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GENE ACTION AND COMBINING ABILITY IN WHEAT FOR DROUGHT TOLERANCE

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ABSTRACT Wheat (*Triticum aestivum* L.) is a globally vital cereal crop, yet its productivity is increasingly constrained by drought stress, particularly in arid and semi-arid regions. Climate change intensifies this challenge, making the development of drought-resilient cultivars a critical breeding priority. Understanding the nature of gene action and combining ability underlying adaptive and yield-related traits is fundamental to genetic improvement. Quantitative genetic approaches, such as Line × Tester analysis, help distinguish between additive and non-additive gene effects, guiding the choice of breeding strategies. Additive gene action, associated with general combining ability (GCA), governs traits with high heritability such as relative water content (RWC) and cell membrane thermostability (CMT), enabling efficient selection in early segregating generations. Conversely, dominance and epistatic effects, reflected by specific combining ability (SCA), predominate in complex yield traits, emphasizing the value of heterosis and hybridization under stress conditions. Genetic variability derived from landraces, synthetic hexaploids, and elite cultivars provides essential allelic diversity for drought adaptation and water-use efficiency. Integrating conventional selection with molecular and physiological tools accelerates the identification of superior parents and hybrids. This review highlights that exploiting both additive and non-additive gene actions through balanced selection and hybrid breeding is key to achieving climate-resilient wheat improvement. Such integrative strategies ensure yield stability and sustainability in the face of global climate variability.

Keywords: *Variability; Heritability; Hybridization; Adaptation; Physiology; Selection*

INTRODUCTION

Wheat (Triticum aestivum L.) is one of the most ancient and widely cultivated cereals in the world, forming a basis for human civilization and food systems. It is an allopolyploid, self-fertilizing species (2n = 6x = 42) belonging to the family Poaceae. It is a very important component in the human diet, supplying carbohydrates, protein, and vitamins and minerals. Approximately 220 million hectares are planted to wheat each year, which is harvested at a total production of over 780 million metric tons. Wheat ranks second only to maize in terms of world grain crops. The distribution of wheat on such distinct ecological zones as the temperate plains or highlands indicates the wide genetic variability and agronomic adaptability of the species (Ikram et al. 2020, Rauf et al. 2023, Vadez et al. 2024).

In nutritional value, wheat kernels contain 70-75% carbohydrates, 10-15% protein, 2% lipids, and various essential micronutrients (iron, zinc, selenium) and vitamins (B-complex vitamins). These components cause wheat to be an indispensable food source for humans and as a feed source for livestock. It is widely consumed in the form of bread, chapatti, noodles, and other products and is the prime source of calories for more than 2.5 billion people of the world. Wheat straw also serves a very important by-product for feed and as a mulching material to promote sustainability of agricultural systems (Guo et al. 2016, Bilgrami et al. 2020).

Challenges to Wheat Productivity under Changing Climatic Conditions

Climate change has emerged as one of the key challenges affecting global agro-systems of food production, with wheat as a predominant cool season crop being particularly sensitive to abiotic stresses. The Intergovernmental Panel on Climate Change (IPCC, 2023) predicts that a temperature increase of 2-3C in mean temperature of South Asia by 2050 will be accompanied by erratic rainfall and prolonged periods of drought. Such climatic aberrations can seriously affect the phenological stage as well as the photosynthetic efficiency and senescent period of the plants, causing serious reduction in yields (Figure 1).

Among the various abiotic stresses, the drought and heat stress are the most deleterious to wheat productivity. Drought affects 50% approximately of the global area under wheat crop but especially in the arid and semi-arid regions such as the Southern Punjab of Pakistan which leads to osmotic stress, decrease turgor of cells, interference with nutrient uptake and metabolic processes disturbances. At the critical stages of growth such as tillering, anthesis and grain filling the plants are at the short end of moisture and drougth leading to decreased number of spikes, poor grain set and shriveled grain. In the same way the heat stress especially at the anthesis and grain filling stages brings about pollen sterility, low grain weights and low harvest indices (Qin et al. 2016, Mehraban et al. 2019).

