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Quantitative evaluation of yield components and their genetic control in bread wheat

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ABSTRACT

Enhancing grain yield in bread wheat (Triticum aestivum L.), a major staple food crop worldwide, is a primary goal of contemporary plant breeding programs. Grain yield is a complex quantitative character influenced by several interrelated traits, including plant height, tiller number, spike length, spikelets per spike, grains per spike, thousand-grain weight, and harvest index. A clear understanding of the genetic mechanisms controlling these traits such as heritability, gene action, and genetic advance is vital for effective selection and yield improvement. Recent developments in molecular breeding have significantly improved the accuracy of wheat improvement through the use of quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), genomic selection (GS), marker-assisted selection (MAS), and high-throughput phenotyping. However, wheat breeding still faces challenges, including strong environmental effects, limited genetic variability, trade-offs among yield components, and the complex regulation of gene networks. Future breeding efforts are expected to benefit from advanced tools such as CRISPR/Cas-based genome editing, the utilization of wild and exotic germplasm, and the integration of phenomics with genomics and machine-learning approaches. The combined application of conventional breeding methods and modern biotechnological strategies offers promising opportunities for developing high-yielding, stable and stress-tolerant wheat cultivars to meet the rising global food demand.

Keywords: Wheat yield, Quantitative traits, QTL mapping, GWAS,Genomic selection,Marker-assisted selection

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Introduction

Wheat is utilized as a basic input for various industrial productsand as animal feed. Increasing wheat productivity is essential to ensuring food security because thethe global population is expected to reach 9.8 billion by 2050 (Fischer, 2011). Although wheat is grown in a variety of agro climatic zones, abiotic stresses such as heat, salinity, and drought often reduce the yield potential of wheatlike heat, salinity, and drought frequently limit the crop's potential yield (Reynolds et al., 2009). Therefore, in order to breed high-yielding and stress-resistant wheat varieties, it is crucial to comprehend the factors that affect wheat yield. Wheat grain yield is a quantitative trait that is influenced by environmental factors and controlled by multiple genes, or polygenes. The number of tillers per plant, spike length, spikelet per spike, grains per spike, and thousand-grain weight (TGW) are all factors that contribute to yield (Singh et al., 2013).

Selection is difficult because grain yield varies continuously due to its polygenic nature. Additionally, the inheritance of yield is complicated by interactions between genotype and environment, since the same genotype can show variable performance under different environmental conditions (Yan & Tinker, 2006). As a result, choosing its constituent parts is frequently more successful than direct selection for grain yield.

Breeders can find traits exhibiting high heritability and stable genetic regulation that show good response to selectionby examining individual yield components (Allard, 1999). For instance, characteristics like thousand-grain weight and grains per spike frequently exhibit high heritability and additive gene action, which makes them appropriate candidates for early-generation selection (Khan et al., 2015). However, characteristics like tiller number and grain yield per plant are more affected by the environment and may need to be improved through multi-location testing or molecular techniques (Chandra et al., 2017). Designing ideotypes or breeding techniques to increase overall yield also benefits from an understanding of trait correlations and genetic architecture.

This review's primary goals are to provide an overview of bread wheat's main yield components and how they affect grain yield, to explain these traits' genetic regulation, heritability, and gene action, to highlight quantitative and molecular methods for studying yield components, such as GWAS and QTL mapping and offer suggestions for breeding techniques that improve wheat stability and productivity in changing conditions.

Major Yield Components in Bread Wheat

Grain yield in wheat is influenced by several interconnected components, each contributing differently to the final output. A clear understanding of these components is essential for developing efficient breeding strategies.

Plant Height: Plant height has a significant influence on wheat productivity by regulating biomass production, resistance to lodging, and the distribution of assimilates within the plant. Semi-dwarf cultivars introduced during the Green Revolution, which possess the dwarfing genes Rht-B1 and Rht-D1, showed reduced lodging and a higher harvest index, ultimately leading to increased grain yields (Hedden, 2003). Although taller plants tend to accumulate greater biomass, they are more susceptible to lodging, which negatively affects harvestable yield. Therefore, selecting plants with moderate height is generally considered optimal for achieving a balance between growth, stability, and yield potential (Fischer, 2011).

