UTILIZATION OF WHEAT RELATIVES TO IMPROVE WHEAT BREEDING FOR RUST RESISTANCE

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Abstract

Wheat is a major food source in a range of countries, thereby largely contributing to food security in vast areas worldwide. Stripe rust *(Puccinia striiformis* f. sp. *tritici*), stem rust (*P. graminis* f. sp. *tritici*) and leaf rust (*P. triticina erikson*) are three major wheat diseases which cause yield and quality loss of wheat. Wild relatives of wheat are dynamic resources for unique traits, not present in cultivated wheat. Different breeding strategies have been used for introgression of alien genes into wheat, to transfer genes contributing tolerance/resistance against biotic and abiotic stresses. The secondary and tertiary gene pools are playing a pivotal role in developing wheat-alien introgression lines. In this paper, the importance of wheat, types of rust, rust resistance types, wheat gene pools, molecular methods used for gene deployment and utilization of alien germplasm are discussed.

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1.0 Introduction

1.1 Wheat

The universal cereal of old world agriculture is wheat, which belongs to *Triticeae* (botanical tribe) and the family *Poaceae*. Almost, 10,000 years ago, when agriculture started, the diploid *Triticum monococcum* (2*n* = 2*x* = 14, AA), and tetraploids *Triticum dicoccum* (2*n* = 4*x* = 28, AABB) and *Triticum timopheevii* (2*n* = 4*x* = 28, AAGG), were domesticated in the Fertile Crescent (Feldman and Levy 2005). Thereafter, the process of natural hybridization occurred between diploid species i.e., *T. monococcum/T. urartu* (2*n* = 2*x* = 14, AA) and *Aegilops speltoides* (2*n* = 2*x* = 14, BB) and as a result tetraploid *T. turgidum* (2*n* = 4*x* = 28, AABB) was originated (Wrigley et al., 2009).

The evolution of hexaploid wheat (*T. aestivum*, 2*n* = 6*x* = 42 AABBDD) resulted from natural polyploidization events between tetraploid *T. turgidum* ssp. *durum* (2n=4x=28, AABB genome) and diploid *Ae. tauschii* (2*n* = 2*x* = 14, DD) (Marcussen et al., 2014). Today, the cultivation of hexaploid wheat (bread wheat), the most widely grown cereal crop in the world, provides a central pillar for national food security and is a daily staple food source for humans. Currently, 95% of the cultivated wheat is hexaploid wheat, and the remaining 5% is durum wheat (Shewry, 2009).

The unique gluten in wheat, contributes to baking and pasting properties resulting in the production of various flavored food (Ragaee et al., 2006). Wheat is broadly cultivated in the Mediterranean Basin, Russia, Australia, Canada, India, United States, and some other countries (Tidiane et al., 2019).

1.2 Economic significance of wheat

Bread wheat has high naturally nutritious values and has become a staple food for ~40% of the human population, thereby contributing more than 20% of the total proteins and 22% of the food energy from wheat (Koehler et al., 2013). Hexaploid wheat is cultivated on ~ 200 million hectares globally (FAOSTAT 2017). By 2050 the global human population is expected to reach almost 10 billion (FAOSTAT 2017), with the population increase taking place mainly in developing countries where wheat is a staple food in some of the countries. According to FAOSTAT (2018), the largest wheat producing countries are China, India, Russia, USA, France, Australia, Canada, Pakistan, Ukraine, and Germany. Europe and Asia are the major continents that produce bread wheat, and the production of wheat in 2028 is also projected to

increase in both continents (Figure.1). Improvement of wheat production is highly needed to obtain global food security. High yield depends largely on crop management strategies i.e., sowing occasion, agricultural management and selection of cultivars (Scarcioffolo et al., 2018). The development of new cultivars resistant against biotic and abiotic stresses is a major challenge for the wheat breeders. Traditional wheat breeding programs have been used to produce cultivars resistant and/or tolerant to biotic and abiotic stresses. Several superior alleles of major genes, such as the vernalization response gene (Chen et al., 2013), photoperiod response gene (Würschum et al., 2018) and kernel size genes (Hou et al., 2014; Wang et al., 2014), have been detected and used for selection in traditional breeding programs.

