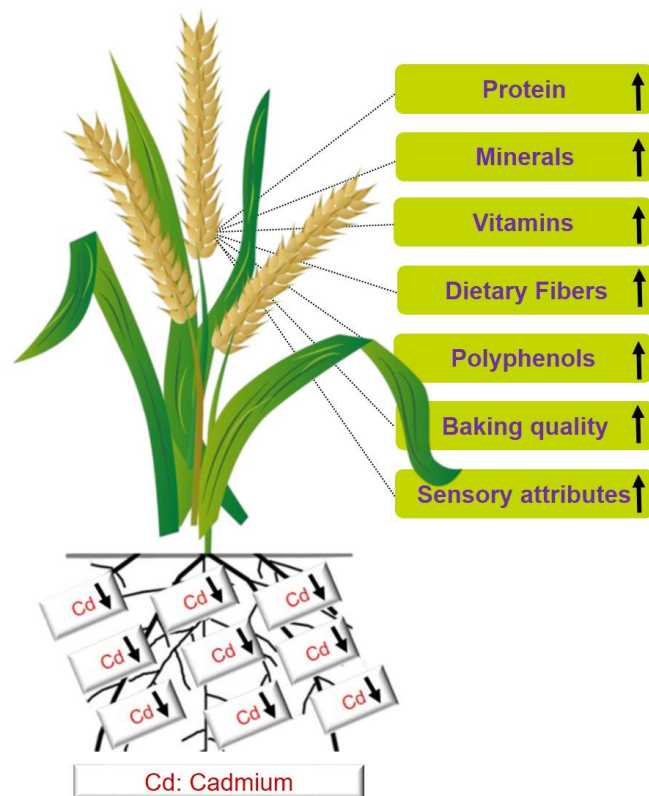# Exploring Ancient and Alien Cereal Germplasms to Advance Sustainable Wheat Breeding for Enhanced Functional, Nutritional, and Sensory Quality

Olawale Olalekan

Exploring Ancient and Alien Cereal Germplasms to Advance Sustainable Wheat Breeding for Enhanced Functional, Nutritional, and Sensory Quality

Olawale Olalekan, https://orcid.org/0000-0003-0627-8807, Swedish University of Agricultural Sciences, Department of Plant Breeding

Sveriges lantbruksuniversitet
Swedish University of agricultural Sciences

Abstract

Global food security is increasingly threatened by numerous challenges, including widespread malnutrition. Nutritional deficiency, particularly in essential micronutrients such as Zinc (Zn) and Iron (Fe), affects over three billion people worldwide, with pregnant women and children being the most vulnerable. Wheat, as principal cereal crop, provides more than 50% of daily caloric for many populations, contributing essential nutrients such as proteins, vitamins, minerals, and phytochemicals. Wheat's adaptability to diverse growing conditions and its wide production and consumption make it the most important staple crop globally, and a strong candidate for addressing nutritional deficiencies. However, enhancement of wheat's quality traits is constrained by the limited genetic diversity within modern cultivars. In contrast, wild relatives and ancient cereals harbor significant genetic variation that can be exploited for crop improvement. Identifying, characterizing, and deploying key genetic loci for quality traits, facilitated by modern breeding tools such as marker-assisted selection (MAS),—offer pathways for the enhancement of both functional and nutritional qualities in wheat. This review examines the current understanding and advancements in wheat quality improvement, with an emphasis on ancient cereals and alien germplasms, and highlights the role of advanced breeding methodologies for optimizing the nutrition, sensory, and end-use qualities of wheat across different growing environments.

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1. Introduction

The world faces numerous challenges, including an increasing population, climate change resulting in extreme weather conditions (Patz *et al.,* 2014), and political instability (Aisen and Veiga, 2013), which threatens food security. Other concerns such as pest and disease infestation on crops (McBeath and McBeath, 2010), increasing changes in food preferences of consumers due to an increased health awareness (Shiferaw *et al.,* 2013), and malnutrition from inappropriate food consumption, aggravate the problem. A coordinated effort is being made to find sustainable and environmentally friendly solutions to these concerns in which breeding plays a crucial role by developing crops rich in nutrients, which can contribute to addressing nutritional deficiencies and improving food security (Bouis, 2002; Welch and Graham, 2004; Agovino *et al.,* 2019; Singh *et al.,* 2021; Reynolds and Braun, 2022). A key aspect of addressing these global challenges is understanding cereal grains' role in human nutrition and food security.

Cereal grains have been a major part of the human diet for thousands of years with a significant impact on the development of the human civilization (Sarwar *et al.,* 2013; Shiferaw *et al.,* 2013). Thus, cereals are essential staples for the everyday existence of billions of people, thereby contributing to over 50% of the global daily calorie intake (Awika, 2011). In addition to protein, cereal grains contain a plethora of other chemical compounds that are beneficial to the body, such as fatty acids, vitamins, elements such as iron, calcium, zinc, phosphorus, manganese, copper, molybdenum, polysaccharides, and bioactive compounds, e.g. phenolics (Borneo and León, 2012). Among the various cereal grains, wheat stands out as a particularly important staple crop due to its wide adaptability and nutritional profile.

Wheat is a major staple crop among the cereals (Shewry and Hey, 2015a; Tadesse *et al.,* 2016) which is grown across the world, specifically in the temperate regions, and it provides both energy and nutrition to the human food (Le Gouis *et al.,* 2020). Wheat is an important source of carbohydrates, protein, vitamins, dietary fiber and phytochemicals, thereby, contributing both to growth cells and the regulation of cell functions (Bálint *et al.,* 2001; Hussain *et al.,* 2012b; Irakli *et al.,* 2015; Guzmán, *et al.,* 2019). The increasing global demand for wheat is driven by its versatility in food production and the need to meet diverse dietary preferences.

Currently, there is an increasing need for wheat in new markets outside its climate adaptation region (Le Gouis *et al.,* 2020). The capacity to create novel food products, each with unique quality components, is raising the consumption of wheat and driving the global demand for it

(Shewry and Hey, 2015a). Wheat grain quality is essential, although the requirements varies across the value chain, e.g. for farmers, millers, food processors, and consumers, and the processing method and end-use product plays a vital role (Hernández-Espinosa *et al.,* 2018). The quality traits of wheat include characters such as grain texture, milling quality, protein attributes, mineral content, vitamin, baking quality, grain and flour colour and flavour. Thereby, specific quality standards are utilized for wheat to suit a wide range of food products (Ganno *et al.,* 2017). Understanding the factors influencing wheat quality, including genetic and environmental interactions, is crucial for meeting these diverse requirements.

Several studies (Graybosch *et al.,* 1995; Curic *et al.,* 2001; Budak *et al.,* 2003; Yong *et al.,* 2004; Johansson *et al.,* 2005; Drezner *et al.,* 2007; Horvat *et al.,* 2012) have shown that end-use quality (EUQ) of wheat is influenced by both genotype and environment (agronomic input and weather), and their interactions. To improve the various quality attributes of wheat, the amount and pattern of genetic diversity in available germplasm need to be utilized (Kronstad, 1986; Warburton *et al.,* 2006, Kashif *et al.,* 2021). Knowledge of genetic control over quality traits, gene-environment interactions, and how these interactions affect the expression of quality traits will improve breeders' selection efficiency (Subedi *et al.,* 2023). To enhance these quality traits, breeders can employ various modern technological approaches to accelerate the development of superior cultivars.

Enhanced selection and accelerated development of cultivars with distinctive grain properties will potentially be achieved through the use of various approaches applying modern technologies such as genomic tools (molecular markers, genomic selection, genetic data platforms, etc.), genome editing, high-throughput phenotyping, speed breeding and big data handling, etc. (Gordeeva *et al.,* 2019; Gordeeva *et al.,* 2020; Loskutov; Khlestkina, 2021; Johansson *et al.,* 2024). In elite cultivars, yield has been prioritized over quality attributes, making them a less suitable source of genes for enhancing unique qualities in wheat (Rajaram and Braun, 2008; Reynolds *et al.,* 2009). Old cultivars, ancient cereals e.g. spelt, einkorn and emmer, wheat wild relatives such as *Aegilops* spp., and wheat introgression lines (crosses between wheat and close relative cereals) are good sources of genetic variation for distinctive quality features (Gadaleta *et al.,* 2023). Additionally, the growing demand for organic products necessitates the development of wheat cultivars that thrive under organic farming conditions.

In recent years, the demand for organically grown crops has increased due to their lower chemical footprint, which is believed to contribute positively to public health and the

environment (Zaccone *et al.,* 2010). This believes may relate to the fact that organically grown crops environment typically exhibit higher microbial biomass and activity, as well as greater biodiversity (Reganold *et al.,* 2010). Thus, there might be a need to develop wheat cultivars for different markets, and for both conventional and organic field production. This trend is particularly relevant in countries like Sweden, where organic farming is on the rise and plays a significant role in the agricultural landscape.

Wheat is a major crop in Sweden and also a major exportable item (FAOSTAT, 2022). Recent years have resulted in significant fluctuations in global wheat yield, although, for Swedish wheat production a general increase is reported from 1971 to 2020, and the total production volume was 3.21 million tonnes in 2020 (FAOSTAT, 2022). Sweden is among the countries in the EU with the highest share of organic farmland in terms of percentage of total EU agricultural land in 2021 and also with a high organic food consumption per capita (Eurostat, 2023). This introductory paper aims to delve deeper into the specific qualities of wheat that are valuable for both conventional and organic production, focusing on ancient and alien cereal lines. It will summarize the current state-of-the-art knowledge related to nutrition, taste, texture, and EUQ in ancient cereals and wheat-alien introgression lines and outline methods for assessing these parameters.

2. Genetic Diversity

Genetic variation refer to the diversity of genetic material within populations or species and arises from differences in DNA sequences among individuals (Cardinale *et al.,* 2012; Bhandari *et al.,* 2017). This diversity lead to a range of phenotypic traits such as height, yield, disease resistance, and environmental tolerance (Ribaut *et al.,* 2002). Genetic variation is generated through several processes, including random mutations during DNA replication, recombination, and genetic drift (Oladosu *et al.,* 2016). Mutations, which are heritable changes in the DNA sequence, can introduce new alleles or genetic variants, thereby contributing to the genetic diversity within a species (Begna, 2021). Genetic variation serves as the foundation for evolution by providing the raw material upon which natural selection acts (Salgotra and Chauhan, 2023). Furthermore, artificial selection harnesses genetic diversity to enhance specific traits for breeding objectives (Gregory, 2009). Genetic variation is important because it can enhance resistance to biotic stresses such as diseases and pests, increase tolerance to abiotic stresses such as drought, heat and salinity, improve yield, influence end-use quality traits, and provide protection against future uncertainties (Jaiswal *et al.,* 2010; Rahmatov *et al.,*

2016a; Lan *et al.,* 2022). However, effectively managing and utilizing genetic variation requires understanding its nature and distribution (Hilbish and Koehn, 1987). This can be determined using morphological, biochemical, or molecular markers which are tools that help in assessing genetic diversity and aid in the selection of desirable traits for breeding programs (Jaiswal *et al.,* 2010; Bhandari *et al.,* 2017).