Number of Tillers: The number of fertile tillers per plant plays a crucial role in determining spike density and total grain number per unit area. While an increase in tiller number can enhance yield potential, excessive tillering often results in increased competition among tillers, leading to a reduction in individual grain size and weight (Mollasadeghi et al., 2012). Tiller development is strongly influenced by environmental conditions such as nutrient availability, planting density, and water stress. Consequently, breeding efforts focus on identifying genotypes that can maintain an optimal number of productive tillers under diverse environmental conditions.

Spike Length: Spike length is closely linked to the number of spikelets per spike and, as a result, influences the potential number of grains. Longer spikes are capable of supporting a greater number of spikelets and grains, thereby contributing to improved yield potential (Sial et al., 2010). This trait generally exhibits moderate heritability and can be effectively utilized in breeding programs as an indirect selection criterion for yield improvement.

Spikelet per Spike: The number of spikelets per spike directly affects a plant's capacity to produce grains. In general, an increase in spikelet number allows for the formation of more grains per spike, making this trait an important target for yield enhancement (Aydogan et al., 2020). However, the actual grain number per spike is also influenced by environmental factors, nutrient supply, and pollination efficiency.

Grains per Spike: Grains per spike is one of the most important traits contributing to grain yield in wheat. This trait typically shows high heritability and is largely controlled by additive genetic effects (Khan et al., 2015). Increasing the number of grains per spike leads to a direct improvement in grain yield without substantially affecting grain size, making it a key focus in breeding programs aimed at developing high-yielding wheat varieties.

Thousand-Grain Weight (TGW): Thousand-grain weight reflects grain size and weight and has a substantial impact on final yield. TGW is a stable and highly heritable trait, predominantly controlled by additive gene effects (Ali et al., 2008). This trait can offset lower grain numbers in certain genotypes, making it essential for maintaining yield stability, particularly under stress conditions such as drought or heat (Kumari, 2022).

Harvest Index (HI): Harvest index refers to the proportion of total above-ground plant biomass that is converted into economic yield, particularly grains. It reflects how efficiently a plant allocates photosynthates toward grain formation rather than vegetative growth. A higher harvest index indicates more effective partitioning of assimilates to reproductive organs. Traits such as plant height, number of tillers, and spike development play a significant role in determining HI. Selecting and breeding genotypes with an optimal harvest index can enhance grain yield while maintaining balanced plant growth.

Genetic Control of Yield Components

Grain yield and its associated traits in wheat are complex in nature and are governed by numerous genes along with their interactions with environmental conditions. Gaining insight into the genetic regulation of these traits is crucial for developing efficient breeding and selection strategies.

Quantitative Nature of Traits

Most yield-associated characteristics in wheat, such as tiller number, spike length, grains per spike, and thousand-grain weight, are quantitative traits controlled by multiple genes. These traits do not follow simple Mendelian inheritance patterns; instead, they show continuous variation within populations. Their expression is influenced by additive, dominance, and epistatic gene effects, which makes direct selection for overall yield more difficult. Consequently, focusing on individual yield components often provides a more effective approach than selecting for grain yield alone.

Heritability (Broad and Narrow Sense)

Heritability measures the extent to which observed variation in a trait is due to genetic factors. It is commonly expressed in two forms. Broad-sense heritability includes all genetic contributions, such as additive, dominance, and epistatic effects, and provides an overview of total genetic influence on a trait. Narrow-sense heritability represents the proportion of variation attributable only to additive genetic effects, which are directly exploitable through selection. Traits like grains per spike and thousand-grain weight often show high heritability, indicating strong genetic control and better selection response. In contrast, traits such as tiller number and grain yield per plant are more influenced by environmental conditions and usually display moderate to low heritability (Kumari et al., *2022*a*)*.

Genetic Advance and Selection Potential

Genetic advance refers to the expected improvement in a trait achieved through selection across generations. It is closely associated with heritability. Traits that exhibit both high heritability and high genetic advance, such as thousand-grain weight and grains per spike, are primarily governed by additive gene effects and respond well to selection. Conversely, traits with low heritability and low genetic advance are strongly affected by environmental factors, making selection less effective. Evaluating heritability alongside genetic advance helps breeders identify the most promising traits for yield improvement.