Novel genomic tools, such as functional and comparative genomics and marker-assisted selection (MAS) provide solutions to the bottlenecks faced by traditional breeding methods (Lei et al., 2017; Uauy, 2017). The exploitation of genetic resources suitable for wheat breeding is expected to contribute a key role developing new resistant and durable wheat cultivars.

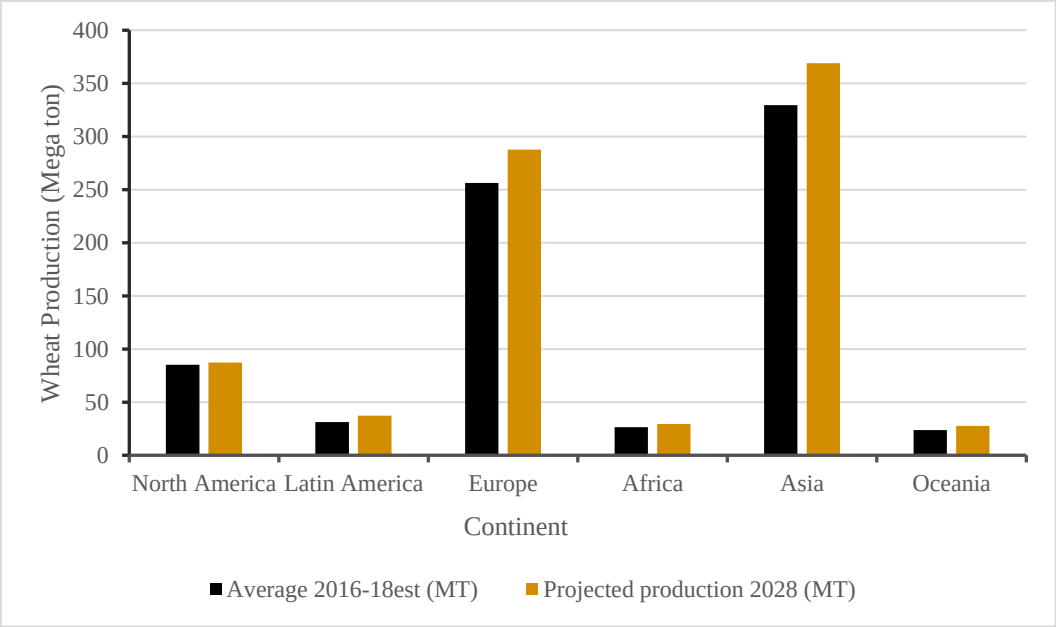

Figure 1: Global Bread wheat production 2016-18 (Mt) and projected production 2028 (Mt) (FAOSTAT 2018)

1.3 Gene pools

Common wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is an allohexaploid containing three closely related homoeologous subgenomes (i.e., A, B, and D) with 7 pairs of chromosomes each (Kihara, 1921; Sears, 1952). A concept of three gene pools (primary, secondary and tertiary) was proposed by Harlan and de Wet (1971), dividing relatives to a population into these groups based on evolutionary and cytogenetically relationship and

crossing ability (homologous/wild type or homoeologous/partially homologous) of chromosomes (Chaudhary et al., 2014). Genotypes in the primary gene pool are genetically close to each other (i.e., *T. Spelta, T. compactum, T. sphaerococcum, T. vavilovii, T. macha, T. yunanense, T. Triticum zhukovskyi, and T. tibetanum*) and easily crossed with common wheat, which results in opportunities to use simple breeding techniques (Qi et al., 2007). Also, when genotypes from the secondary gene pool is used for gene transfer, crossing and backcrossing can be used for homoeologous chromosomal pairing with little difficulty between common genomes (i.e., *T. timopheevi, T. monococcum, T. Urartu and T. timopheevii*).

An exception from this is *Aegilops speltoides*, which require cytogenetic manipulative methods for genetic transfer due to massive hybridization barriers (Nevo et al., 2012). Wild wheat relatives are non-homologous to wheat and belong to the tertiary gene pool of wheat. The tertiary gene pool includes annual (e.g. *Secale cereale*) and perennial (e.g. *Thinopyrum* spp., *Lophopyrum and Agropyron* spp.) cereal species. For gene transfer from the tertiary gene pool, wheat-alien introgressions have been used, e.g. *S. cereale* has served as a source of resistance to rusts and powdery mildew (*Sr31/Yr9/Lr26/Pm8*) (Friebe et al., 1996), resistance to cereal aphid and Hessian fly (Crespo Herrera 2014; Hysing et al., 2007) and significant genetic diversity for yield increase, drought and salinity tolerance, micronutrient content, and further additive genetic variation for wheat improvement (Mujeeb-Kazi et al., 2013; Peake et al., 2011).

