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## Wheat genetic diversity trends as a result of domestication and plant breeding

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### Abstract

Genetic diversity is essential for plant survival in nature and crop enhancement. The significance of genetic diversity is now being identified as a distinct topic, due to the susceptibility of crops to pest and diseases and limited adaptability to climatic changes. The assessment of genetic diversity in crops has significant implications for plant breeding programmes and genetic resource conservation. The current cultivated wheat's are the results of long evolution taken place around 10000 years ago. Due to hybridization, polyploidization, domestication, and mutation, the wheat genome exhibited fast and random changes during this evolutionary process. This has resulted in certain character modifications as well as gene loss. Even after then, genes were lost from landraces as a result of repetitive cultivation for certain characteristics. During 1960's improvement in genetic diversity was observed due to green revolution by incorporating semi dwarf genes. Although modern cultivars does not contain all the genes of their progenitors. So it is important to incorporate lost genes into the modern cultivars for wheat improvement. With the advent of molecular techniques helps the plant breeders to develop new varieties by incorporating lost genes from landraces.

**Keywords:** Genetic diversity, domestication, molecular techniques, hybridization, polyploidization, landraces

### Introduction

Wheat is the most domesticated food crop which is grown in mild temperature. It is one of the important cereal crop grown in worldwide which provides various important nutritional components such as carbohydrates, vitamins, phytochemicals, minerals, essential fibers and amino acids. The cultivation of wheat as a pioneer crop happened 10 centuries ago, due to "Neolithic revolution" [Heun *et al.*, Nesbitt, 1998; Dubcovsky and Dvorak, 2007] <sup>[37, 18]</sup>. Through archaeological evidence it was proved that in the Iberian peninsula, wheat was cultivated since the fifth millennium B.C., following that the fertile crescent was responsible for developing wild wheat, traditional wheat varieties and other crops [Diamonds, 2002]. But as a result of migration from the region of fertile crescent and also natural and human selection, local wheat landraces was developed, these land races refers to a traditional wheat variety possessing tolerance to stress and producing high- yielding stability with moderate level of crop yield under minimum input conditions [Zeven, 1998] <sup>[79]</sup>.

Domestication of wheat was responsible for the increase in human population by enabling humans to produce food in large quantities, thereby contributing to the emergence of human civilization [Zohary&Hopf, 2000] <sup>[80]</sup>. The domestication of wild emmer (*Triticum dicoccoids*) the progenitor of all cultivated wheat [Feldman and Kislev, 2007] <sup>[23]</sup> and it is the pre-requisite for the evolution of tetraploid durum and hexaploid bread wheat.

However the domestication of wild emmer in the fertile crescent and the subsequent breeding of domesticated durum and bread wheat drastically narrowed their genetic diversity [Dvorak *et al.*, 1998] <sup>[19]</sup>. On the depletion of genetic variability, plants are unable to stand with unfavorable environmental conditions or pathogens and pests.

It is therefore vital for plant breeding programs to maintain sufficient genetic diversity to allow for production of new and diverse varieties suitable for cultivation under a variety of biotic and abiotic stresses. The main objective of this review is to focus on the loss of genetic diversity in wheat which taken place during domestication and plant breeding and the techniques which helpful in improving the genetic diversity.

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## Genetic diversity

Crop plant evolution, whether natural or induced by humans, is essentially determined by genetic diversity in the population (Bhandari *et al.*, 2017) [6]. The degree of differentiation between or within species is referred to as diversity. The presence of diversity in Plant genetic resource allows plant breeders to generate new and better cultivars with desired qualities, which include both farmer-preferred traits (high yield potential, big seed, etc.) and breeder-preferred attributes (pest and disease resistance and photosensitivity, etc.). If all of the individuals within the species were the same, there would have been no progress to be made in plant performance for various factors. Natural variability and divergence amongst crops have been extensively discovered and utilized in crop improvement since the beginning of systematic plant breeding. However, natural variability has been depleted over time due to (i) lopsided breeding practices focusing on improving only a few traits (such as yield and its component traits), (ii) frequent use of a few selected genotypes as parents in varietal development programmes, and (iii) introduction of a few outstanding lines to many countries, resulting in increased genetic similarity between modern crop cultivars (Bhandari *et al.*, 2017) [6]. Persistent narrowing of germplasm diversity would inevitably result in some of the unfavorable outcomes, including decreased potential to improve crop production, increased susceptibility to pests and diseases, decreased ability to adapt to changing weather patterns, increased instability in agricultural production, and genetic resource loss (Govindaraj *et al.*, 2015) [29]. With the changing environmental scenario, it is becoming increasingly necessary to create climate resistant cultivars (Wheeler *et al.*, 2013) [76]. The presence of genetic variety, manifested as wild species, related species, breeding stocks, mutant lines, and so on, may serve as a source of desirable alleles (Begna, 2021) [5]. Diversity analysis can be carried out using morphological, cytological, biochemical and molecular characterization.