3. The Wheat Crop

Wheat belongs to the grass family (Poaceae), includes a variety of species whose seed are cultivated as staple foods globally (Devos, 2010). Alongside rice and maize, wheat is one of the three major crops that contribute more than 55% of the crop-based food energy to the human global population (Awika, 2011). The origin and domestication of wheat can be traced to the Fertile Crescent, where its wild ancestors first emerged (Feldman, 2001; Zohary *et al.,* 2012). The genus (*Triticum*) encompasses species that are diploid (2n = 2x = 14, AA), tetraploid (2n = 4x = 28, AABB), and hexaploid (2n = 6x = 42, AABBDD) (Vishwakarma *et al.,* 2018; Sharma *et al.,* 2021). The domesticated wheat species are derived from wild ancestors: *Triticum urartu*, *Aegilops speltoides*, and *Aegilops tauschii*, which contributed the AA, BB, and DD genomes, respectively (Levy and Feldman, 2022). Wild emmer (*Triticum turgidum* ssp *dicoccoides)* was domesticated as *T. turgidum* ssp *dicoccum*, from which *T. turgidum* ssp durum and other tetraploid species are thought to have originated, potentially from a cross between *T. Urartu* and *Ae. speltoides* (Zeibig *et al.,* 2022).

Wheat is cultivated across various climates, ranging from temperate to tropical regions (Mondal *et al.,* 2016), with a significant role as staple crop in temperate regions (Shewry, 2009). It is grown as both winter wheat, sown in autumn and harvested in summer, and spring wheat, sown and harvested within the same year. Wheat is classified based on characteristics such as texture, color, and gluten content (Guzmán *et al.,* 2014; Vishwakarma *et al.,* 2018), resulting in classes such as hard red spring wheat, hard red winter wheat, soft red winter wheat, and soft white wheat (Posner, 2000; Finney *et al.,* 1987). Wheat is used to produce a wide range of food products, including bread, pasta, breakfast cereals, pastries, and snacks (Posner, 2000; Mastrangelo and Cattivelli, 2021). Additionally, wheat is utilized in animal feed (Adamović *et al.,* 1998), beverages (Pasqualone *et al.,* 2018), and for biofuel production (Tishler *et al.,* 2015).

Wheat plays a relevant role in food security especially global nutrition (Shewry and Hey, 2015a). However, its cultivation is increasingly threatened by various diseases (Figueroa *et al.,*

2018), pests (Lopes *et al.,* 2016), and environmental stresses such as drought (Steenwerth *et al.,* 2014), and frost (Xiao *et al.,* 2018), which can adversely affect both yields and quality.

4. Importance of Genetic Diversity for Wheat Improvement

One major prerequisite for developing new cultivars or achieving breeding objectives is the presence of genetic diversity for the targeted trait of interest (Monasterio and Graham, 2000). Modern wheat cultivars are bred to adapt to the environments in which they are grown. They are designed to achieve high yield, resist prevailing diseases, and tolerate abiotic stresses such as drought (Bedő and Láng, 2015). As a result, the genetic base of these cultivars is often narrower than that found in old, ancient and alien wheat lines (Raman *et al.,* 2010). With climate change expected to alter cultivation conditions significantly, novel genetic variation might be required to maintain functionality, enhance nutritional value, reduce grain heavy metal uptake, and provide resistance to emerging pathogenic strains (Rahmatov, 2016b; Alvarez and Guzmán, 2018; Bashir *et al.,* 2023; Gadaleta *et al.,* 2023; Lan *et al.,* 2024). Several methods can introduce novel genetic diversity into an adapted wheat background, including hybridization, mutation, asexual reproduction, recombination, and genetic engineering (Rauf *et al.,* 2010; Li *et al.,* 2012; Nadeem *et al.,* 2018). To date, hybridization has been the primary method for gene transfer (Molnár-Láng and Linc, 2015; Alvarez and Guzmán, 2018). Wheat-alien introgression lines, old and ancestral cultivars, heritage crops, wild wheat relatives, and landraces are abundant reservoirs of valuable traits (Cakmak *et al.,* 2000; Kashif *et al.,* 2021). These resources offer potential for enriching breeding programs aimed at improving modern cultivars (Chhuneja *et al.,* 2006; Johansson *et al.,* 2020b; Gadaleta *et al.,* 2023).
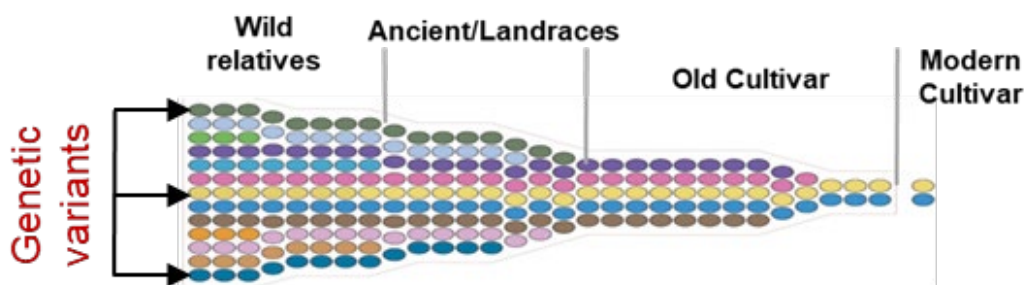

Figure 1: Genetic variations in wheat wild relatives. Adapted from (Voss-Fels et al., 2019) with modifications.

5. Plant Breeding-Based Solutions

Plant breeding provides powerful tools for developing new crop cultivars to address various challenges facing modern agriculture (Ceccarelli and Grando, 2020), including feeding an increasing population (Fedoroff *et al.,* 2010; Hawkesford *et al.,* 2013), combating climate change (Snowdon *et al.,* 2021; Messina and Cooper, 2022), tackling food insecurity (Lenaerts *et al.,* 2019), and alleviating nutritional deficiencies (Srinivasa *et al.,* 2014). Leveraging the latest advancements in breeding technologies (Yu *et al.,* 2020) and genetic research (Sun *et al.,* 2022), plant breeders can substantially contribute to developing a more sustainable and resilient food system for the future (Nestel *et al.,* 2006; Cooper and Messina, 2022).

Historically, plant breeding has focused on selecting plants with desirable traits such as larger grains and a greater number of flowers and fruits resulting in increasingly productive crop cultivars (Fischer and Edmeades, 2010). Recent studies have demonstrated the opportunity to develop climate-smart crops designed to be resilient, adaptable to varying climatic conditions, and capable of thriving in stressful environments (Cooper and Messina, 2022). Such crops could play a vital role in ensuring food security even under climate change conditions, which brings extremes and increasingly frequent and severe droughts (Ceccarelli and Grando, 2020). With predicted climate change scenarios, crops tolerant to dry conditions will become increasingly important (Cooper and Messina, 2022). Drought-tolerant crops can be developed through traditional breeding methods or modern technologies. Traits associated with drought tolerance include deeper root systems (Lan *et al.,* 2022; Liu *et al.,* 2023), improved heat stress tolerance (Bellundagi *et al.,* 2022), and enhanced water use efficiency (Hou *et al.,* 2023). Additionally, many people globally suffer from nutrient deficiencies (Stein, 2010; WHO, 2022), leading to various health problems (Black, 2003). Developing crops with higher levels of essential nutrients, such as iron, zinc, and vitamins, is crucial for improving the nutritional content of the food supply (Ortiz-Monasterio *et al.,* 2007; Velu *et al.,* 2022). Furthermore, crop diseases cause significant yield losses, thereby threatening global food security (Mahmuti *et al.,* 2009). Developing disease-resistant crops is crucial for global food security (Piquerez *et al.,* 2014). This involves identifying resistance-conferring genes or traits and using them to breed new cultivars via traditional or molecular breeding methods such as genetic engineering (Li *et al.,* 2012; Rahmatov *et al.,* 2019). Furthermore, breeders have the potential to develop nitrogen-use efficient crops, contributing to sustainability by reducing the need for chemical fertilizers (Hitz *et al.,* 2017).

6. Wheat Nutrient Composition

Wheat is arguably the most important food crop globally, given its significant consumption and impact on human nutrition (Shewry and Tatham, 2016). Wheat contributes approximately 30% of the calories, more than 20% of the protein, 37-40% of the dietary fiber, 38-40% of iron (Fe), and nearly 30% of the folates to the daily intake of adults in highly industrialised countries (Shewry and Tatham, 2016). Wheat is also a valuable source of vitamins and minerals such as thiamine, riboflavin, niacin, and folate (Batifoulier *et al.,* 2006; Shewry and Hey 2015a). Aside from its nutritional properties, wheat is a valuable source of other minerals such as phosphorus, potassium, calcium, and magnesium (Li *et al.,* 2004).
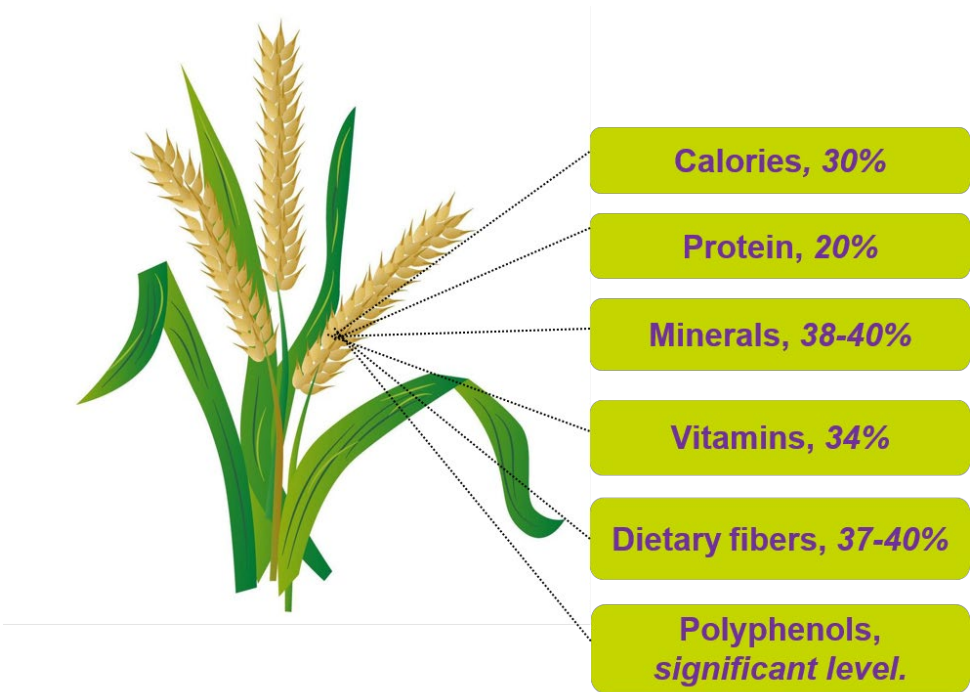
Figure 2: Some important quality traits in wheat (Contribution of 100g of whole wheat to the daily recommended intake (DRI))

6.1 Wheat Energy Contribution

Energy is essential for all living organisms, including humans, for whom carbohydrates are the primary source, contributing 45-70% of the total energy intake (Lafiandra *et al.,* 2014). Carbohydrates are classified based on their degree of polymerization and sugar composition into monosaccharides, disaccharides, oligosaccharides, starch (amylose and amylopectin) and non-starch polysaccharides (fibers). Mature wheat grain contains approximately 65-75% carbohydrates, the majority of which is starch. Around 1% consist of monosaccharides (glucose and fructose) and disaccharides (maltose and sucrose), another 1% is oligosaccharides

(raffinose and fructo-oligosaccharides), 1-2% is fructans, and about 10% comprises cell wall polysaccharides (cellulose, arabinoxylan and dietary fibers). Wheat bran consists of 50% of polysaccharides with a low starch content, whereas the starchy endosperm is composed of approximately 83-84% starch (Shewry *et al.,* 2020). The remaining 16-17% comprises proteins, fats, vitamins, and minerals. Wheat bran also contains bioactive compounds such as polyphenols and antioxidants, which offer various health benefits, like reducing inflammation, improving digestion, and protecting against chronic diseases (Stevenson *et al.,* 2012).