Additive vs. Non-Additive Gene Action

Additive gene action occurs when the effects of individual alleles accumulate to influence trait expression. Traits controlled mainly by additive effects respond efficiently to selection, particularly in early generations, such as thousand-grain weight and grains per spike.Non-additive gene action: Includes dominance and epistatic effects. Traits controlled by non-additive genes often require hybridization, recurrent selection, or exploitation of heterosis to achieve improvement (Comstock & Robinson, 1952). Recognizing the type of gene action is crucial for developing appropriate breeding strategies.

Genotype × Environment (G×E) Interaction

Genotype × Environment (G×E) interaction refers to the phenomenon where different genotypes respond differently under changing environmental conditions. This variation makes selection more challenging because a genotype that performs well in one environment may show poor performance in another (Yan & Tinker, 2006). To overcome this issue, plant breeders commonly conduct multi-environment or multi-location trials to identify genotypes that consistently perform well and show stability across environments. In addition, modern tools such as QTL mapping and genomic selection help predict genotype performance under diverse environmental conditions, thereby minimizing the negative impact of G×E interactions (Crossa et al., 2017).

Advances in Genetic Dissection of Yield Components

Recent progress in molecular genetics and genomics has greatly improved wheat breeding by enhancing understanding of the genetic mechanisms controlling yield-related traits. Earlier breeding approaches mainly depended on phenotypic selection, which is laborious, time-consuming, and strongly affected by environmental variation. In contrast, contemporary breeding strategies such as QTL mapping, genome-wide association studies (GWAS), genomic selection (GS), marker-assisted selection (MAS), and high-throughput phenotyping (HTP) allow breeders to improve yield components with greater accuracy, speed, and efficiency.

QTL Mapping for Yield Traits

Quantitative Trait Loci (QTL) mapping is used to locate specific genomic regions linked to traits of interest by studying segregating populations. Numerous QTLs influencing thousand-grain weight (TGW), grain number per spike, spike length, and plant height have been identified in different wheat populations (Griffiths et al., 2009). For example, major QTLs for TGW have been reported on chromosomes 2D, 5A, and 7A, while QTLs controlling grains per spike have been mapped on chromosomes 3A and 4D.QTL mapping enables breeders to identify beneficial alleles and develop effective marker-assisted selection strategies. The combined effect of multiple QTLs can contribute additively, leading to improved grain yield stability across a range of environments (Cuthbert et al., 2008).

Genome-Wide Association Studies (GWAS)

Genome-wide association studies (GWAS) utilize natural genetic variation present in diverse germplasm to establish associations between genetic markers and phenotypic traits. Unlike traditional QTL mapping, GWAS does not rely on biparental populations and captures a broader spectrum of allelic diversity from breeding lines and landraces. GWAS has successfully identified important markers associated with thousand-grain weight, grains per spike, spike length, and tiller number, allowing breeders to uncover novel and previously underutilized alleles (Juliana et al., 2019). Integrating GWAS with QTL mapping strengthens the reliability of marker-trait associations and supports the development of precision breeding strategies.

Genomic Selection (GS)

Genomic selection estimates the breeding potential of individuals by using markers spread across the entire genome. This approach is particularly valuable for complex traits such as yield, which are controlled by many genes with small individual effects that together influence performance. One major advantage of genomic selection is that it shortens the breeding cycle by allowing breeders to choose superior genotypes without relying heavily on detailed phenotypic evaluation. It also identifies small-effect alleles that are often overlooked by marker-assisted selection (MAS), resulting in higher selection precision and greater genetic improvement over time. In wheat breeding programs, genomic selection has successfully been used to enhance yield, grain quality, and tolerance to various stresses at the same time.

Marker-Assisted Selection (MAS)

Marker-assisted selection uses DNA markers associated with important genes or quantitative trait loci (QTLs) to enable early and accurate selection. This method works best for traits with high heritability, such as thousand-grain weight, plant height, and resistance to diseases. It is especially effective when traits are controlled by a small number of major QTLs, allowing selection to be carried out before the trait is fully expressed. When combined with conventional breeding methods, MAS speeds up the development of high-yielding crop varieties, lowers the cost of field evaluations, and allows breeders to select for several traits simultaneously.