Genetic variation may occur through a number of mechanisms, resulting in genotype alterations and the emergence of new alleles. Allopolyploid species can withstand genetic modifications that are either impossible or detrimental in diploid species. Thus, genetic diversity in polyploid species is much higher than predicted by polyploid formation models involving a single origin. (Soltis *et al.*, 2000) [72].

Tetraploid and hexaploid wheat were developed by allopolyploidization, or inter-generic hybridization followed by chromosomal doubling, which is responsible for some of the plant's genetic variability (Feldman *et al.*, 2005) [25]. Genetic diversity causes the agriculturally significant phenomena of hybrid vigour in polyploids (Chen *et al.*, 2010) [14]. As wheat is a polyploid plant, including tetraploid and hexaploid types in genetic variability assessment programmes is advantageous (Khan *et al.*, 2015) [41].

Wheat developed enough genetic variation throughout the evolutionary path from einkorn to bread wheat (Faris *et al.*, 2014) [22]. However, due to repeated cultivation of landraces for particular characteristics, limited adaptation, farmers' varietal selection, and the demand of uniform variety in industrial seed grain processing, its diversity is declining now. The introduction of high-yielding commercial cultivars contributed significantly to the loss of genetic variation (Wouw *et al.*, 2013) [74]. As a result, maintaining adequate

genetic variation for the development of new varieties is critical for plant breeding programmes.

## Status of genetic diversity

In recent years a lot of research has been done to study the genetic diversity in wheat by using molecular markers. Restriction fragment length polymorphism (RFLP Bostein *et al.*, 1980) was one of the first DNA marker technique used to characterize wheat cultivar (Vaccino *et al.*, 1993) [73] and assess genetic diversity (Kim and ward 1997; paull *et al.*; 1998) [42, 52]. Reduction in genetic diversity was reported among Canadian hard red spring wheat cultivars, French bread wheat and Chinese core collection (Roussel *et al.*, 2004; Hao *et al.*, 2006; Fu *et al.*, 2005) [63, 31]. While increase in genetic diversity were observed among Nordic spring wheat (Christiansen *et al.*, 2002) [15].

R.R. Mir *et al.*, 2012 [48] has examined the genetic diversity in 263 Indian bread wheat cultivars by using 90 SSR markers. These cultivars classified into group 1(pre green revolution) and group 2(Post green revolution). The results of both groups suggest a higher level of genetic diversity in group 2 than in the group 1. But in the group 2 also there was a fluctuation with significant increase in diversity from 1960 to 1970 followed by a decrease in 1990 and then again slight increase in 2000. Finally the estimates of gene diversity suggest that the wheat breeding in post green revolution period did not lead to any loss of genetic diversity in Indian bread wheat cultivars rather there was a slight increase in diversity it is due to the introduction of Mexican semi dwarf genes into the Indian bread wheat during 1960s.

Ren *et al.*, (2013) explained by categorizing 97 cultivars into three groups: OC, EGR, and PGR. As indicated in Table 1, there was a loss of genetic diversity from OC to EGR, although there was an increase in PGR. That means, genetic diversity decreased from 1930 to 1980 but increased from 1981 to 2009.

**Table 1:** Genetic diversity generated by 946 SNP markers was compared between landraces and cultivars.

| Gene diversity       |          |
|----------------------|----------|
| level of Improvement |          |
| landrace             | 0.2192 b |
| cultivar             | 0.2310 a |
| Time group           |          |
| Landrace             | 0.2192 b |
| OC                   | 0.2192 b |
| EGR                  | 0.2034 c |
| PGR                  | 0.2474 a |

\*OC-old cultivars released before 1965; EGR, cultivars released during the period of early Green Revolution (1965–1980); PGR, cultivars released during the period of post Green Revolution (1981–2009) (Ren *et al.*, 2013)

Alipour *et al.*, (2017) [3] studied the genetic diversity between landraces and cultivars (GBS-SNP) markers. Molecular study of variance revealed that genetic diversity across groups was greater than within groups.