6.2. Wheat Protein

Wheat is renowned for its versatility and ability to be processed into various food products (Shewry and Tatham, 2016). These characteristics are primarily determined by the protein concentration and composition in the wheat caryopsis (Gupta *et al.,* 1996). The wheat grain is formed by two sperm cells fertilizing the egg, where one develops into the starchy endosperm and the other forms the germ and bran (Bechtel *et al.,* 2009). The starchy endosperm, which contains mainly starch, also contributes storage proteins known to significantly impact the bread-making quality of wheat (Payne, 1987). The protein content in a mature wheat seed is normally 7 – 22% of the dry weight (Vogel *et al.,* 1976; Shewry and Hey, 2015a).

Wheat proteins are classified into two major types based on solubility: gluten and non-gluten proteins (Ma *et al.,* 2019). Non-gluten proteins include albumin, which is soluble in water, and globulin, which is soluble in a saline solution. Among the non-gluten proteins are the alpha-amylase inhibitors, which modulate starch digestion (Singh *et al.,* 2001). Gluten proteins form the cohesive mass known as gluten, which remains after washing dough made from flour and water with a substantial volume of water or saline solution (Shewry, 2019). These proteins constitute approximately 80% of the total protein content in mature wheat grain (Shewry and Hey, 2015a; Bromilow *et al.,* 2017) and are composed of gliadin, which is soluble in 60-70% alcohol, and glutenin, which is soluble in either alkali or acid solutions (Shewry and Tatham, 2016). Gliadin imparts viscosity and extensibility to the dough, enhancing its ability to stretch without deforming easily, while glutenin contributes strength and elasticity (Shewry *et al.,* 2003a).

The combined influence of gluten proteins is pivotal for wheat processing, as they provide a range of functional attributes critical for baking (Johansson and Svensson, 1995). Numerous studies (Johansson, 1989; Ma *et al.,* 2019; Shewry, 2019) have shown that the composition of the gluten proteins plays a central role in determining the fundamental characteristics of both

flour and dough, ultimately influencing their suitability for transformation into finished products.

6.2.1 Wheat Gluten Protein

The properties that underpin dynamic functionalities and end-use qualities of wheat are influenced not only by the gluten protein concentrations but also by the composition and combination of different gluten proteins and their subunits (Johansson *et al.,* 1994; Shewry *et al.,* 2003a; Liu *et al.,* 2023). The balance between gliadin and glutenin components in wheat flour significantly affects its functional properties (Johansson *et al.,* 2013; Ma *et al.,* 2019). Glutenins are particularly influential in the bread-making characteristic of wheat flour due to the formation of intra- and inter-chain disulphide bridges (covalent bonds) within and between subunits (Johansson and Svensson, 1998; Johansson *et al.,* 2013; Shewry and Hey, 2015a). This property of the glutenins contributes to the formation of the dough and its complex matrix of a continuous network, resulting in elastic properties and strength (Johansson *et al.,* 2013). Gliadins, on the other hand, primarily form intra-molecular disulphide cross-links in their native state (Markgren *et al.,* 2020, 2022) and contribute to the viscosity of wheat dough, allowing it to stretch without easily breaking (Shewry *et al.,* 2003a).

6.2.2 Wheat Gluten Subunits

The processing, functional, and end-use qualities of wheat flour are strongly influenced by the composition of the gluten proteins (Payne, 1987; Johansson and Svensson, 1995). Techniques such as sodium dodecyl sulphate-polyacrylamide gel electrophoresis (SDS-PAGE) are widely utilized to separate gluten proteins and subunits based on size or molecular weight; thus, aiding in understanding their composition (Gupta *et al.,* 1996). Additional analytical methods, including isoelectric focusing (IEF), high-performance liquid chromatography (HPLC), capillary electrophoresis and mass spectroscopy, have also been adapted to analyse compositional variation and the polymerisation behaviour of these proteins. Gliadin, a component recognized for imparting viscosity and extensibility to wheat dough, primarily comprises individual gluten protein units in their monomeric form (Wrigley *et al.,* 2006). Gliadin can be further divided into distinct subunits, namely alpha, beta, gamma, and omega, each contributing to its overall structure and functionality (Shewry *et al.,* 2003a). A newly identified subunit referred to as delta has been reported in recent studies (Altenbach *et al.,* 2019), although ongoing research is dedicated to confirming its existence and characteristics. Due to the similarity of their amino acid sequences, alpha and beta gliadin subunits are collectively designated as alpha-type gliadin subunits (Wrigley *et al.,* 2006). In contrast, the

Glutenin component, which imparts elastic properties to wheat gluten, is divided into high molecular weight glutenin subunits (HMW-GS) and low molecular weight glutenin subunits (LMW-GS) monomers (Wieser *et al.,* 2023). HMW-GS are generally known as polymers, while LMW-GS are referred to as monomers in their native state. LMW-GS can be further separated, based on size, isoelectric points, and composition into B, C, and D subunits (Shewry, 2019). The B-type subunit of LMW-GS has two groups differentiated by methionine and serine amino acids (Wrigley *et al.,* 2006). HMW-GS are polymeric gluten proteins and can be divided into x- and y-type subunits (Shewry *et al.,* 2003b). Examples of HMW-GS pairs include 1, 2*, 21* from the 1A chromosome, 6+8, 7+9 from the 1B chromosome, and 5+10, and 2+12 from the 1D chromosome (Johansson and Svensson, 1995). Molecular and biochemical studies have revealed that gluten proteins are structurally and evolutionary associated, and that they are either soluble in alcohol-water mixture as monomers (gliadins) or in basic or acidic condition as reduced subunits (glutenin polymers) (Bromilow *et al.,* 2017). Based on solubility, gluten proteins are classified into three groups (Shewry and Tatham, 2016). The HMW subunits group; the sulfur-rich group, which includes alpha-type gliadin, gamma-gliadins, and B- and C-type LMW glutenin subunits; and the sulfur-poor group, which consists of omega-gliadins and D-type LMW glutenin subunits (Shewry and Halford, 2002). The amino acid sequence of C- and D-type LMW glutenin subunits is similar to omega gliadins, with the former exhibiting additional cysteine residues that enable interchain disulfide bridge formation, an effect of mutation (Bromilow *et al.,* 2017).
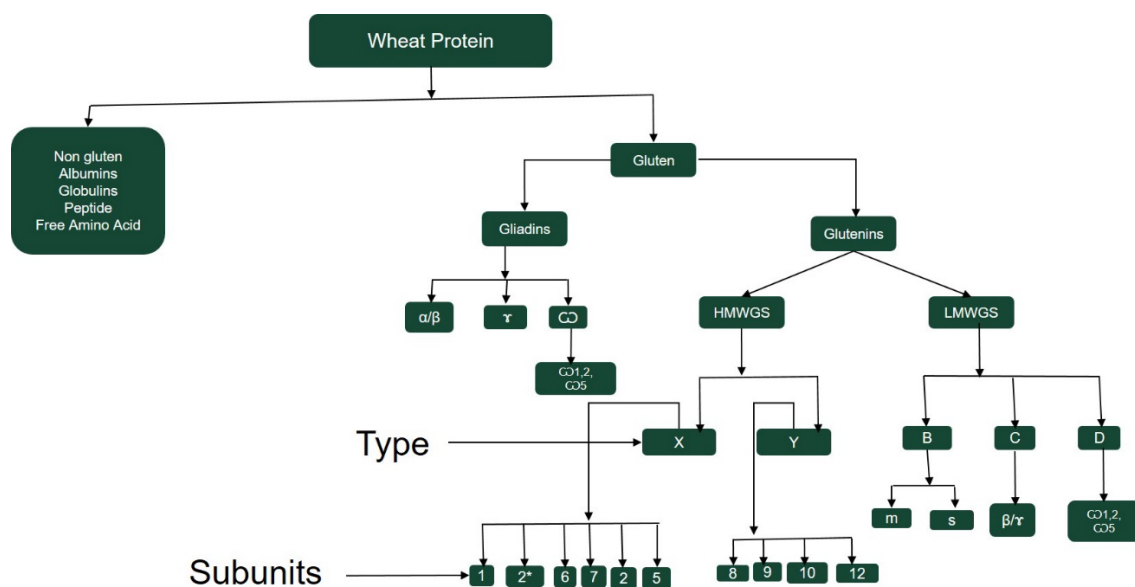
Figure 3: Protein composition and Gluten subunits in wheat

6.2.3 Genetic Control of Wheat Gluten

Several studies have reported chromosomal locations of gluten protein genes, which is crucial for identifying genes controlling gluten protein and developing markers for rapid selection of these traits among different wheat genotypes (Shewry *et al.,* 2003a; Distelfeld *et al.,* 2006; Wang *et al.,* 2020; Zhou *et al.,* 2021). Gliadin protein genes are located on *Gli-A1*, *Gli-B1* and *Gli-D1* loci of hexaploid wheat (Camerlengo *et al.,* 2017). These loci linked to omega and gamma-gliadins subunits and are located on the short arms of chromosomes 1A, 1B and 1D, respectively (Hsia and Anderson, 2001). Similarly, alpha-type gliadins are linked to genes located on *Gli-A2*, *Gli-B2* and *Gli-D2* loci on the short arms of Chromosomes 6A, 6B and 6D, respectively (Dubois *et al.,* 2016). The genes encoding HMW-GS are complex and located in *Glu-A1, Glu-B1* and *Glu-D1* loci on the long arm of chromosomes 1A, 1B and 1D, respectively, where eaach locus are containing x- and y-type subunits based on size and biochemical properties (Shewry, 2019). However, due to gene silencing, wheat genotypes typically have between three to five HMW-GS genes. For instance, *Glu-A1* may contribute none or one subunit, *Glu-B1* may contribute one or two, and *Glu-D1* consistently contribute two subunits (Johansson *et al.,* 1993). Notably, the *x- type* is the only expressed HMW-GS at *Glu-A1* and *Glu-B1* when only one subunit is expressed at these loci (Shewry *et al.,* 2003a). There are also allelic differences among HMW-GS that contributing to genetic variation influencing baking properties of wheat. These differences can be analyzed using the SDS sedimentation test (Johansson *et al.,* 1993; Johansson and Svensson, 1995). The differences include subunits such as 1x, 2*x, 6x, 7x, 8y, 9y, 5x, 2x, 10y and 12y HMW-GS. The subunit 1Ax5 has a unique disulfide structure, and 1Ax7 is consistently present in high amounts compared to other HMWGS. (Johansson *et al.,* 1993; Johansson and Svensson, 1995). The LMW-GS are controlled by genes located at the *GLU-A3*, *Glu-B3* and *Glu-D3* loci on the short arm of the homoelogous chromosomes 1A, 1B and 1D (Shewry and Tatham, 2016).