Integration of Genomics and Phenotyping

The integration of QTL or GWAS analysis, genomic selection, and high-throughput phenotyping helps breeders detect and confirm genes responsible for yield-related traits. This combined approach supports the design of ideal plant types with balanced trait combinations and assists in selecting stable, high-performing genotypes across different environments. Recent research shows that combining genomic information with phenotypic data can lead to significantly higher genetic gains in yield compared to using traditional selection methods alone (Kumari et al., *2022b)*.

Breeding Implications

A thorough understanding of the genetic control and relationships among yield components is essential for guiding wheat breeding programs. Efficient breeding strategies depend on selecting appropriate traits, combining classical and modern approaches, and evaluating genotypes across diverse environments.

Selection Based on High-Heritability Traits

Breeding programs are most effective when selection focuses on traits with high heritability and genetic advance, as these traits respond predictably to selection. In wheat, traits such as thousand-grain weight (TGW), grains per spike, and spike length consistently exhibit high heritability (Khan et al., 2015; Singh et al., 2013). Selecting for these traits, especially in early generations, can efficiently improve grain yield because additive gene action predominates, making genetic gains more reliable (Kumari and Sharma, 2022a)

Multi-Environment Testing

Traits with moderate to low heritability, such as tiller number or grain yield per plant, are strongly influenced by environmental factors (Kumari and Sharma, 2022b). Multi-environment trials are therefore crucial to identify stable and high-performing genotypes (Kumari and Sharma, 2021 and Yan & Tinker, 2006). Evaluating genotypes across different locations and seasons allows breeders to:

Assess genotype × environment interactions.

Identify varieties adapted to target regions.

Reduce the risk of releasing genotypes that perform well only under specific conditions. This approach is particularly important in wheat, as environmental stresses like drought, heat, and soil fertility can significantly affect yield components.

Hybridization and Ideotype Breeding

Hybridization remains a key strategy in wheat breeding, enabling the combination of favorable alleles from different parents. Ideotype breeding focuses on designing plant types with optimal trait combinations, such as:

Moderate plant height to improve lodging resistance.

Optimal tiller number.

Long spikes with high grain numbers per spike.

High TGW.

By crossing parents with complementary traits, breeders can develop lines that combine multiple desirable characteristics, enhancing grain yield and adaptability (Fischer, 2011; Reynolds et al., 2009). Hybridization also allows exploitation of non-additive gene action, which is important for traits influenced by dominance or epistasis.

Integration of Classical and Molecular Approaches

Modern wheat breeding increasingly combines traditional phenotypic selection with molecular tools. For instance:

Marker-assisted selection (MAS): Enables precise selection for major genes controlling yield components.

Genomic selection (GS): Predicts polygenic traits such as yield, reducing breeding cycles (Crossa et al., 2017).

High-throughput phenotyping (HTP): Provides accurate measurements of traits under field conditions (Araus & Cairns, 2014).

Integrating classical and molecular approaches ensures that breeders can target both major and minor effect genes, improve selection accuracy, and accelerate the development of high-yielding and stable wheat varieties.

Challenges in Improving Yield Components

Improving yield components in bread wheat is a complex process due to the interplay of genetic, environmental, and physiological factors. Despite significant advances in breeding and molecular genetics, several challenges continue to limit the efficiency of selecting high-yielding varieties.

Environmental Influence

Environmental conditions, such as temperature, rainfall, soil fertility, and water availability, strongly influence the expression of yield components. Traits like tiller number, grains per spike, and spikelets per spike are particularly sensitive to environmental fluctuations, resulting in variable performance across different locations and seasons (Yan & Tinker, 2006). These genotype × environment interactions make it difficult to identify stable, high-yielding genotypes. Breeders often rely on multi-location trials and advanced modeling approaches to account for environmental variability.