Kabbaj *et al.*, (2017) [40] analysis revealed that Ethiopian landraces had a low amount of segregating alleles, and the Central and South Asian landraces were the most genetically varied sub-population.

Sansaloni *et al.*, (2020) [66] large-scale genotyping and diversity analysis, 56,342 domesticated hexaploids, 18,946 domesticated tetraploids, and 3,903 crop wild relatives were

studied. The study shows recently unknown landraces and genetic imprints characterised by locations under selection. This provides fertile ground for developing future wheat varieties by focusing on specific gene or chromosomal areas and locating germplasm that preserves allelic variation that is lacking in present breeding efforts.

Furthermore, a comparison of genetic variety across the ten main ecogeographical areas revealed that South America, North America, and Europe had the most genetic variability, whereas the Middle East had intermediate amounts (Jing ren *et al.*, 2013).

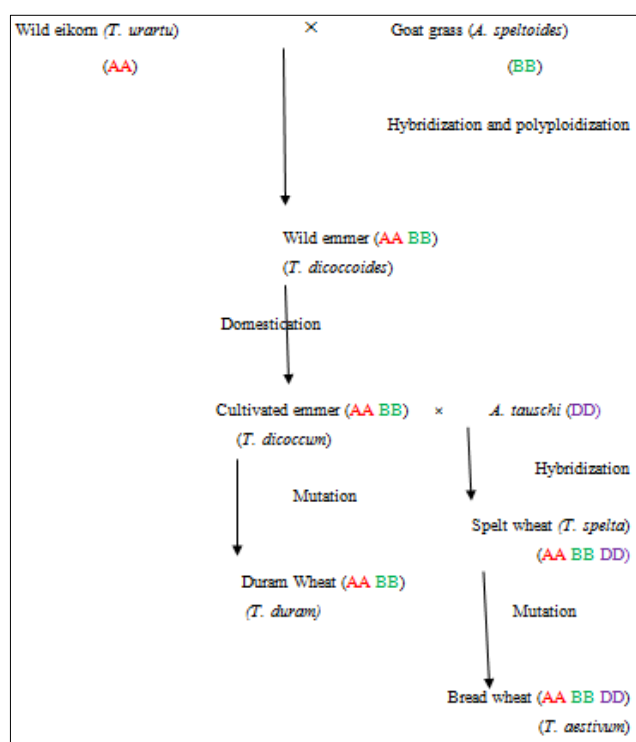
It was clear that genetic diversity in wheat decreased from landraces to cultivars released before green revolution. The cultivars released after green revolution showed increased genetic diversity. More genetic diversity was present between the groups rather than among the groups (Wikipedia).

### Domestication in wheat

Domesticated crop species evolved as a result of wild species being exposed to novel selective situations involved with human cultivation and use (Purugganan *et al.*, 2009) [57]. The process involves numerous commonly observed phases that transform a wild organism into one more suited to human use—that is, a domesticate. These steps are roughly as follows: (a) wild harvesting; (b) conscious and unconscious

selection to modify plant characteristics (e.g., architecture, flowering time, dormancy, size, and defensive structure reduction) (Harlan, 1992) [32].

Bread wheat (*Triticum aestivum* L.) is a major crop species that has fed and continues to feed a large portion of the world's population for many centuries (Salamini *et al.*, 2002 and Shewry, 2009) [65, 67]. It is an important energy source (supplying around 20% of global population requirement), protein (also giving approximately 20%), vitamins, and other useful substances, not only for humans, but also for animal feed (Hawkesford *et al.*, 2013 and Shewry, 2009) [35, 67]. It is an allohexaploid species ( $2n = 6 \times = 42$ , AABBDD genomes) that resulted from two rounds of hybridization with combination of 3 interrelated diploid genomes (El Baidouri *et al.*, 2017, Marcussen *et al.*, 2014, Petersen *et al.*, 2006, Pont *et al.*, 2017) [21, 45, 54, 55]. The initial hybridization, that occurred approximately 10,000 years ago it is believed to have been between the two grass species *T. urartu* (the A genome donor) and *T. speltoides* (the B genome donor), the result of this hybridization is tetraploid (emmer) wheat *T. turgidum ssp. dicoccoides*. A second hybridization event occurred some 8,000 years ago between cultivated emmer wheat and the donor of the D genome, *Ae. tauschii*, giving rise to current bread wheat (Venske *et al.*, 2019) [75].