Genetic Improvement for Sustainability under Climate Variability

The mounting pressures of climate change, resource depletion and population growth make it crucial that continued genetic improvement of wheat is undertaken. The classical methods of increasing yields based most especially on the use of fertilizers and irrigation have reached biological and environmental ceilings. Consequently, breeding for genetic vigour is now the mainstay of modern wheat improvement programmes (Figure 2). The approach to genetic improvement is concerned with using the natural variation in existing germplasm collections and wild relatives to identify allele combinations conferring drought, heat and saline tolerances. The important factor in the efficient design of selection and hybridization program is a knowledge of the nature of gene action controlling quantitative traits, such as yield, efficiency of water use and retention of chlorophyll. A number of techniques, e.g. Line × Tester (L × T) analysis, yield vital information as to the combining ability and relative importance of additive and nonadditive genetic effects, thus facilitating the identification of superior combinations of parents for the production of hybrids (Ferrari et al. 2018, Gramaje et al. 2020, Yildirim et al. 2022).

In addition, the combination of phenotypic selection with molecular breeding techniques, including genomic selection and physiological selection will expedite the production of climate-resilient cultivars. This is especially important for countries like Pakistan, where the limits to wheat productivity are imposed by scarcity of water, high evapotranspiration and erratic climate (Berry et al. 2015, Khaled et al. 2015, Zhou et al. 2016). The production of climate-resilient wheat genotypes is not only a scientific necessity but a socio-economic imperative, in order to provide food and nutritional security for the future generations. Genetics combined with agronomic and technological advance will enable breeders to produce cultivars, which can sustain productivity under normal and also stressed situations, a necessary advance towards a sustainable agricultural technology and the meeting of climate adaptation goals based on wheat systems (Abdolshahi et al. 2015, Muneer et al. 2016, Hakeem et al. 2020).

Impact of Climate Change on Wheat Production

Global climate change has arisen as one of the most important threats to agricultural productivity in general and to crops like wheat (Triticum aestivum L.) in particular. The forecasts of climate changes show that increased concentrations of CO_2 in the atmosphere, variable precipitation, and high temperatures can be expected to affect the frequency and severity of heat waves, droughts, and other abiotic stresses(Michaletti et al. 2018, Rai et al. 2018). As wheat is one of the crops most sensitive to temperature changes during the reproductive phases, it suffers generally large declines in yield when under conditions of high temperatures and moisture stress (Figure 3).

Importance of breeding wheat for water-use efficiency and resilience.

Breeding for enhanced water-use efficiency (WUE) and climate resilience have become a strategic priority in wheat improvement program. Conventional selection methods have been successfully used, but these are often limited by the complex inheritance of drought and heat tolerance traits (Figure 2.4). Therefore, quantitative genetic methods such as combining ability and estimation of gene action are increasingly being used to dissect the genetic basis of these adaptive traits. Traits such as relative water content, canopy temperature depression, chlorophyll stability index, and membrane thermostability are dependable physiological indicators to use in the screening of resilient genotypes. The use of physiological markers in combination with molecular markers in hybrid breeding increases the accuracy of selecting for parents and crosses with superior tolerance to abiotic stresses (Fasahat et al. 2016, Gupta et al. 2017).

Role of variability in selection, adaptation, and hybridization.

Importance of variability in wheat breeding can be related to its relationship with adaptability, stability of yields and tolerance against stresses. Wheat (*Triticum aestivum* L.), an autogenous crop by nature, does not undergo natural recombination and hence the amount of genetic diversity is limited in cultivars. It is, therefore, necessary to know and retain viability for broadening genetic base of stock in breeding material development. It opens up ways for the selection of allelic combinations which leads to important polygenic traits e.g. in case of grain production, drought resistance and cause of heat resistance. It plays a great role in hybridization and selection by which breeders can choose parents possessing homogeneous characters and desirable gene actions. Utilization of genetic potential hidden in hybridization and selection of various germplasm can be made possible to develop climate proof wheat varieties with superior physiological and yield characters (Banerjee et al. 2020, Nardino et al. 2022).

Sources of variability in wheat

Diversity in sources for genetic variability in wheat exists which can be grouped in three main categories. They are landraces, synthetic hexaploids, and modern cultivars. Landraces are a storehouse of natural variation which has evolved through centuries of adaptation to growing in certain agro-climatic conditions (Figure 5). They contain valuable alleles for abiotic stress tolerance, disease resistance and grain quality traits (Grzesiak et al. 2019, Poudel et al. 2020).