Table 1: Protein and corresponding genes related to wheat grain quality

Protein/Enzymes	Gene	Chromosome location	Reference
Granule-bound starch synthase 1	Wx-1	7AS, 7BL, 7DS	Chao *et al.* (1987), Ainsworth *et al.* (1993), Yamamori *et al.* (1994)
Starch Snythase II or SGP-1 (SGP-A1, SGP-B1 and SGP-D1)	SS-IIa	7AS, 7BS, 7DS	Li et al (1999, 2003) Shimbatal *et al.* (2005)
Starch branching enzyme SGP2 Grain Hardness	SBE IIa, -IIb	2AL, 2BL, 2DL	Nair *et al.* (1997), Rahman *et al.* (2001)
Puroindoline A (Pin A)	Pina- D1	5DL	Li *et al.* (2008)
Puroindoline B (PIN B)	Pin b-D1	5DS	Ali *et al.* (2015)
Grain softness Protein	Gsp-1	5DS	Jolly *et al.* (1996)
α- and β- gliadins	Gli-2	6AS, 6BS, 6DS	Metakosvsky *et al.* (1984)
ɤ- and ꞷ-gliadins	Gli-1	1AS, 1BS, 1DS	Metakosvsky *et al.* (1984)
HMW-GS	Glu-1	1AL, 1BL, 1DL	Payne (1987)
LMW-GS	Glu-3	1AS, 1BS, 1DS	Singh and Sheperd (1988). Liu (1995)

6.2.4 Measurement of Wheat Protein Content and Gluten Composition

Protein plays a significant role in the human diet, it helps in biochemical and enzymatic processes in support of the body's optimal growth and development, hormonal regulation, and disease prevention, among others (Hoffman and Falvo, 2004; Mæhre *et al.,* 2018; Hayes, 2020). Protein is a critical component of wheat, and the quality of wheat protein indicate not only its nutritional value, which is essential for human health and well-being (Johansson *et al.,* 2014; Shewry and Hey, 2015a), but also affects the economic value of the various products made from it (Hayes, 2020). The concentration of protein is a key factor in determining wheat protein value (Hayes, 2020). Several researchers have employed different techniques to quantify protein content, including the Kjeldahl technique, Dumas technique, Near-infrared reflectance spectrometry (NIR), Size-exclusion high-performance liquid chromatography (SE-HPLC) and UV-spectroscopy (Mæhre *et al.,* 2018). All of these methods have their advantages and limitations, and most of the more recent techniques are correlated to the Kjeldahl method, which involves sample digestion in the presence of strong acid for nitrogen release and quantification

using a titration method (Mariotti *et al.,* 2008). The protein content is then calculated by multiplying the nitrogen concentration with a specific conversion factor of the wheat part used (Whole grain, flour, or bran) (Maclean *et al.,* 2003). However, the accuracy of protein measurement of this method is still debatable (Mariotti *et al.,* 2008). The SE-HPLC method is considered a more reliable techniques for measuring protein quantity (Hayes, 2020). This method often involves the digestion of wheat flour by Sodium dodecyl sulfate (SDS) and sodium phosphate buffer in two extraction steps to obtain SDS-extractable and SDS-unextractable proteins (sonicated sample), with the amount and size distribution of proteins later analyzed using SE-HPLC system (Lan *et al.,* 2023). From the chromatogram, large polymer protein (LPP), small polymer protein (SPP), large monomer protein (LMP), and small monomer protein (SMP) are calculated separately for both SDS-extractable and SDS-unextractable proteins according to the specified retention time (Lan *et al.,* 2023). Total SDS-extractable protein (TOTE) calculated from the sum of all SDS-extractable large and small polymers along with large and small monomers, correlates well with protein content as shown by several authors (Johansson *et al.,* 1995; Johansson *et al.,* 2013; Alvarez and Guzmán, 2018; Lan *et al.,* 2023). TOTE demonstrates a strong correlation with alternative protein quantification techniques such as the Kjeldahl and Dumas methods, as evidenced by the research conducted by Lan *et al.* (2023). Likewise, the percentage of SDS-unextractable polymer protein in total polymer protein (%UPP) serves as a valuable metric for assessing gluten strength (Wrigley *et al.,* 2006). This metric is derived by summing the quantities of SDS-unextractable large and small polymer proteins and then dividing by the total sum of SDS-unextractable large and small polymer proteins, as well as SDS-extractable large and small polymer proteins, and then multiplying by 100%. This parameter has been established as a significant gauge of gluten's cohesive strength, substantially influencing functional attributes and bread-making proficiency of wheat dough (Johansson *et al.,* 2013; Lama *et al.,* 2023).

6.3 Wheat Amino Acid Composition

Amino acids are fundamental components of proteins and serve as the building blocks for neurotransmitters and hormones (Dietzen, 2018). Each amino acid is an organic compound containing an amino (-NH2) and a carboxylic acid (-COOH) functional groups. Proteins consist of chains of alpha-amino acids, distinguished by the separation of amino and carboxylic acid groups (side chain R-group) by a single carbon atom, often chiral, which impart unique properties to each amino acid. The further arrangement of amino acids within a protein chain

and their interactions with the environment determine the protein's distinctiveness and complexity (Zeece, 2020).

Approximately 20,000 genes encode about 100,000 distinct proteins in the human body (Lopez and Mohiuddin, 2024). Despite the existence of hundreds of natural amino acids, only about 20 are essential for producing proteins in humans and most other life forms. These amino acids are primarily L-isomers, with exceptions such as glycine, which lacks a chiral center, and cysteine, which has an S-absolute configuration due to its sulfur-containing R-group. Selenocysteine and pyrrolysine have been reported with functional significance as the 21st and 22nd amino acids, respectively, by recent studies, but they do not apply to human protein synthesis (Zhang and Gladyshev, 2007). These 22 amino acids, upon translation, can undergo post-translational modifications, further enhancing protein diversity. The production of neurotransmitters, hormones, muscle development, and other cellular processes in the human body requires a specific quantity of amino acids (Lopez and Mohiuddin, 2024).

After ingestion, dietary are broken down into amino acids, which then assist in food digestion, tissue growth and repair, energy provision, and other bodily functions. Several metabolic pathways involve amino acids within human cells. Amino acids are classified into three groups (Table 2) based on their necessity for growth, nitrogen balance and how they are absorbed into the body. The first group consist of non-essential amino acids, which are synthesized in the body from metabolic intermediates (Wu *et al.,* 2013). The second group includes essential amino acids, which cannot be synthesized by the body and must be obtained from food (Lopez and Mohiuddin, 2024). Conditional amino acids make up the last group and these are considered conditionally essential due to the inability of the body to produce them in adequate amounts during periods of physiological stress, such as growth illness, stress, injury or gestation (Grimble, 1993).

These essential amino acids are available from complete proteins, primarily sourced from animal products except for soybeans, which are a notable plant-based source. Incomplete proteins, often plant-based, also provide these essential amino acids. Wheat protein concentration and amino acid composition are critical factors influencing its processing into various food products (Johansson and Svensson, 1998; Siddiqi *et al.,* 2020; Shewry, 2023).

Table 2: List of important amino acids and minimum recommended adult intake (RAI) of essential amino acid (g/100 g protein) from protein (%N × 5.7) according to WHO/FAO/UNU Expert Consultation (2002, Geneva, Switzerland).

Amino Acid	Necessity from Food	WHO adult intake (g/100 g protein)	Sufficient availability in wheat
Alanine	Non-essential	-	Yes
Asparagine	Non-essential	-	Yes
Aspartic acid	Non-essential	-	Yes
Glutamic acid	Non-essential	-	Yes
Lysine	Essential	4.5	Limited
Isoleucine	Essential	3.0	Yes
Leucine	Essential	5.9	Yes
Phenylalanine	Essential	3.8	Yes
Phytophan	Essential	0.6	Yes
Histine	Essential	1.5	Yes
Threonine	Essential	2.3	Limited
Methionine	Essential	1.6	Limited
Valine	Essential	3.9	Yes
Arginine	Non-essential/Conditional	-	Yes
Cysteine	Non-essential/Conditional	-	Yes
Glutamine	Non-essential/Conditional	-	Yes
Tyrosine	Non-essential/Conditional	-	Yes
Glycine	Non-essential/Conditional	-	Yes
Proline	Non-essential/Conditional	-	Yes
Serine	Non-essential/Conditional	-	Yes

Wheat is rich in most of the essential amino acid when compared to the recommended adult intake, except for lysine, which is present in limiting amounts, with this disparity being more pronounced in white flour compared to wholemeal flour (Tkachuk, 1966; Simmonds, 1962; McDermott and Pace, 1957; Shoup *et al.,* 1966.). The starchy endosperm, from which white flour is derived, contains a significant amount of gluten protein that is specific to it. This gluten protein, which constitutes approximately 80 % of wheat protein, is limited in lysine but boasts a substantial abundance of proline and glutamine (Shewry and Hey, 2015a).

6.4 Wheat Mineral Composition

Staple crops like cereals need to be improved nutritionally, as public concern has increased in recent years regarding the daily diet's nutrient and health value (Hefferon, 2015). This is unsurprising, as micronutrient deficiency drastically affects human health globally, with a call to address this by incorporation of a dense quantity of essential nutrients into staple diet (Johansson *et al.,* 2020b; Bansode and Kumar, 2015; Gupta *et al.,* 2021). Wheat is an important cereal source of minerals and other nutrients in daily human diet (Welch and Graham, 1999; Hussain *et al.,* 2010). Wheat contributes approximately 15%, 11%, 13% and 14% of Fe, Zn, Mg and Cu, respectively, from bread alone (Henderson *et al.,* 2003). Until recently, wheat improvement focused on yield and disease resistance, but now the focus is shifting toward breeding for nutritional qualities alongside with the aforementioned traits (Welch and Graham, 1999; Morris and Sands, 2006). The condition of having less than adequate levels of essential minerals in human daily diet is known as malnutrition, which can lead to hidden hunger (Bansode and Kumar, 2015). Hidden hunger, recognized as a significant contributor to diseases and infections on a global scale, persists extensively in developing nations and also affects developed countries (Puntis, 2009; Kiran *et al.,* 2022). Among the essential minerals required in the human diet, Fe and Zn are the most critical, affecting over 2 billion people worldwide, most of whom are women and children (Gupta *et al.,* 2021). Lack of Fe causes anaemia, impaired cognition and fatigue, while Zn deficiency results in stunted growth, cell damage, and increased susceptibility to infections (Cakmak *et al.,* 2004). Children aged 0 to 24 months, as well as pregnant and lactating women, are most affected (Gupta *et al.,* 2021). The increasing number of people adopting vegetarian diets, especially in developed countries, may exacerbate hidden hunger, as meat is a primary source of these minerals. Generally, hidden hunger not only affects general health but also has economic implication, as an unhealthy population may not be optimally productive (Welch and Graham, 1999). Among the strategies to mitigate hidden hunger is food fortification (Bouis and Welch, 2010), which involves supplementing grains

with essential nutrients (Borrill *et al.,* 2014). However, this strategy has limitations, including limited availability to rural dwellers and the significant cost implications over time. Another strategy is improving existing cultivars through the use of wild relatives of the crop, which are rich in these micronutrients, a process known as biofortification (Aigul *et al.,* 2019). This approach can be economical, sustainable and more accessible to everyone. To optimize biofortification strategies, it is essential to understand the genetic mechanisms that control iron Fe and zinc Zn accumulation in wheat grains. By leveraging genetic tools such as Genome-Wide Association Studies (GWAS) and Quantitative Trait Locus (QTL) mapping, researchers can identify specific genes and loci that contribute to the accumulation of these essential micronutrients. Recent genetic studies on wheat have identified key QTLs and genes responsible for the accumulation of Zn and Fe, critical for biofortification efforts. For Zn, a significant QTL on chromosome 6D plays a major role in grain Zn concentration, with additional QTLs mapped on chromosomes 1A, 3A, 4A, 5B, and 7A. The gene TraesCS6D01G234600 has been linked to Zn translocation (Roy *et al.,* 2022; Ma *et al.,* 2023). For Fe, several QTLs, particularly on chromosome 4B, regulate Fe uptake, overlapping with Zn QTLs. Other important loci for Fe are located on chromosomes 3A, 2B, and 5A (Harrington *et al.,* 2023). Chromosome 4B is a hotspot for both Zn and Fe accumulation, suggesting shared genetic pathways (Crespo-Herrera *et al.,* 2016). This knowledge can then be used to develop wheat varieties that are richer in Fe and Zn, addressing nutritional deficiencies in populations that rely heavily on wheat as a staple.