**Fig 1:** Flow chart of evolution of wheat - (Rahman *et al.*, 2020) [44]

### Changes in wheat due to domestication

A variety of phenotypic changes occur between domesticated and wild species, which are paralleled by genetic differences. These variations, such as non-dehiscent spikes, free-threshing grain, decreased seed dormancy, and changed flowering time, are critical to domestication because they govern features that allow human gathering and eating but would be detrimental in nature (Haas *et al.*, 2019) [30]. Other features associated with domestication and crop evolution include glume reduction (easy threshing), changes in plant architecture, changes in ear and kernel size, loss of seed dormancy, decreased grain

protein and mineral concentrations, and higher grain carbohydrate content (Harlan *et al.*, 1973) [32]. It has been broadly accepted that significant genetic erosion occurred throughout the wheat domestication process. As a result, there has been a loss of diversity, selective sweeps, and adaptive variation, resulting in significant genetic alteration. By using molecular marker and QTL analysis techniques it was identified that nucleotide diversity at 21 gene loci was examined in wild, domesticated, and cultivated durum and bread wheat's, and got to know that diversity was reduced by 69 percent in bread wheat and 84 percent in durum wheat

during domestication (Haudry *et al.*, 2007) <sup>[33]</sup>. During evolution, some genes are lost forever. Natural wheat and similar allopolyploids have 2–10% less DNA than the total of their parents, indicating that DNA was lost throughout evolution (Nishikawa and Furuta 1969; Furuta *et al.*, 1974; Eilam *et al.*, 2008, 2010) <sup>[28, 20]</sup>.

### Impact of Plant breeding on wheat genetic diversity

During the process of domestication only a specific species were selected which are suitable for new environments as well as which fulfill the requirements of early farmers (Charmet, 2011; Peng *et al.*, 2011) <sup>[13, 53]</sup>. This practice led to the development of landrace which are traditional crop varieties developed by farmers through years of natural and human selection (Jaradat, 2013; Zeven, 1999) <sup>[38, 79]</sup> to meet their social, economic, cultural, and environmental needs. These are also known as farmers' varieties or folk varieties (Belay *et al.*, 1995) <sup>[10]</sup>. These landraces have a variety of features, including growth habit, cold, heat, or drought resistance, early growth vigour, time to heading and maturity, seed filling duration, and quality attributes. (Masood *et al.*, 2005) <sup>[10]</sup>.

Since 1900's plant breeding played an important role in improving food production with the development of new varieties (Borlaug, 1983) <sup>[7]</sup> by using the methods ranging from introduction, phenotypic selection, controlled mating to marker assisted selection for desired genes (Allard, 1999) <sup>[4]</sup>. During the early stages of plant breeding, breeders used landraces as a primary source for developing varieties by systematic cross breeding with the invention of line and pedigree selection (Nilsson, 1898) <sup>[50]</sup>. Due to this selection it causes the development of more uniform varieties, which leads to the change in diversity present in landraces (Louwaars 2018) <sup>[43]</sup>.