Combining Ability Analysis in Wheat Improvement

Combining ability refers to the capacity of the parent genotypes to transmit desirable characters to the progeny. It is an important concept in quantitative genetics and plant breeding. It indicates the nature and magnitude of gene action underlying the complicated characters of plants, e.g. yield, drought resistance, physiological characters, etc., in wheat (Triticum æstivum L.). There are two distinct classifications of combining ability, namely, general combining ability (GCA) and specific combining ability (SCA). The factor which denotes the performance of individual lines in hybrid combinations is characterized as the general combining ability, and this factor is associated closely with the additive gene effects, which are capable of fixation through selection. The factor which expresses the difference of any cross from the level that is expected on the average performances of the parents is termed specific combining ability, a concept which is associated primarily with gene actions which are non-additive, e.g. dominance and epistasis. Hence, an understanding of the relative importance of GCA and SCA is of utmost importance in the application of proper methods of breeding, whether pure lines are to be developed, or whether the heterosis is to be invoked to assist in the production of hybrid varieties (Ashraf et al. 2015, Ashfaq et al. 2016, Al-Naggar et al. 2017, Fatima et al. 2023).

Significance of GCA for Additive Effects and SCA for Heterotic Effects

The relative importance of GCA and SCA is a guide as to the kind of gene action that is involved in the inheritance of the important characters. The predominance of the GCA variance indicates the importance of additive effects and implies that the selection of early segregating generations will be effective. In contrast, the predominance of the SCA means to expect non-additive gene action and the crop improvement strategy to be hybridization and recurrent selection. The best possible utilization of the additive and non-additive types of genetic variance in climate-resilient wheat breeding will be to develop genotypes which show high yields under normal conditions and also good yield under abiotic stress (Grzesiak et al. 2019, Gramaje et al. 2020, Ghatak et al. 2021).

Gene Action and Its Role in Quantitative Trait Inheritance

Gene action describes the manner in which the alleles present at one or more loci act together to affect the expression of a given character. In quantitative genetics, the expression of a character such as yield, drought resistance, or resistance to heat in wheat is determined by the cumulative effect of the action of a number of genes, each contributing a small proportion of the total phenotypic expression, which may lead to the conclusion of which kind of gene action was concerned in the respective inter-specific hybridisation. The chief forms of gene action are represented by additive, dominance and epistatic effect. Additive gene action denotes the independent action of two alleles whereby the phenotypic value due to the expression of a given genotype is equal to the sum of the effects of the various alleles of which it is composed (Guo et al. 2016, Gupta et al. 2017, Hakeem et al. 2020).

This kind of gene action can be fixed by selection and plays an important part in the genetic improvement of self fertile crops. In contrast dominance as a form of gene action indicates the action of alleles, which are on the same locus whereby one allele hides the expression of the other allele. On the other hand, epistatic gene action denotes the action of one or more alleles on other genes on different loci which renders the inheritance of complex characters more difficult. Knowledge of the nature of gene action is accordingly essential in designing a practical breeding program for the improvement of quantitative characters when they are subjected to any program of selection and testing under diverse conditions of environment (Hannachi et al. 2017, Jamil et al. 2019, Ikram et al. 2020).

Relationship between Gene Action and Trait Heritability

The type of gene action that governs a particular trait will determine its heritability and the efficiency of selection that can be employed. Traits that are mainly controlled by additive gene effects have high values of narrow sense heritability, which means that the phenotypic variation that is observed is attributable nearly entirely to genetic causes and can be effectively passed on to succeeding generations in the breeding procedure. This allows plant breeders to obtain a steady gain under selection in the early segregating generations. Traits which are the result of dominance and epistatic action show low heritability instead, since their expression is affected largely by none-fixable arrangements due to environmental influences and by genetic interactions. This throws an obstacle in the effectiveness of selection and necessitates alternative means for the exploitation of heterosis, like recurrent selection or hybrid breeding. It is apparent then that the determination of heritability through the employment of a knowledge of the gene action will give a good means of analyzing the inherited constitution and predictability of the more complex traits, such as yield, relative water content, and shrub temperature depression in wheat (Khaled et al. 2015, Khadka et al. 2020, Kamara et al. 2021)