6.5 Dietary Fiber in Wheat

Adequate level of dietary fiber in daily human diet are known to have a positive impact on human health (Lovegrove *et al.,* 2020). Dietary fibers consist of carbohydrates that resist digestion and absorption in the small intestine, instead traveling intact to the colon, where they undergo either complete or partial bacterial fermentation (Ibba *et al.,* 2021). Regular intake of dietary fibre has been linked to lower risk of cardiovascular disease, diabetes, obesity, and colorectal cancer. It also supports colon health by improving digestion, regulating blood sugar levels and intestinal movement (Barber *et al.,* 2020). Given its widespread consumption as a staple cereal, wheat plays a significant role in providing dietary fibre to human diets (Lovegrove *et al.,* 2020). However, it is worth noting that wheat is mainly consumed as white flour containing 2-3 % dry weight of fibre. In contrast, health-promoting components, such as dietary fiber, are primarily concentrated in the bran of a whole grains, which contain 11-15% dry weight of fibre (Gebruers *et al.,* 2008; Andersson *et al.,* 2013). This preference for refined products

contributes to increased obesity and chronic diseases. The key components of dietary fibre in wheat are arabinoxylan (AX), β-glucan, cellulose, and lignin, which are constituent of non-starch polysaccharides and non-polysaccharide compound found mainly in the cell wall (Gebruers *et al.,* 2008). Arabinoxylans (AX) constitute the major portion of dietary fiber (DF) within wheat grain, mainly concentrated in the bran, where they make up 13–22% of its dry weight (Ibba *et al.,* 2021). Improving wheat cultivars with elevated arabinoxylan (AX) content could prove to be an effective strategy for enhancing daily dietary fiber (DF) intake. While tocols, sterols, and arabinoxylan fiber exhibit high heritability (Shewry *et al.,* 2010), researchers have identified significant genomic regions for arabinoxylan (AX) on chromosomes 1A, 1B, 2B, 3B, 5A, 5B, 7A, and 7B (Lovegrove *et al.,* 2020). The identification of these genomic regions can facilitate targeted breeding programs aimed at increasing fiber content in wheat. The recommended daily intake of dietary fiber for adults ranges from 30 to 35 grams for men and 25 to 32 grams for women (Burley *et al.,* 2017). A recent study reviewed dietary fibre intake in European countries, finding that adults typically consume 18 to 24 grams per day for men and 16 to 20 grams per day for women, indicating a significant gap between recommended and actual intake (Barber *et al.,* 2020).

7. Wheat Phytochemicals

Wheat, an essential cereal in the human diet, comprises three main components: germ, starchy endosperm, and bran (consisting of pericarp, testa, hyaline, and aleurone layers) accounting for approximately 2–3%, 81–84%, and 14–16% of the grain weight, respectively (Tian *et al.,* 2022). Whole grains are abundant sources of various health-prompting compounds, including dietary fibre, vitamins and phytochemicals (Onipe *et al.,* 2015). Phytochemicals, biologically active compounds of plant origin, offer significant health benefits beyond basic nutrition and may reduce the risk of chronic diseases (Okarter *et al.,* 2010). The primary phytochemical groups found in whole grains include polyphenols, carotenoids, flavonoids, vitamin E compounds, β-glucan, inulin, and curcumin (Liu, 2007). While over 5,000 individual phytochemicals have been identified in fruits, vegetables, and grains, many remain undiscovered, necessitating further research to fully elucidate the health-promoting effects of phytochemicals in whole-grain foods (Liu, 2004). Epidemiological studies have linked the consumption of whole grain products to a reduced risk of chronic diseases such as obesity, type 2 diabetes, cardiovascular diseases (CVDs), and cancer (Okarter *et al.,* 2010).

Despite the potential health benefits, phytochemicals in grains have received less attention compared to those in fruits and vegetables, partly due to the lower concentration of antioxidant

capacity reported in earlier studies (Liu, 2004). This discrepancy may be attributed to limitation in extraction methods, primarily aqueous solutions of methanol, ethanol, and acetone, which predominantly extract free phenolic compounds, overlooking the bound phenolics, which constitute approximately 75% of the total (Adom and Liu, 2002). Recent advancements in extraction techniques, such as high-performance liquid chromatography (HPLC), have revealed a more comprehensive profile of phytochemicals in whole grains, indicating their richness beyond previous estimations (Kool *et al.,* 2011). The underestimation of phytochemicals in whole wheat grains may have obscured their potential as valuable sources of health-promoting compounds, comparable to those in fruits and vegetables (Adom and Liu, 2002). The bran and germ of whole wheat are concentrated sources of bioactive compounds and may impart greater health benefits when consumed as part of a diet, thus helping to reduce the risk of chronic diseases (Adom *et al.,* 2003). Phytochemicals in whole grains are distributed as free, soluble-conjugated, and bound forms, with a significant portion bound to cell wall materials (Menga *et al.,* 2023). These bound phytochemicals, resistant to digestion in the upper gastrointestinal tract, may undergo colonic fermentation, releasing their beneficial effects locally and systemically (Liu, 2007).

The cumulative and synergistic effects of various bioactive components present in whole grain foods, some unique to them, may confer greater health benefits than isolated compounds (Liu, 2004). The synthesis and accumulation of phytochemicals in wheat are influenced by genotype (Shewry and Hey, 2015), the growing environment (Shewry *et al.,* 2010), and their interaction (Lu *et al.,* 2015). Further research into these factors is vital for enhancing the phytochemical content of wheat, thereby promoting its potential health benefits. Recognizing the growing consumer demand for healthy food options, wheat breeders and producers are increasingly considering phytochemical content as a quality parameter alongside conventional end-use properties (Shewry *et al.,* 2012a), in which wild relatives of wheat could be a potential foundation for such variation (Shewry and Ward, 2012b).

7.1 Polyphenols in Wheat

The quantity and composition of polyphenols in wheat products are crucial for health and well-being due to their antioxidant and anti-inflammatory properties (Kiani *et al.,* 2021). Polyphenols are a diverse group of phytochemicals that share a common chemical structure characterized by an aromatic ring with one or more hydroxyl substituents (Ayad and Akkal, 2019). These compounds can be categorized into several classes, with the principal groups

encompassing flavonoids, phenolic acids, tannins, stilbenes, alkylresorcinols and lignans (Shewry and Ward, 2012b; Luna-Guevara *et al.,* 2018). Phenolic acids are the most abundant polyphenol in wheat and include ferulic acid, vanillic acid, caffeic acid, syringic acid, and p-coumaric acid (Buczek *et al.,* 2023). Most phenolic acids in wheat are bound to cell wall components, accounting more than 90% of their total content, with ferulic acid being the predominant form (Sosulski *et al.,* 1982). Ferulic acid is especially abundant in the aleurone, pericarp, and embryo cell walls of various grains and is present in trace amounts in the starchy endosperm (Zhang *et al.,* 2023). It comprises 70–90% of the total polyphenol content in wheat, with derivatives such as dihydroferulic, sinapic, caffeic, vanillic, syringic, p-coumaric, and phydroxybenzoic acid also detected, primarily in the bran and occurring in both free and bound forms (Bresciani *et al.,* 2016). Among phenolic acids, diferulic acids (DFAs) are of particular interest due to their ability to form cross-links between polysaccharide chains, thereby influencing the structural integrity of cell walls. Diferulic acids include isomers such as 8-8 FA, 8-5 DFA, 5-5 DFA, 8-O-4′ DFA, and 8-5 benzofuran DFA, existing in monomeric and oligomeric forms. DFAs, particularly dimers of ferulic acid, can be extracted alongside other phenolic acids, with most present in insoluble fractions (Parker *et al.,* 2005; khosravi *et al.,* 2020). Flavonoids, is another major polyphenol group in wheat, especially prominent in colored cultivars and include apigenin, chrysoeriol, kaempferol, quercetin, and luteolin, predominantly found in conjugated forms with various sugars (Dinelli *et al.,* 2011). Anthocyanins, specific flavonoid compounds present in colored wheat cultivars, include cyanidin, malvidin, petunidin, and delphinidin, occurring mainly in their sugar derivatives, albeit in lower concentrations compared to phenolic acids (Liu *et al.,* 2010). These pigments provide color and also contribute to the antioxidant capacity of wheat products. Polyphenols contribute to the color, taste, and nutritional value of wheat and have been studied for their potential health benefits, including anti-inflammatory, anticancer and antioxidant properties.

7.1.1 Antioxidants in Wheat

Polyphenols are a diverse group of phytochemicals renowned for their potent antioxidant properties, largely due to their ability to donate electrons and neutralize free radicals. These phenolic compounds, abundant in whole grains, play a significant role in combating oxidative stress, with high phenolic content strongly correlated with increased antioxidant potential (Khosravi *et al.,* 2020). Antioxidants, which include both naturally occurring and synthetic compounds such as vitamins and minerals, are crucial in neutralizing free radicals within the body (Mamta *et al.,* 2014). Their essential role extends to reducing the risk of chronic conditions

such as cancer, coronary artery disease, muscular degeneration, and serious eye diseases, while simultaneously enhancing immune function (Akond *et al.,* 2010). Polyphenols, as part of these antioxidant systems, offer numerous health benefits. They help reduce the risk of diabetes, cardiovascular diseases, and obesity and they serve as anti-mutagenic, anti-allergenic, anti-inflammatory, antimicrobial, and anti-apoptosis agents (Balasundram *et al.,* 2006). For instance, polyphenols exhibit antioxidant activities by inhibiting oxidase enzymes, protecting antioxidant enzymes, reducing free radical generation, and inactivating free radicals. These mechanisms make polyphenols effective antibacterial, anticancer, and anti-inflammatory agents (Kardum *et al.,* 2014; Zhao *et al.,* 2017). Polyphenols are synthesized in plants in response to physiological and oxidative stresses, serving protective roles against pathogen attacks, UV radiation, and physical damage (Al-Rawahi *et al.,* 2013). The antioxidant activity of whole grain wheat varies among different species and genotypes, emphasizing the potential to exploit genetic variation to enhance the polyphenol content in wheat, thereby promoting human health benefits (Shewry and Hey, 2015b). Efforts to breed wheat varieties with higher antioxidant capacities could lead to healthier dietary options and align with consumer demand for nutrient-rich foods.
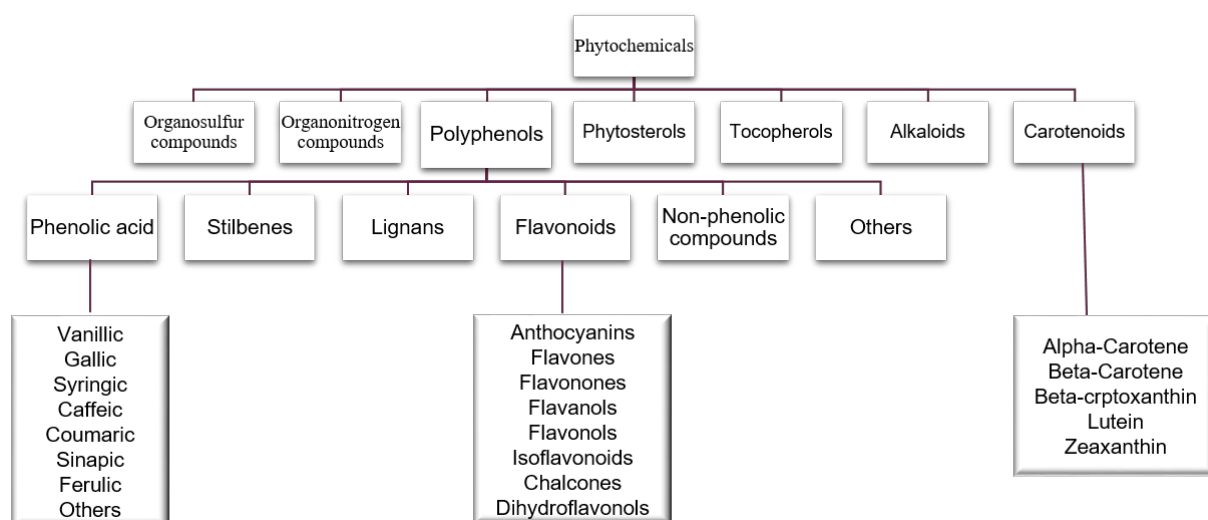

Figure 4: Phytochemicals composition in wholegrain wheat (Adapted from Ammar et al., 2023 and Tian et al., 2022).