The two main reasons causes the uniformity in varieties are 1. Plant breeders combine different varieties in one genotype thus reduces the diversity within the species. The second one is early mechanization which requires more uniform crops and large scale processing of agriculture produce (Louwaars, 2018) <sup>[43]</sup>. Due to the presence of narrow genetic diversity in improved varieties causes genetic vulnerability thus leads to susceptibility of plants to biotic and abiotic stresses (Singh, 2002; Marshall, 1977; Wolfe and Barrett, 1977; Agrios, 1978; Simmonds, 1979) <sup>[69, 46, 78, 2]</sup>. The Green Revolution in wheat began in the late 1960s in the Indian Punjab, as did worries over genetic degradation caused by the relocation of indigenous landraces (Frankel 1970; Hawkes 1983; Harlan 1992) <sup>[24, 32]</sup>. Semi-dwarf cultivars showed the significance the varieties they replaced when cultivated with higher rates of fertiliser application and a regulated water supply (Smale *et al.*, 2008) <sup>[71]</sup>. Rht-B1b and Rht-D1b is the semi dwarf genes induced in semi dwarf cultivars (Pearce *et al.*, 2021). The early Green Revolution cultivars' success contributed considerably to the realization that plant genetic resources must be protected (Harlan, 1992) <sup>[32]</sup>. The experiment conducted by (Ren *et al.*, 2013), data demonstrated that genetic diversity decreased between 1930 and 1980, but increased from 1981 and 2009, showing that breeders were effective in increasing genetic variety through the introgression of numerous new wheat materials (Rajaram *et al.*, 2001 & Reeves *et al.*, 1999) <sup>[59, 61]</sup>. However, after a while, several unintentional and besides negative consequences of the green revolution were discovered (John *et al.*, 2021) <sup>[39]</sup>.

After certain period of time narrowing of genetic diversity was noticed with the emergence of epidemics of yellow rust in wheat and also other factors like environment factors. So, it is necessary to improve genetic diversity by transferring the desired traits from landraces, wild relatives to modern cultivars by using various techniques.

### Techniques used to improve genetic diversity in wheat

Despite massive improvements made in wheat breeding programmes across the world, there are still various problems to solve in order to enhance production levels (Casassola, 2013) <sup>[12]</sup>. In the field of crop improvement genetics was acknowledged as the most effective strategy for improving yields through the development of new superior varieties, whether by assisted selection, genetic engineering, or traditional breeding methods (Butler, 2010) <sup>[11]</sup>. After that to increase the genetic diversity accessible for wheat breeding, several strategies such as double haploids, wide hybridization, induce mutation, genetic transformation, genome editing, and introgressions from secondary and tertiary gene pools would need to be used. The advent of NGS, however, has enabled new approaches to tackle sequencing of the wheat genome. The first sequence of wheat was published in 2012 (Brenchley *et al.*, 2012) <sup>[9]</sup> based on a whole-genome shotgun (WGS) assembly of 'long' sequence reads using 454 technology (Borrill, 2015). Drought tolerance in wheat should be improved using new technologies such as high-throughput phenotyping, NGS, and genetic engineering. (Mwadingeni *et al.*, 2016) <sup>[49]</sup>. Especially Marker-assisted selection (MAS) to increase breeding efficiency, has become popular in breeding operations (Tanksley *et al.*, 1989) <sup>[64]</sup>. Other than these techniques genomic selection, Genomics and related technologies, proteomics and metabolomics also played a key role in improving genetic diversity. Transgenic methods result in the creation of genetically modified creatures by introducing foreign DNA, which are not always well accepted by consumers (Slade, 2004) <sup>[70]</sup>. A reverse genetic, non transgenic approach to wheat crop improvement by TILLING. TILLING is a reverse genetic approach for mutation generation and discovery that does not rely on transgenic technology (Henikoff *et al.*, 2004) <sup>[36]</sup>. (Garcia *et al.*) applied the non-transgenic TILLING method to find mutant candidates in the TaMlo genes in an EMS-mutagenized population of spring wheat cv. Cadenza (Acevedo-Garcia *et al.*, 2017) <sup>[11]</sup>.

### Conclusion

This review is mainly focused on the importance and status of genetic diversity in wheat evolution from domestication to modern cultivars developed by plant breeders. Wheat has undergone a long evolutionary process, including hybridization, domestication, polyploidization, mutation (Rahman *et al.*, 2020) <sup>[44]</sup>, as well as genomic alterations. It has been observed that wheat gained a sufficient variation from einkorn to bread wheat but due to the repeated cultivation of landraces for specific characters the loss of genetic diversity was observed in cultivated varieties. After introducing semi dwarf varieties there was little increase in genetic diversity however the presence of more uniformity in modern cultivars than landraces, result in some of the unfavorable outcomes, including increased susceptibility to pests and diseases, decreased ability to adapt to changing weather patterns. A current task is to find and clone essential

strategic genes from landraces and wild relatives that impart agronomic, qualitative, biotic, and abiotic stress-related properties by using modern breeding techniques (Rahman *et al.*, 2020)<sup>[44]</sup>

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