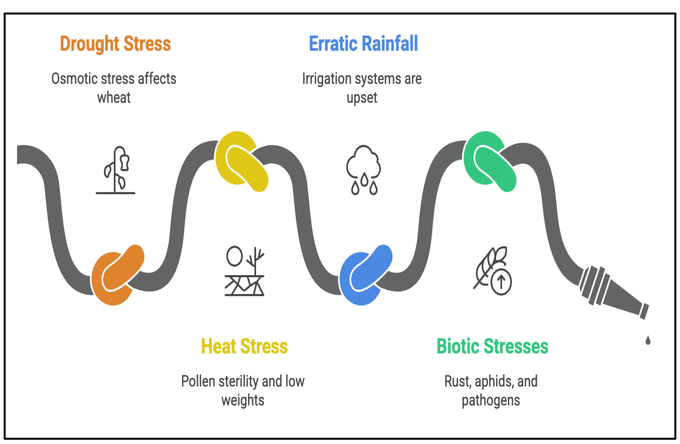

Figure 1: Stressed Wheat: Climate Change Impacts

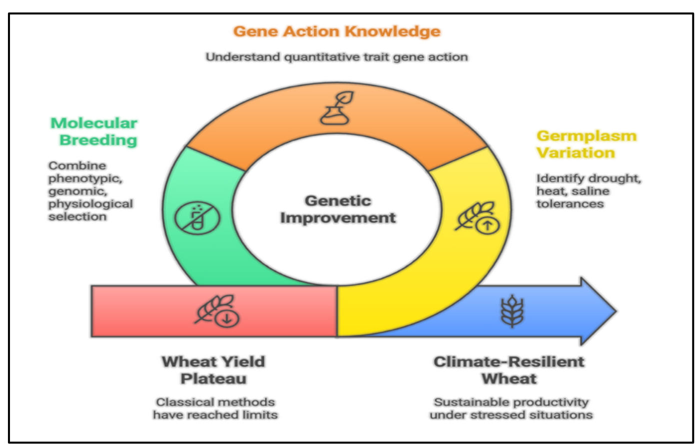

Figure 2: Breeding Climate-Resilient Wheat

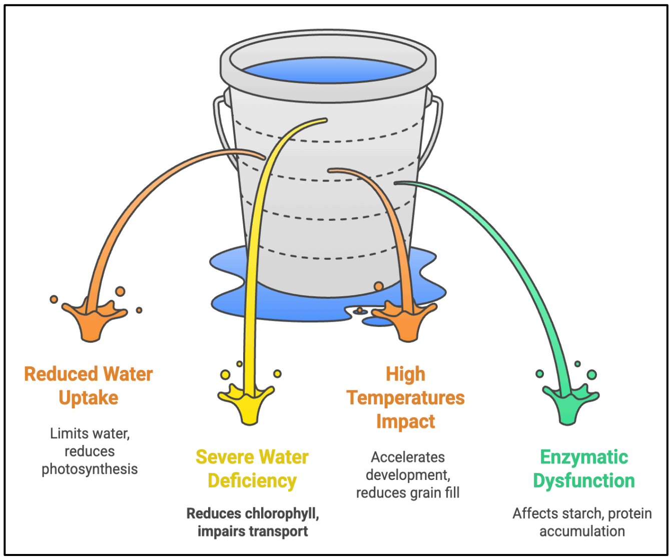

Figure 3: A biotic stress effects on yield

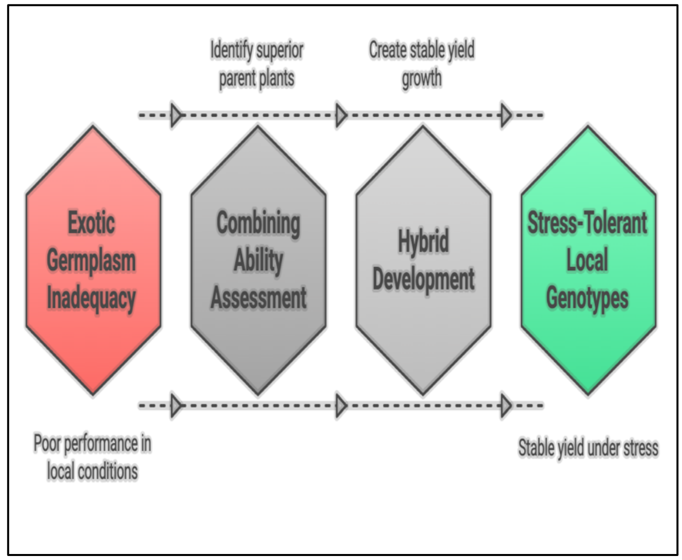

Figure 4: Developing Stress-Tolerant Local Genotypes

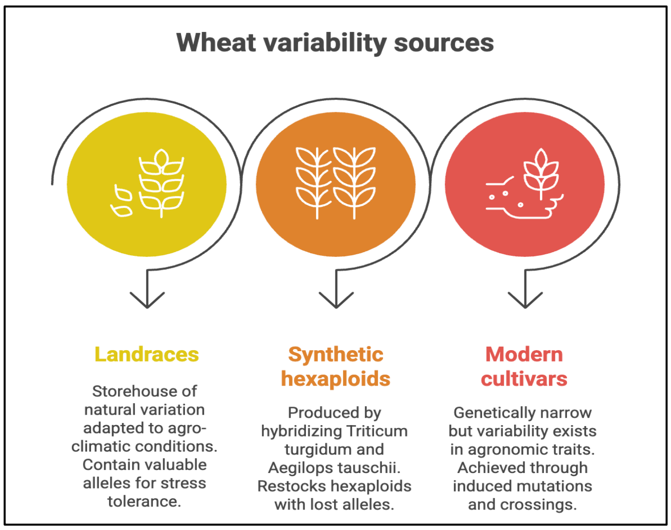

Figure 5: Sources of variability in wheat

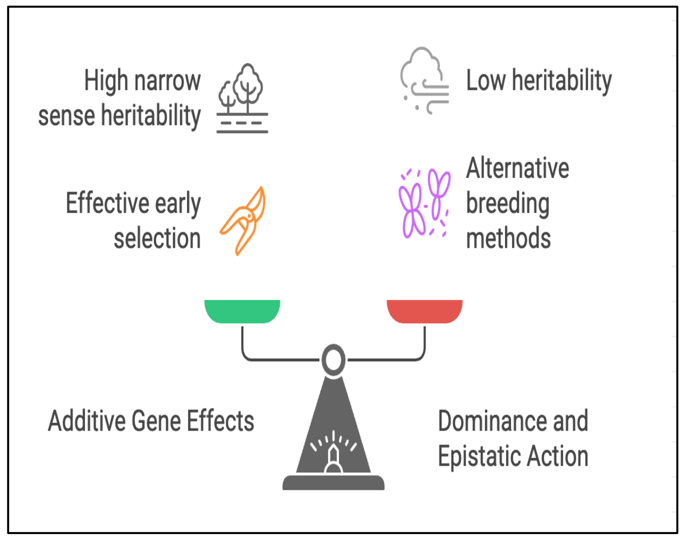

Figure 6: Comparing Gene Action and Heritability

CONCLUSION

Understanding gene action and combining ability is central to the genetic enhancement of wheat for drought tolerance under changing climatic conditions. The identification of additive and non-additive genetic effects provides a scientific basis for designing effective breeding strategies. Additive gene action, associated with general combining ability (GCA), governs heritable traits like relative water content, chlorophyll stability, and membrane thermostability, allowing efficient selection in early segregating generations. In contrast, dominance and epistatic effects, reflected through specific combining ability (SCA), play a vital role in complex yield traits and heterosis expression under water-deficit conditions. Therefore, integrating both additive and non-additive gene actions through complementary breeding methods—such as recurrent selection, hybridization, and molecular-assisted selection—ensures sustained progress in developing resilient cultivars. Genetic variability from landraces, synthetic hexaploids, and modern cultivars must be systematically utilized to broaden the genetic base for drought adaptation. The integration of physiological and molecular markers further accelerates the identification of superior parents and hybrids. Ultimately, a balanced exploitation of both GCA and SCA effects will facilitate the breeding of climate-resilient wheat genotypes, ensuring yield stability, enhanced water-use efficiency, and sustainable food security in drought-prone regions worldwide.

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