8. Different Genetic Origin of Wheat

8.1 Wheat-Alien Introgression Lines

Common wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) originated from a series of hybridizations involving *Triticum urartu,* which contributes the AA genome, a species believed to be *Aegilops speltoides* that provides the BB genome and *Aegilops tauschii*, which carries the DD genome (Sarka and Stebbins 1956; Dvořák *et al.,* 1993; Matsuoka, 2011; Levy and Feldman, 2022). Common wheat belongs to the *Poaceae* (grass family), which includes important cereals such as durum wheat, barley, and rye, and falls under the tribe *Triticeae*. This tribe encompasses over 500 wild and cultivated species across several genera, including *Aegilops, Leymus, Secale, Triticum, Agropyron,* and *Thinopyrum* (Rey *et al.,* 2015). Members of this tribe are recognized for their beneficial agronomic characters which includes resistance to biotic and abiotic stresses, enhanced nutritional profile, increased yield, wide environmental adaptation, reduced lodging, and earliness (Bedő and Láng, 2015; Rahmatov *et al.,* 2016; Johansson *et al.,* 2020b). Species carrying these traits have been hybridized with common wheat, followed by the subsequent identification and mapping of the genes associated with the traits of interest to specific loci (Rabinovich, 1998). Wheat-alien introgression, which involves transferring chromosome segments from wild wheat relatives into cultivated wheat, has been a valuable tool in wheat breeding programs by introducing new genetic variability into the common wheat gene pool (Molnar-Lang *et al.,* 2016; Rahmatov, 2016b; Johansson *et al.,* 2020b). This is complex and time-consuming process that requires careful planning, precise breeding, and thorough selection to incorporate new traits while maintaining desirable characteristics. Additional breeding and selection are often necessary to ensure stable and consistent trait expression across generations.

Homologous chromosome pairing in wheat, particularly with chromosomes from the tertiary gene pool, is controlled by the pairing homoeologous loci, Ph1 and Ph2, located on chromosomes 5BL and 3DS, respectively (Gill *et al.,* 1993; Sutton *et al.,* 2003). The Ph1 locus plays a dominant role during meiosis, ensuring that only true homologous chromosomes pair and preventing recombination between homoeologous chromosomes (Rawale *et al.,* 2019). This mechanism is essential for maintaining the genomic stability of hexaploid wheat (Triticum aestivum), which has genomes from three ancestral species (AA, BB, and DD). The deletion of the Ph1 locus, as seen in the ph1b mutation in hexaploid wheat and ph1c mutation in tetraploid wheat, reduces the strict control over chromosome pairing, facilitating homoeologous recombination and genetic material transfer between wheat and other species (Giorgi and

Barbera 1981; Sears 1977). This process provides valuable opportunities for wheat breeding by introducing desirable traits, such as disease resistance, drought tolerance, and improved quality, from the tertiary gene pool into the wheat genome (Yazdani *et al.,* 2023; Lan *et al.,* 2023).

Alien gene introgressions are well-known for their notable impact on disease resistance, though they typically display limited influence on product quality, except for the 1BL.1RS translocation (Kaur *et al.,* 2022). While this translocation is known to have a negative effect on baking quality, it has proven extremely useful in combating several strains of wheat rust and powdery mildew diseases. However, the recent shift in plant breeding focus towards quality traits, driven by health and environmental concerns, underscores the need for proactive pursuit of attributes aligned with these priorities. Recent research has revealed increased levels of iron (Fe) and zinc (Zn) in wheat resulting from the incorporation of genes from *Leymus racemosus* and *Leymus mollis*, and additional reports indicate increased levels of these minerals alongside reduced cadmium content through introgressions from 1R, 2R, 5R, and *Leymus spp*. Furthermore, wheat-*Leymus* hybrids have shown promising enhancements in protein content and gluten strength, suggesting potential improvements in bread-making attributes. The gene complex *SR31/Yr9/Lr26/Pm9* has notably contributed to agricultural productivity, and recent gene introductions such as *Sr59*, *Pm56*, and *Yr83* offer further prospects for enhanced agricultural performance through targeted gene transfer approaches.

Successful introgression has been reported for rye (*Secale cereale*), *Thinopyrum junceiforme*, *leymus racemosus* and *leymus mollis* (Merker and Rogalska, 1984; Merker and Lantai, 1997; Ellneskog-Staam and Merker, 2002; Kole, 2011) with 1BL/1RS wheat-rye translocation proving to be extremely useful in the fight against several strains of wheat rust and powdery mildew diseases. Introgressed chromosome segments from rye into wheat genome such as 1AL/1RS (from Amigo), 1BL.1RS, 1DL.1RS, 2BL.2RS, 3BL.3RS, 5AL.5RS, 1R + 2R, 1R +3R, 5R + 4R + 7R AND 1R + 6R +4R +7R, and 1B(R) substitutions have been documented to be useful against several insects and different strains of stem, stripe and leaf rusts wheat pathogens (Rabinovich, 1998; Rahmatov *et al.,* 2016; Johansson *et al.,* 2020b).

8.2 Landraces, Old and Ancient Wheat

The importance of landraces in safeguarding genetic diversity is rooted in their inherent competitiveness and capacity to thrive in distinct environments, a trait developed from numerous cycles of human-driven evolution, and supported by a diverse genetic foundation (Gadaleta *et al.,* 2023). Emerging as dynamic populations, landraces were cultivated during the evolutionary progression of crops through human selection in recently inhabited areas

following the onset of agriculture until the late 19th century. This period saw the emergence of inbred lines and cultivars in the early 20th century, making a transition away from genetically heterogeneous collections of plants. (Peleg *et al*., 2011). Due to their extensive genetic diversity, landraces manifest substantial allelic variability associated with diverse traits including end-use functionality and nutritional quality, including micronutrient content (Zn and Fe), fatty acid profiles, phytochemicals, vitamins, amino acid, protein composition, baking properties, sensory attributes, as well as factors such as disease resistance, and adaptability (Johansson *et al.,* 2020b, 2021; Sönmez *et al.,* 2023). Despite the contention that the yield potential of landraces is considered a notable limitation, they remain a valuable resource for reintroducing lost alleles into modern cultivars. This process serves to enhance the functional and nutritional potential of these cultivars. Wheat cultivars grown in Sweden from 1900 to 1960 are classified as "old cultivars" according to research by Hussain *et al.,* in 2010 and Johansson *et al.,* in 2021. These cultivars have been notably recognised as a distinct reservoir of essential minerals within the human dietary context, as documented by Hussain *et al.,* in 2010. Furthermore, they represent a potential reservoir for achieving elevated and consistent gluten strength, as highlighted by Lan *et al.,* in 2023. Additionally, these cultivars exhibit adaptability to resource-constrained environments, primarily attributed to their efficient nitrogen utilization mechanisms, as elucidated by Pourazari *et al.,* (2015). These exceptional attributes, despite their well-documented yield reduction compared to modern cultivars as reported by Pourazari *et al.* (2015), offer valuable prospects for harnessing these distinctive features in the strategic development of novel cultivars designed to enhance end-use qualities.

Heritage crops bear significant agricultural importance, rooted in their historical and cultural significance (Shewry and Hey, 2015b). These plants harbour extensive genetic diversity, offering potential contributions to human nutrition, crop enhancement, and resilience against environmental challenges, beyond their cultural value. Heritage crops embody a blend of biodiversity, culture, and sustainability, yielding insights into a resilient agricultural approach that bridges the past with the present (Cabas-Lühmann *et al.,* 2023). Integrating heritage crops into contemporary food systems through strategic plant breeding holds promise for addressing current challenges.

Certain wild and primitive wheat cultivars, including *Triticum monococum, Triticum dicoccon, Triticum dicoccoides,* and *Aegilops speltoides*, exhibit promise as genetic sources for essential micronutrients, surpassing cultivated wheat cultivars and advanced breeding lines (Cakmak *et al.,* 1999, 2000). Literature consistently reports elevated levels of the carotenoid lutein (resulting in a yellow colour) in einkorn, emmer, and Khorasan (Kamut) wheat, in contrast to

bread wheat, often chosen for its white appearance (Shewry and Hey, 2015b). Additionally, discernible differences emerge between ancient crops and modern cultivars concerning phenolic acids, other phytochemical compounds, polar metabolites, and dietary fibres (Shewry *et al.,* 2015b, 2017).

9. Wheat Growing Conditions in Sweden

9.1 Organic Farming and Its Importance

To meet one of the United Nations' goals of responsible consumption (SDG 12), consumers' desires for nourishing and delicious food options that contribute to overall well-being and safeguard against chronic ailments need to be satisfied, which could change attitudes toward food wastage, leading to its reduction (Johansson *et al.,* 2014). However, this must be accompanied by responsible and sustainable production, promoting biodiversity and positively impacting the environment. The conventional farming system, characterized by its extensive reliance on synthetic chemicals (fertilizers and pesticides) that gained prominence post World War II (1939–1945), has been identified as having detrimental effects on agricultural sustainability (Tudi *et al.,* 2021). Remarkably, while this system has historically delivered high yields, it has also resulted in enduring negative consequences for human health, animal welfare, biodiversity, and environmental integrity (Scherer *et al.,* 2018; Agovino *et al.,* 2019). Numerous reports have highlighted organic farming as a potential solution to these challenges (Hussain *et al.,* 2012a; Tuomisto *et al.,* 2012; Reganold and Wachter, 2016; Meemken and Qaim, 2018; Pekala, 2020), and it also offers the prospect of supplying nutritious food to our growing global population (Foley *et al.,* 2011). According to the International Federation of Organic Agriculture's (IFOAM) definition, organic agriculture, which includes practices like organic farming, is a production system that puts the health of soils, ecosystems, and people first. It depends on ecological processes, biodiversity, and local adaptations rather than the use of inputs with harmful effects. Organic agriculture integrates tradition, innovation, and scientific knowledge to enhance the overall environment and foster equitable relationships, aiming to improve the quality of life for all involved (IFOAM, 2008). The principles of organic agriculture, founded on the values of health, ecology, fairness, and care, have driven the growing global demand for organic food products (Willer, 2010; Gamage *et al.,* 2023). This growth in demand has resulted in a worldwide expansion of organic production areas, notably in Europe, where Sweden stands out as one of the leading countries (Hussain *et al.,* 2012a; Statistics Sweden, 2021). The European Union aims to allocate at least 25% of agricultural land

to organic production by 2030 through initiatives like the EU Green Deal and Farm to Fork strategies, while Sweden has set a more ambitious target of 30% (European Commission, 2020; Moschitz *et al.,* 2021; Statistics Sweden, 2021). Notably, Sweden experienced an annual growth rate of 8% in organic food demand between 2015 and 2018, and the Green Public Procurement (GPP) Act has set a goal of sourcing 60% of all food purchased by the public sector from organic sources by 2030 (Swedish Government, 2017; EkoWeb, 2020). The cultivation of nutritionally enriched and tasty wheat cultivars, integral to Swedish culture as the most produced and consumed cereal crop, can be effectively advanced through organic farming practices, offering a scientific approach to promote both end-use qualities and well-being.