1.4 Role of pairing homoeologous loci

Two pairing homoeologous (*Ph*) loci have been identified in the wheat genome, i.e., *Ph1* and *Ph2*. The primary pairing homoeologous locus, *Ph1*, is present on the long arm of the 5B (5BL) chromosome and has been shown to control homoeologous chromosome pairing (Riley and Chapman 1958, 1959; Sears 1976., Griffiths et al., 2006). The secondary *Ph2* locus is located on the short arm of chromosomes 3D (3DS) and 3A (3AS) and generally shows lower activity than the *Ph1* locus (Mello-Sampayo 1971, 1968; Driscoll, 1972).

The *Ph* loci have been shown to contribute stability to the wheat genome as they prevent homoeologous recombination among wheat relatives. Several mutants have been used in wheat breeding to suppress the activity of the *Ph* loci, which prevent the homoeologous recombination. Thus, X-ray irradiation has been used to develop wheat with mutant loci of *Ph1*, e.g. the *ph1b* mutant in *Triticum aestivum* (hexaploid, 2n=6x=42) and *ph1c* mutant in durum wheat (tetraploid, 2n=4x=28) (Sears, 1977; Giorgi, 1978). Furthermore, Sears (1982)

and Wall (1971) developed *Ph2* mutants for *ph2a* on short arm of 3D (3DS) and *ph2b* on the short arm of 3A (3AS) in hexaploid wheat.

The Chinese Spring wheat *ph1b* mutant has been widely used to induce homoeologous recombination for gene introgressions across wheat sub-genomes and from related grass species into the wheat genome (Qi et al., 2007, 2008; Niu et al., 2011; Zhang et al., 2016; Boehm et al., 2017).

Therefore, the *Ph1b* mutant plays a pivotal role in identifying novel sources of resistance genes in wheat and its relatives to the stem rust, stripe rust and leaf rust. For example, *Sr32, Sr39, Sr43, Sr47, Sr51, Sr53* and *Sr59, Yr83* and *Lr19* resistance genes have been identified from wheat relatives by using the *Ph1b* locus (Zhang &Gassmann 2007; Marais et al., 2005,2018; Mago et al., 2011; Niu et al., 2011; Liu et al., 2011; Rahmatov et al., 2016)

2.0 Wheat Diseases

2.1 Rust Fungi

Rusts are obligate bio-trophic pathogenic fungi and one of the most complex groups of plant pathogens. Rusts of cereal crops are an old group of plant diseases reported 12,000 years ago (Haldorsen et al., 2011). The rust fungi belong to *Uredinales*, a highly specialized order of the Basidiomycetes, estimated to include 14 families and 166 genera. It belongs to the order *Pucciniales*, which is the largest fungal order containing more than 8000 species (Aime et al., 2014).

The rust fungi' bio-trophic lifestyle is described as an ancestral adaptation because the rusts use a wide range of host species from various genera (gymnosperms, angiosperms, monocots, and ferns) (Aime et al., 2014). However, specific rust species have complete dependence on the host plants, resulting in a complicated life cycle for the rusts and difficulties in producing the fungi in laboratory environments (Aime et al., 2017).

Due to their many races and large effects on yield, rusts are considered one of the most devastating diseases for a wide array of agricultural crops, e.g. cereals, soybean, alfalfa, coffee etc. (Cummins & Hiratsuka, 2003), and wood trees, e.g. poplar, eucalypt or pines (Dean et al., 2012). The continuous emergence of new races of rust fungi causes major threats to agricultural crops, and in particular to cereals. Rust fungi causes significant loss by decreasing the productivity of wheat at a global level (Figueroa et al., 2018). To overcome the rusts' threats, breeding has focused predominantly on developing and producing novel rust resistant cultivars.