Limited Genetic Variability

Genetic variability is the foundation of successful selection, yet modern wheat cultivars often have a narrow genetic base, particularly among elite breeding lines, due to repeated use of similar parents (Tanksley & McCouch, 1997). This limited diversity constrains the potential to improve key yield components, such as grain number, spike length, and harvest index. To overcome this limitation, breeders incorporate wild relatives, landraces, and exotic germplasm to introduce new alleles and broaden the genetic base.

Trait Trade-Offs

Enhancing one yield component can sometimes negatively impact another due to physiological or genetic trade-offs. For example: Increasing grains per spike may reduce thousand-grain weight (TGW) because of competition for assimilates. Excessive tillering may result in smaller grains or delayed maturity (Fischer, 2011).

Breeders must carefully balance improvements across traits to optimize overall grain yield and stability, rather than focusing on individual components in isolation.

Complexity of Gene Networks

Yield components are controlled by polygenic networks involving additive, dominance, and epistatic interactions. Genes influencing different traits often interact in complex ways, making it challenging to predict the outcome of selection (Griffiths et al., 2009). For instance, QTLs for grain number may interact with QTLs for spike length or TGW, and environmental factors may further modulate these effects. Fully understanding these networks requires integrating molecular tools, genomic selection, and precise phenotyping, yet the complexity remains a major bottleneck in wheat improvement.

Future Prospects: Recent advances in genomics, phenomics, and computational tools are creating new opportunities to improve yield components in wheat. Combining these modern technologies with traditional breeding approaches promises faster development of high-yielding, stress-resilient varieties.

CRISPR/Cas Gene Editing

CRISPR/Cas technology allows precise modification of specific genes that control yield-related traits. In wheat, CRISPR has been successfully applied to alter genes affecting plant height, spikelet number, and grain size (Zhang et al., 2019). This method enables breeders to introduce beneficial alleles or eliminate negative regulators without inserting foreign DNA, making it faster and more precise than conventional breeding. CRISPR also offers the potential to improve complex traits like yield by targeting multiple genes simultaneously.

Use of Wild and Exotic Germplasm

Wild wheat relatives and traditional landraces represent an important reservoir of genetic diversity for yield-related traits, resistance to diseases, and tolerance to non-living environmental stresses. Introducing genes from these sources into elite wheat varieties can broaden the genetic base, address the constraints of modern breeding, and improve characteristics such as grain number per spike, tillering capacity, and harvest index. The use of advanced molecular approaches, including marker-assisted selection and genomic selection, has greatly improved the efficiency of incorporating exotic germplasm into breeding programs.

Machine Learning and Predictive Breeding–Rewritten

Machine learning (ML) and artificial intelligence are increasingly applied to predict the performance of plant genotypes by processing large datasets that include genetic, phenotypic, and environmental information. These techniques are capable of uncovering complex relationships within data, identifying superior high-yielding genotypes, and refining breeding decision-making processes. When genomic data are integrated with phenotypic observations, ML enhances the speed and precision of modern breeding and increases the accuracy of selection for traits controlled by many genes.

Integration of Phenomics and Genomics

The combination of high-throughput phenotyping (phenomics) with genomic data enables breeders to simultaneously assess observable plant traits and underlying genetic potential. Modern tools such as drone-based imaging systems, LiDAR, and spectral sensors allow rapid measurement of traits including biomass, canopy temperature, and growth behavior. These phenotypic measurements can then be connected to genomic markers through QTL analysis or genomic selection, supporting the identification of genotypes that show high yield performance and stability across different environmental conditions.

Conclusions

Grain yield in bread wheat is a complex quantitative trait influenced by many genes as well as environmental conditions. Key yield-related traits such as plant height, tiller number, spike length, spikelets per spike, grains per spike, thousand-grain weight, and harvest index play an essential role in enhancing wheat productivity. Traits with high heritability and additive genetic effects, including grains per spike and thousand-grain weight, provide strong opportunities for selection, whereas traits that are highly affected by environmental factors require multi-location evaluation to ensure consistent performance.

Recent progress in genetic analysis techniques, including QTL mapping, genome-wide association studies (GWAS), genomic selection, and marker-assisted selection, has supplied powerful approaches for understanding and improving the genetic control of yield components. In addition, high-throughput phenotyping enables fast and accurate assessment of complex traits, further increasing breeding efficiency.

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