9.2 Heavy Metals

Heavy metals, defined as metallic elements with an atomic weight greater than 40.04 atomic mass units, can act as toxic contaminants impacting human health (Agency for toxic substances and disease registry (ATSDR), Castro-Gonzalez and Mendez-Armenta, 2008). These metals enter the environment through both natural processes, such as weathering of the earth's crust, and human activities such as mining, industrial discharge, chemical fertilizers and pesticides and urban runoff (Martin and Griswold 2009; Jorhem *et al.,* 2013). Human exposure to heavy metals primarily occurs through the consumption of contaminated food and water, establishing a cyclic pathway involving industry, atmosphere, soil, water, food, and humans (Ming-Ho, 2005; Morais *et al.,* 2012). To mitigate health risks, Commission Regulation (EU) 2021/1323 sets maximum allowable concentrations for heavy metals such as lead, mercury, cadmium, tin, and arsenic in food and feed (European Commission, 2021).

9.2.1 Cadmium Impact on Food Security Challenges in Sweden and Possible Solution

In Sweden, the concentrations of cadmium, a naturally occurring heavy metal in soil, fluctuate based on geographical and soil variations, entering the food chain through crop absorption and raising concerns (The Swedish National Chemicals Inspectorate, 1998; Edirisinghe and Jinadasa, 2019). Dietary exposure is influenced by the consumption of larger food quantities including wheat (European Food Safety Authority, 2012; Jorhem *et al.,* 2013). This metal, which persists in the body and accumulates in the kidneys, poses health risks such as cardiovascular diseases, osteoporosis, cancer, renal tubular dysfunction with prolonged exposure (Hallenbeck, 1984; Rafati-Rahimzadeh *et al.,* 2017). Plant breeding techniques can be employed to effectively decrease the absorption of cadmium, alongside reducing the activities that contribute to its accumulation (Grant *et al.,* 2008; Zaid *et al.,* 2018; Chen and

Wu, 2020). Cadmium although non-essential for plant growth, disrupts vital metabolic pathways by competing with essential elements such as Fe and Mn (Gao *et al.,* 2018), as well as Zn and Ca (Clemens and Ma, 2016), potentially causing health issues and imbalance within biological systems (European Food Safety Authority, 2012; Rafati-Rahimzadeh *et al.,* 2017; Rubio *et al.,* 2023). Identifying genes responsible for Cd accumulation is crucial for breeding wheat varieties with low Cd content. Several studies have reported genes linked to Cd uptake in wheat, including *TaHMA2* and *TpNRAMP5* (Wiebe *et al.,* 2010; Tan *et al.,* 2013). Additionally, 26 QTLs related to Cd stress have been identified, with two QTLs on chromosomes 4A and 5D specifically influencing Cd accumulation in roots (Ci *et al.,* 2012). In durum wheat, the *Cdu1* gene, located on chromosome arm 5BL, plays a major role in regulating Cd concentration in grains (Penner *et al.,* 1995; Knox *et al.,* 2009; Wiebe *et al.,* 2010). These findings provide valuable genetic targets for developing wheat varieties with reduced Cd accumulation, improving food safety and crop quality.
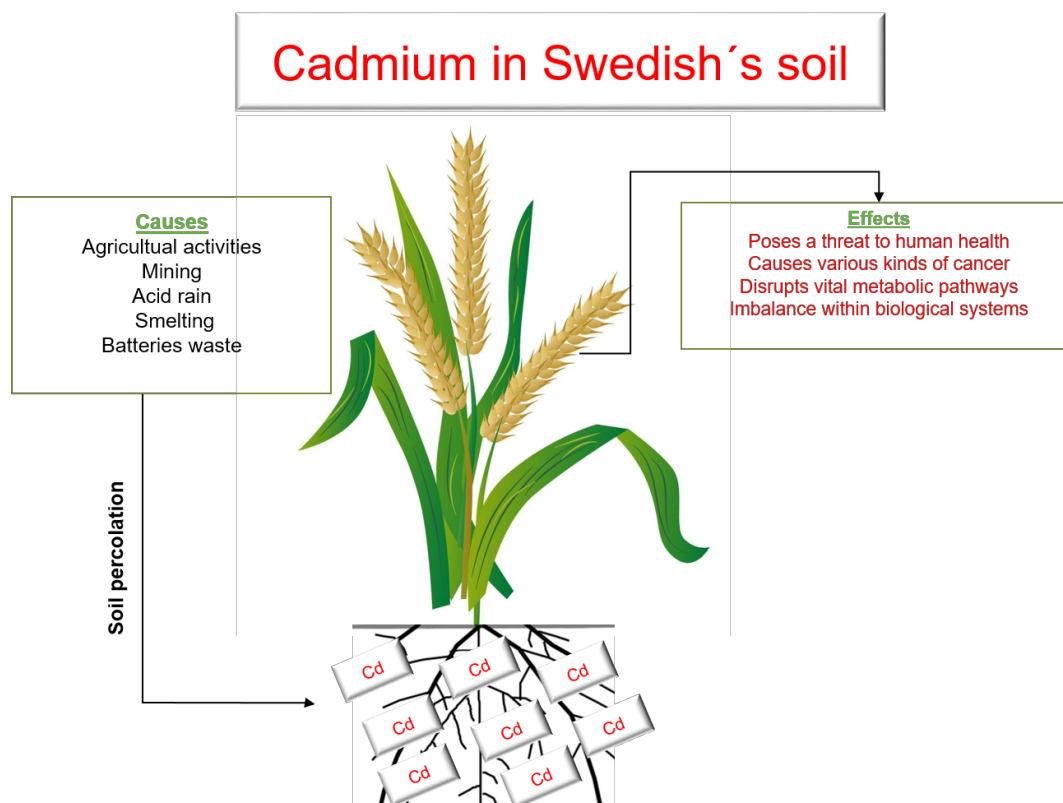
Figure 5: Causes and effects of Cadmium uptake in wheat grain

Cadmium thresholds for foodstuffs in the European Union (EU) are governed by specific regulations aimed at minimizing exposure to this toxic metal. The EU has set maximum permissible levels of cadmium in various food categories, with thresholds based on the type of crop or product. These thresholds are laid out in regulations such as EU 2023/915 and earlier ones like EU 488/2014 and EC 1881/2006.

Table 3: Comparative table showing the maximum allowable cadmium levels (in mg/kg wet weight) for different crops in Sweden and the EU (Commission regulation, 2023).

Crop/Foodstuff	Sweden (Aligned with EU)	Sweden Cadmium Threshold (mg/kg)
Durum wheat (Triticum durum)	0.18	0.18
Wheat germ	0.2	0.2
Rice, quinoa, wheat bran and wheat gluten	0.15	0.15
Maize	0.1	0.1
Barley and rye	0.05	0.05
Oat	0.1	0.1
Citrus fruits, pome fruits, stone fruits, table olives, kiwi fruits, bananas, mangoes, papayas and pineapples	0.02	0.02
Berries and small fruits,	0.03	0.03
Raspberries	0.04	0.04
Root and tuber vegetables	0.1	0.1
Pine nuts	0.3	0.3
Radishes	0.02	0.02
Tropical roots and tubers, parsley roots, turnips	0.05	0.05
Onions	0.03	0.03
Garlic	0.05	0.05
Fruiting vegetables	0.02	0.02
Brassica vegetables	0.04	0.04
Spinaches and similar leaves, mustard seedlings and fresh herbs	0.2	0.2
Legume vegetables	0.02	0.02
Proteins from pulses	0.1	0.1
Rape seeds	0.15	0.15
Peanuts and soybeans	0.2	0.2
Linseeds and sunflower seeds	0.5	0.5

10. Wheat Bread-Making

10.1 Bread-Making Quality

Wheat is primarily consumed as bread, which is a major source of food and nutrition including protein, starch, dietary fibres, phytochemicals, amino acid composition, minerals and vitamins in many households (Chikpah *et al.,* 2021). For bread-making, wheat flour is utilized due to its gluten-network, which imparts dough extensibility, strength, viscoelasticity and gas retention properties (Marchetti *et al.,* 2012; Bashir *et al.,* 2023). The compositional balance between

gliadin and glutenin, the two main protein fractions in gluten, plays a crucial role in determining the texture, structure, and appearance of bread (Barak *et al.,* 2013; Shewry, 2019). The HMW-GS subunit is critical for bread-making quality, with its concentration influencing bread volumes positively or negatively (Johansson and Svensson, 1995). In addition to gluten proteins, grain physical, chemical and nutritional characteristics, rheological properties of dough, falling number, and Zeleny sedimentation volume also influence bread-making quality (Poblaciones *et al.,* 2009; Al-Saleh and Brennan, 2012; Barak *et al.,* 2013). However, these characteristics vary depending on wheat genotypes and the environment in which wheat is cultivated (Carcea *et al.,* 2006; Shewry *et al.,* 2010; Hussain *et al.,* 2012; Bashir *et al.,* 2023).

10.2 Bread-Making Quality Testing

There are various methods for testing bread-making quality, but the most common are the Chopin alveograph, Mixograph, Amylograph, Farinograph, Consistograph, Mixolab, Texture Analysis, Falling Number Test and Extensograph (Song and Zheng, 2007; Marchetti *et al.,* 2012; Guzmán *et al.,* 2015; Cappelli *et al.,* 2020; Best *et al.,* 2023). These methods assist bakers and researchers in understanding the characteristics of flour and dough, enabling them to optimize formulations and processes for desired bread and baked product qualities. Each method provides specific insights into different aspects of dough rheology and behaviour.

11. Other Quality Test

11.2 Sensory Evaluation

Consumers seek both nutritional and energy benefits from food and derive pleasure based on sensory attributes during its consumption. The assessment of food quality relies significantly on sensory analysis, and its scientific underpinning is continually reinforced by growing understanding of human behaviour, together with advancements in sensory analytical methods (Haglund *et al.,* 1998). Nutritional qualities such as protein, starch, fiber content, minerals and biochemical compounds have been shown to affect different sensory attributes of wheat (Bustos *et al.,* 2011; Irakli *et al.,* 2015; Torbica *et al.,* 2019), with important attributes such as taste, colour, appearance, texture, and odour being crucial for evaluating the end-use quality of wheat flour, complementing its functionality and baking characteristics (Haglund *et al.,* 1998). Since both genotype and growing environment are known to influence the nutritional quality of wheat (Haglund *et al.,* 1998; Carcea *et al.,* 2006; Hussain *et al.,* 2012b, 2013; Johansson *et al.,* 2020a), exploring the impact of these factors on the sensory characteristics of wheat products is a

compelling area of study. For food to be accepted and incorporated into the diet, it should not only be sustainable and nutritious but also possess attractive and appealing qualities to consumers. Assessment of sensory attributes is carried out through the use of human senses with a particular objective in mind.

11.2.2 Sensory Evaluation Techniques

There are different methods for analyzing sensory attributes (Gillette, 1990), but the commonly used ones are Difference Testing (Ennis *et al.,* 2014), Affective Testing (Gillette, 1990) and Descriptive analysis (Murray *et al.,* 2001; Lawless and Heymann, 2010b) with the choice of techniques depending on the objective of the study. While Difference Testing is used to determine if significant sensory differences exist between samples (Amerine *et al.,* 2013), Affective Testing assesses consumers' liking or acceptance of one sample over another (Lawless and Heymann, 2010a). In contrast, Descriptive Analysis is among the most comprehensive techniques, involving the identification and description of sensory attributes both qualitatively (taste, colour, appearance, texture, aroma) and quantitatively (level of intensity in each qualitative components using line scale) by specially selected and trained panel of assessors (Meilgaard *et al.,* 1999; Murray *et al.,* 2001).