2.2 Life cycle of rust fungi

Rusts have five different spore forms; *Pycniospores, Aeciospores, Urediniospores, Teliospores, and Basidiospore,* and requires two unrelated host plants to complete their life cycles (Aime et al., 2017). Some rust fungi, e.g. the flax rust fungus *Melampsora lini,* are macrocyclic or autoecious, which means that they produce all five types of spores (Lawrence et al., 2007). Other rust fungi have only two types of spores, either *basidiospores* and *teliospores,* or *pycniospores* and *teliospores.* Such rust fungi with only two types of spores are defined as microcyclic, of which *Puccinia graminis* is one example, using barberry and cereals as hosts. If only the *urediniospore* stage is absent, the rust fungi are considered as autoecious or heteroecious and is determined demicyclic i.e. *Gynoconia peckiana* is an autoecious demicyclic rust (Aime et al., 2017).

2.2.1 Wheat stem rust

Stem rust in wheat is caused by *Puccinia graminis* f. sp. *tritici* Ericks and Henn (*Pgt*), and is continuously threatening the global wheat production (Leonard & Szabo, 2005; Singh et al., 2015). The stem rust symptoms of infection are typically manifested as masses of brick-red urediniospores on leaf sheaths, stems, glumes and awns of susceptible plants (Singh et al., 2015). Barberry is known as the second host of *Pgt,* and therefore, barberry was eradicated in the United Kingdom and Scandinavia already in 1959, to break the disease cycle of the stem rust (Hessayon, 1982). These actions were enormously successful in breaking the disease cycle and driving wheat stem rust to near extinction in Western Europe. However, in 2017 Sweden reported the first occurrence of wheat stem rust that was derived from barberry representing a worrying turn for wheat stem rust in Europe (Berlin et al., 2017).

Despite the fact that stem rust has been well controlled in many parts of the world, there is a high requirement for cultivars with durable resistance. The presence of such cultivars may contribute additionally at least 6.2 million metric tons of yield in years with severe epidemics (Pardey et al., 2013). Recent newly emerged races of stem rust have resulted in that the majority of cultivars have become vulnerable to the disease (Pretorius et al., 2000; Singh et al., 2015).

The first of these newly emerged *Pgt* races was Ug99, which appeared in Uganda in 1998, and which was found virulent to the widely deployed stem rust resistance genes *Sr31* and *Sr38* (Jin et al., 2008; Pretorius et al., 2000). This race, also known as TTKSK using the North American system of nomenclature for *Pgt* races, was found to spread throughout Africa to Middle East causing major yield losses since its detection. It is also found to be virulent to the *Sr24*, *Sr36*,

Sr9h and *SrTmp* resistance genes (Rouse et al., 2014; Patpour et al., 2016; Jin et al., 2010; Singh et al., 2015).

Since 1988, several additional novel virulent *Pgt* races have emerged, breaking resistance in the majority of the currently grown wheat cultivars. Thus, the resistance of the *Sr24* gene was defeated by the TTKST race, resulting in epidemics of stem rust (Jin et al., 2008). Generally, the emergence of these novel *Pgt* races have led to an increasing number of devastating epidemics, e.g. in Ethiopia in 2014 by the 'Digalu' race (TKTTF), and a similar race has been reported present in Germany (Olivera et al., 2018).

Generally, only few resistance genes are available that has proven to be effective against all races of *Ug99*, one of those reported is *Sr13* in tetraploid durum wheat lines (Zheng et al., 2017). Additionally, a resistance gene, *Sr59*, contributing resistance to all currently known stem rust races have been reported in Swedish rye-translocation lines (Rahmatov et al., 2016)

The tertiary gene pool is a useful source of new durable stem rust resistance genes to stem rust. *Sr31* has been deployed from wheat-rye introgressions and resulted in a stable resistance against stem rust for 30 years in commercial wheat until it was first broken by *Ug99* (Singh et al., 2008). Thus, pyramiding of resistance genes is necessary to protect wheat against stem rust; 90% of the current wheat cultivars are vulnerable to *Ug99* (Singh et al., 2019), and including other emerging races of stem rust, the proportion of sensitive cultivars are even higher.

