic value of a trait expected in the selected population relative to the original population after one cycle of selection. It is a composite function of three parameters: selection intensity (i or k), phenotypic standard deviation (σ_P), and narrow-sense heritability (h^2). The formula is expressed as: $GA = i \times h^2 \times \sigma_P$, where i is the standardized selection differential corresponding to the proportion of individuals selected (e.g., $i = 2.06$ for selecting the top 5% of a population). Genetic advance as a percentage of the mean (GA%) is routinely computed to facilitate comparison across traits measured on different scales: $GA\% = (GA / \bar{x}) \times 100$, where $\bar{x}$ is the population mean. This standardized measure is particularly informative when evaluating the potential for improvement in traits such as yield components, where absolute values vary widely across crop species and environments. High heritability with low genetic advance suggests the presence of significant non-additive variance (dominance or epistasis), favouring heterosis-based breeding or recurrent selection schemes. Low heritability with high genetic advance, though relatively rare, may indicate that epistatic interactions contribute substantially to phenotypic expression, necessitating biparental mating designs to recombine favourable allele combinations.

Environmental Variance and Genotype $\times$ Environment Interaction

Environmental variance (VE) encompasses all phenotypic variation not attributable to genotypic differences, including systematic effects of soil fertility gradients, micro-climatic variation, pest and disease pressure differentials, and random measurement error. The partition of VE into predictable (systematic) and unpredictable (random) components has practical implications for experimental design — systematic environmental effects are controlled through blocking and replication, while random error is minimized through precision in measurement and standardization of cultural practices. Genotype $\times$ environment interaction (G $\times$ E) represents a particularly important component of variance in multi-location trials, as it determines the consistency of genotypic performance across diverse environments. High G $\times$ E interaction reduces the reliability of selection decisions made in one environment for performance in others and necessitates multi-environment testing for the identification of stable, broadly adapted varieties. Statistical tools including AMMI (Additive Main Effects and Multiplicative Interaction) analysis and GGE biplot methodology are widely employed to quantify and graphically represent G $\times$ E interactions in plant breeding programmes.

Authors' Perspectives

From the perspective of the authors, the classical framework of variance component analysis remains indispensable in contemporary plant breeding, despite the transformative advances brought about by molecular markers and genomic technologies. The fundamental equations partitioning phenotypic variance into additive, dominance, epistatic, and environmental components provide the logical scaffolding upon which all quantitative breeding decisions rest, whether those decisions are made using phenotypic data alone or in combination with genomic information. The authors emphasize that heritability is a population- and environment-specific parameter, and its misinterpretation as an intrinsic property of a trait — rather than a ratio contingent upon the genetic and environmental context of estimation — remains a persistent source of confusion in applied breeding programmes. Breeders must exercise caution in extrapolating heritability estimates obtained in one population or environment to guide selection decisions in different genetic backgrounds or agro-climatic zones. Investment in multi-location, multi-season trials for reliable estimation of variance components and heritability across target environments is strongly advocated.

Conclusion

The components of variance framework — encompassing phenotypic, genotypic, and environmental variance — constitutes the bedrock of quantitative genetics and applied plant breeding. The partitioning of phenotypic variation into its constituent sources enables breeders to understand the genetic architecture of complex traits, predict the response to selection, and design efficient breeding strategies aligned with specific improvement objectives. Heritability as the of additive genetic variance to total phenotypic variance, serves as the pivotal indicator of selection efficiency, while genetic advance quantifies the expected improvement per selection cycle under defined conditions. As agriculture confronts increasing environmental uncertainty driven by climate change, the accurate characterization of genotype $\times$ environment interaction and environmental variance assumes greater urgency. Breeders who master the theory and application of variance components are equipped to design robust, efficient, and resource-optimal breeding programmes capable of delivering sustained genetic gain in the face of complex biotic and abiotic challenges. The intellectual legacy of quantitative genetics, built upon the mathematical elegance of variance partitioning, continues to illuminate the path toward a more productive and resilient agricultural future.

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