11.2.3 Descriptive Analytical Analysis Assessment

For this technique, a minimum of six assessors are selected based on their sensory skills and awareness. Using a line scale from 1 to 100, and following ISO standard, the assessor panel is trained on a selection of the samples to reach a consensus on the sensory attributes to be used for evaluation (Guld *et al.,* 2020). The quantitatively analysed sensory attributes can be further subjected to statistical analysis to identify significant differences between the samples.

12. Molecular Markers

Molecular markers are DNA fragments with genetic linkage to a target gene and are inherited from one generation to another (Nadeem *et al.,* 2018). Molecular markers serve as landmarks to the gene of interest and, like genes, occupy a particular region on the chromosome (Kumar *et al.,* 2009). Markers can be found abundantly throughout the genome, have wide applications in science, and have been used to improve several crops (Kumar, 2009). Genetic markers are used to track variations in DNA segments within and between species and enable the creation of novel sources of genetic variations by introducing traits of interest from wild relatives into modern cultivars (Rahmatov *et al.,* 2016b). Due to technological advancements, molecular

markers have been developed from non-PCR based to PCR-based methods (Bhagyawant, 2016), with newer techniques overcoming the limitation of the previous one. Restriction Fragment Length Polymorphism (RFLP) marker is a DNA-based technique used in genetic linkage map construction, but it has limitations including complex hybridization, exposure to radioactive compounds, high cost, labour intensive, and a limited number of hybridization probes (Bernatzky and Tanksley, 1986; Liu, 2007). However, PCR-based markers, including Random Amplification of Polymorphic DNA (RAPD) (Williams *et al.,* 1990), Amplified Fragment Length Polymorphisms (AFLP) (Vos *et al.,* 1995), Cleaved Amplified Polymorphic Sequences (CAPS) (Shavrukov, 2016), Sequence Characterized Amplified Region (SCAR) (Liu *et al.,* 1999); Simple Sequence Repeats (SSR) (Song *et al.,* 2001); Direct Amplification of Length Polymorphisms (DALPs) (Langar *et al.,* 2003) and Single Nucleotide Polymorphism (SNP) (Shavrukov, 2016) all have a relative advantages over non-PCR based molecular markers (Akbari *et al.,* 2006; Bhatia and Bajwa, 2022). An ideal molecular marker should meet requirements such as high polymorphism, codominance in expression, even genome-wide distribution, distinct allelic features, no pleiotropic effect, multiplex capability, cost-effectiveness in use and analysis, easy detection, high availability, high reproducibility, genome-specific and no negative impact on phenotype (Kumar *et al.,* 2009; Andersen, 2013).

12.1 High-throughput genotyping in wheat

DNA-based molecular markers are essential for identifying genome sequence differences between organisms, and their early development has greatly advanced plant breeding by providing improved tools and techniques that enable breeders to select traits more effectively for better crop varieties (Kondić-Špika *et al.,* 2023). The evolution of SNP chips has marked a transformative shift in genetic research, beginning with the 9k chip, which provided initial genetic insights. This progressed to the 35k, 90k, 660k and 820k chips in wheat, which offer much higher resolution and a broader range of genetic markers, enhancing the ability to conduct detailed genetic analyses and facilitate targeted breeding MAS (Rasheed *et al.,* 2017; Thudi *et al.,* 2021). Genotyping by sequencing (GBS is a high multiplexed method to obtain genome-wide variability information for a population (Crossa *et al.,* 2013; Morris *et al.,* 2013; Spindel *et al.,* 2015). It involves determining the nucleic acid sequence within a DNA molecule. The sequence of nucleotides (A, T, C, and G) encodes the biological information cells use to develop and perform their functions. Unraveling the DNA sequence is essential to understanding the role of genes and the overall genome. GBS is a low-cost, time-saving, and labor-effective way of capturing SNPs for genetic analysis and genotyping using the next generation sequencing

(NGS) platforms (Beissinger *et al.,* 2013; Bhatia *et al.,* 2018). It has advantages over regular markers such as RFLP, RAPD, AFLP, and SSR (He *et al.,* 2014). GBS is utilized in various applications, including quantitative trait locus (QTL) mapping, molecular diversity, Genome-wide-association study (GWAS), construction of high-density genome maps, haplotypes map, phylogenetics, identification of candidate genes, genetic linkage analysis, molecular marker discovery, and genomic selection/prediction (Romay *et al.,* 2013; He *et al.,* 2014; Spindel *et al.,* 2015). The GBS procedure includes DNA isolation, quantification, and normalization from samples, followed by digestion with methylation-sensitive restriction enzymes, such as ApeKI (a rare cutter PSTl and frequent cutter Mspl) for wheat, with enzyme choices varying for other plant species to reduce genome complexity (Poland *et al.,* 2012; Yazdani *et al.,* 2023). *ApeKI* cuts DNA at specific 5-base pair sequences, targeting gene-rich regions to reduce genome complexity in GBS, which simplifies sequencing and variant identification (Elshire *et al.,* 2011). This is followed by the litigation of adaptors (ADP) with barcodes to allow multiplex sequencing, forming a library panel (Elshire *et al.,* 2011). Sequence analysis is conducted using an appropriate NGS platforms such as Illumina platforms, Ion Torrent, Beijing Genomic Institute-SEQ, MGI-SEQ and Oxford Nanopore (Poland *et al.,* 2012; Pérez-De-Castro and Cañizares, 2017; Scheben and Edwards, 2018 and Meyer and Kirkness, 2019). These platforms generate high-throughput sequence data, which are then processed through bioinformatics pipelines to identify genetic variations by aligning sequence reads to a reference genome. The development and availability of reference genomes have been pivotal for such bioinformatics analysis, allowing for the accurate detection and identification of single nucleotide polymorphisms (SNPs) for marker-assisted selection in breeding programs (Bentley *et al.,* 2008). One of the most significant milestones in wheat genetics was sequencing the 'Chinese Spring' wheat genome, which provided a comprehensive reference genome and laid the foundation for more advanced genetic studies (Han *et al.,* 2015; Hao *et al.,* 2020). This advancement enabled the use of Whole Genome Sequencing (WGS) and Whole Genome Resequencing (WGR) techniques, which have expanded our understanding of wheat genetics and facilitated the identification of genomic regions associated with important traits (Can *et al.,* 2019; Sahu *et al.,* 2020). Building on this foundation, several studies have employed GBS to investigate various research objectives in wheat, such as adaptability and yield traits (Akram *et al.,* 2021), generating a dense linkage map and mapping the high-density three-pistil gene (Pis1) (Yang *et al.,* 2017), and creating a high-density genetic map for milling and the homologous transformation sterility gene (hts) (Yang *et al.,* 2018). Additional research includes identifying GBS tags associated with milling performance and end-use quality traits (Boehm *et al.,* 2017)

and searching for genetic variants underlying baking quality in 462 hard winter wheat lines (Zhang-Biehn *et al.*, 2021). These examples demonstrate how GBS, combined with advanced sequencing technologies and bioinformatics tools, has become essential for understanding wheat genetic architecture and accelerating marker-assisted breeding. Thus, it improves wheat breeding efficiency and facilitates the development of high-quality wheat varieties.

12.2 Genome-Wide Association Studies (GWAS)

In recent years, GWAS have become a powerful tool for detecting and mapping- genomic loci control traits of interest in crops (Yoosefzadeh-Najafabadi *et al.*, 2022). This method has broad applications across many crop species, including wheat (Rathan *et al.*, 2022; Mulugeta *et al.*, 2023), sorghum (Enyew *et al.*, 2022) rice (Spindel *et al.*, 2016), oat (Newell *et al.*, 2012), barley (Jabbari *et al.*, 2018), millet (Jaiswal *et al.*, 2019) and maize (Wu *et al.*, 2022). GWAS involves several key steps: assembling and phenotyping of an association panel (Belzile and Torkamaneh, 2022), genotyping the population (Wang *et al.*, 2014; Kang *et al.*, 2020), conducting association analysis (Zhou *et al.*, 2020), and identifying candidate genes (Rathan *et al.*, 2022). This approach has successfully identified genomic regions associated with essential traits in wheat, such as yield (Li *et al.*, 2019), disease resistance (Mihalyov *et al.*, 2017), climate resilience (Mérida-García *et al.*, 2020; Phuke *et al.*, 2022), and quality attributes (Liu *et al.*, 2017). The development of SNP arrays through high-throughput genotyping technologies have facilitated the way for widespread use of GWAS. Unlike bi-parental QTL mapping, GWAS requires significant marker coverage across the genome of interest and allows for the identification of multi-allelic variants associated with the traits of interest (Uffelmann *et al.*, 2021). GWAS can significantly enhance our understanding of the genetic basis of heritable traits, enabling marker-assisted selection to improve traits in breeding programs (Spindel *et al.*, 2016). Several powerful tools are available for conducting GWAS, such as PLINK for fast statistical analysis, BOLT-LMM and SAIGE for mixed models and addressing population structure, FaST-LMM for efficient mixed model analysis, and GEMMA for mixed-model association with both quantitative and binary traits (Purcell *et al.*, 2007; Lippert *et al.*, 2011; Zhou *et al.*, 2012 and Bi *et al.*, 2021). Additionally, R statistical tool has gained popularity for GWAS, particularly with the GAPIT (Genomic Association and Prediction Integrated Tool) package (Wang *et al.*, 2022). Common GWAS models implemented in R include the General Linear Model (GLM), Mixed Linear Model (MLM), Compressed Mixed Linear Model (CMLM) and Multi Locus Mixed Model Approach (MLMM) (Pritchard *et al.*, 2001; Yu *et al.*, 2006 and Segura *et al.*, 2012). Advanced models such as SUPER (Settlement of Mixed Linear

Models Under Progressively Exclusive Relationship), FARMCPU (Fixed and Random Model Circulating Probability Unification), and BLINK (Bayesian-information and Linkage-disequilibrium Iteratively Nested Keyway) improve computational speed and statistical power, making them highly effective for large datasets (Huang *et al.,* 2019; Wang *et al.,* 2014 and Liu *et al.,* 2016).

12.3 Kompetitive Allele Specific PCR (KASP)

Two cost-effective methods for converting flanking SNP markers from array-based genotyping (GenFlex^{TM}, GeneChip^{TM}, Infinitum, BeadXpress^{TM}, GoldenGate^{TM}) and GBS into more specific assays are Semi-Thermal Asymmetric Reverse PCR (STARP) and KASP markers (Long *et al.,* 2017; Semagn *et al.,* 2014). KASP markers are generally preferred due to their higher throughput, enhanced accuracy, and robustness across diverse samples. Their cost-effectiveness and compatibility with standard real-time PCR machines make them a practical choice for many genotyping projects (Long *et al.,* 2017; Jagtap *et al.,* 2020). KASP markers have become popular among cereal researchers and breeders, especially for validation and marker-assisted selection (Rasheed *et al.,* 2016). This popularity is attributed to their ability to produce reliable and reproducible results across different genetic backgrounds, which is critical in breeding programs. KASP assays depend heavily on the quality and quantity of the DNA template, as these markers function through allele-specific oligo extension and fluorescence resonance energy transfer (FRET) for signal generation. DNA can be extracted efficiently from leaves or seeds, making KASP markers versatile at various stages of plant development. Using KASP with other genotyping methods allows researchers to validate SNPs identified in high-throughput sequencing or array-based approaches, thus ensuring marker-assisted selection accuracy and reliability in crop breeding programs (Roncallo *et al.,* 2019). This integration helps bridge the gap between high-throughput discovery platforms and practical breeding applications, providing a comprehensive and cost-effective approach to genetic analysis.

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