2.2.2 Wheat stripe rust

Puccinia striiformis f. sp. *tritici*. (*Pst*) is the causal agent of yellow rust/stripe rust, which is a devastating disease that is threatening global wheat production (Singh et al., 2005; Wellings, 2011). However, several additional factors are also involved in yield loss of wheat e.g. unfavorable climatic conditions, evolution of new pathogen races, vulnerability of cultivars and length of disease (Begum et al., 2014). Stripe rust can infect wheat plants already at the one-leaf stage and then throughout the whole plant growth period, and the disease is able to cause 100% yield loss on highly susceptible wheat cultivars. In 2009, major outbreaks of stripe rust (5.5 million tons per year) were reported from different parts of West and Central Asia as well from Morocco (Beddow et al., 2015).

During 2010, an epidemic of yellow rust caused major decreases in wheat production in several parts of Tajikistan and also in other countries of central Asia (Singh et al., 2017; Rahmatov 2013). A range of common yellow rust (*Yr)* genes have been identified in European wheat cultivars, i.e. *Yr1, Yr2, Yr6, Yr9, Yr17,* and *Yr32* (Hovmøller., 2007). Additional yellow rust genes that have been proven with effective resistance are *Yr5* and *Yr15*, although they have never

been employed in the breeding of European elite wheat cultivars (Hanzalová et al., 2016; Goyeau & Lannou., 2011; Hovmøller et al., 2018).

A new race in a new unique genetic group, termed PstS15, was detected in France in 2017, 2018 and 2019 and in 2019 also in Denmark (Hovmøller et al., 2018). Thus, there is an urgent need to understand host-pathogen interactions as well as the mechanisms behind the evolution of new races in order to facilitate the development of new resistant cultivars and establish new management strategies to control pathogens (Johnson, 1992; Hawkesford et al., 2013). Pathologist have focused on identifying factors that contribute to the spreading of the pathogen and its genetic structure in the Himalayan and near-Himalayan regions (Ali et al., 2014; Thach et al., 2016; Walter et al., 2016).

However, the virulence structure of the pathogen has often only been described at country or regional scales, limiting a broader concept and understanding (Hovmøller et al., 2008; Wellings, 2007; Bahri et al., 2009; Ali et al., 2014; Hovmøller et al., 2016). Till now, only one single study (Sharma-Poudyal et al., 2013) has focused on stripe rust virulence patterns covering the period from the 1950s to the 1980s at an international level (Thach et al., 2015).

Due to the continuous emergence of virulent *Pst* races, the identification and characterization of novel sources of resistance is a necessity. Resistant wheat cultivars are a highly effective and environment friendly solution for the control of stripe rust outbreaks (Zhang & Gassmann, 2007). Due to the fact that *Pst* races have continuously broken the resistance of most major genes available in wheat cultivars, particularly in Africa, and Asia (Figueroa et al., 2018), wheat stripe rust has dramatically been spreading across the globe and epidemics have been reported in almost 60 countries during the last 50 years (Beddow et al., 2015; Chen, 2005).

To date, approximately 83 yellow rust resistance (*Yr*) genes have been permanently named in wheat, including the newly mapped *Yr79* (Feng et al., 2018), *Yr80* (Nsabiyera et al., 2018) *Yr82* (Pakeerathan et al., 2019), *Yr83* and $6R^{afr}$ (Li et al., 2020). Additionally, 67 stripe rust resistance genes have been temporarily designated, including both all-stage resistance (also termed seedling resistance) and adult-plant resistance (APR) (Wang and Chen, 2017). Among these, APR genes comprise a minority, where several gene loci are pleiotropic for biotrophic fungal diseases, i.e., *Yr18*/*Lr34*/*Pm38*/*Sr57*, *Yr29*/*Lr46*/*Pm39*/*Sr58*, *Yr30*/*Lr27*/*Pm48*/*Sr2* and *Yr46*/*Lr67*/*Pm46*/*Sr55*. During the last 18 years, more than 160 quantitative trait loci have been tentatively designated in 49 regions of 21 chromosomes (Rosewarne et al., 2013; Maccaferri et al., 2015). Many resistance genes, such as *Yr2, Yr6, Yr7, Yr8, Yr9, Yr17* and *Yr27*, have been overcome by new vulnerable races of stripe rust. Therefore, wheat breeders are currently struggling to identify new genetic resources with possible durable resistant genes.

2.2.3 Wheat leaf rust

Puccinia triticina Eriks. (*Pt*) is the causal agent of leaf rust (Anikster et al., 1997; Bolton et al., 2008), the most common and widely distributed among the three (stem, stripe and leaf) wheat rust diseases (Bolton et al., 2008; Huerta-Espino et al., 2011). A humid temperature is required for the spread of the wheat leaf rust pathogen. The Fertile Crescent of the Middle East is the origin of leaf rust (*Puccinia triticina*), and in this region, both the primary (wheat) and the secondary (*Thalictrum* spp.) hosts of the pathogen are abundantly present (Bolton et al., 2008; Kolmer et al., 2007).

Leaf rust is known to decrease the yield in wheat by a negative impact both on amount and weight of wheat grains (Huerta-Espino et al., 2011; Kolmer et al., 2007). Losses caused by *Pt* is reported to reach over US$ 350 million only in the USA (Huerta-Espino et al., 2011). Globally, leaf rust epidemics is projected to cause economic losses in the range of US$1.5 to US$3.3 billion per year during the period of 2000-2050 (Chai et al., 2020).

Genetic resources (transfer of resistance genes from gene pools) have successfully been used to control leaf rust, although the pathogen have changed constantly (Kolmar et al., 2007). For leaf rust, the evolution of new pathogen races have beaten a range of the resistance genes, such as, *Lr9, Lr14a, Lr16, Lr17a, Lr24, Lr26 and Lr41* (Huerta-Espino et al., 2011). Of the 76 identified *Lr* genes, only four genes are known as slow rusting i.e., *Lr34* (Dyck, 1987), *Lr46* (Singh et al., 1998), *Lr67* (Hiebert et al., 2010), and *Lr68* (Herrera-Foessel et al., 2012) because they are race non-specific resistance genes and give durable resistance during adult plant stage. Therefore, the identification of new sources of unique resistance genes, which are useful to produce new durable resistant cultivars of wheat, is highly desired, to fulfill the high demands of wheat production.

3.0 Resistance to rust

Biffen (1905) demonstrated that the resistance against yellow (stripe) rust in the wheat variety "Rivet" was due to a single, recessive gene. The epidemiologist, Van der Plank (1963), define the concept of resistance. Later, in the late 1960s and the early 1970s, the theory of general (race-nonspecific) resistance and its application in crop resistance breeding was described (Caldwell, 1968). Thus, the theory of general resistance was used and implemented to protect wheat against stem rust by Borlaug (1972), against leaf rust by Caldwell (1968) and yellow rust by Johnson (1988). In general, the host ranges of rust fungi are narrow and the capability of the fungi to infect related non-host species is poor. Recent studies have indicated non-host

resistance as a more durable, broad-spectrum form of resistance that can complement the host plant resistance (Lee et al., 2016).

3.1 Types of disease resistance

In principal, there are two methods to control a plant diseases i.e., by host resistance or through pesticide applications. The host resistance is genetically determined and is broadly classed into two forms: seedling or all stage resistance (ASR) and adult-plant resistance (APR).

3.1.1 Seedling resistance

Seedling resistance genes are often governed by a single major gene and they are effective only against specific races of the pathogen. Therefore, these genes are designated as qualitative, race-specific, vertical, major, seedling and/or nucleotide-binding-site (NBS) and leucine-rich-repeats (LRR) genes (Line and Chen 1995; Qiu et al., 2010). Seedling resistance or 'all stage resistance' (ASR), is usually expressed at all growth stages of the plant. The resistance is often associated with a hypersensitive response of the plant.

The ASR is race specific, it is often easily broken down by the evolution of evolving new pathogens. Thus, the following resistance genes such as *Sr13, Sr24, Sr31, Sr36, Sr38, SrTmp* and *Sr1RSAmigo* for stem rust, the *Yr2, Yr6, Yr7, Yr8, Yr9, Yr17* and *Yr27* for stripe rust and *Lr9, Lr14a, Lr16, Lr17a, Lr24, Lr26* and *Lr39* for leaf rust have been overcome by newly rusts pathogen races (Huerta-Espino et al., 2011; Singh et al., 2015; Ali et al., 2017). The ASR follows the gene-for-gene interaction described by Flor & Comstock (1971). In the gene-for-gene interaction, R-proteins interact with avirulence proteins produced by the pathogen, which induces the resistance reaction.

A susceptible reaction occur, if the resistant allele is not present in the host or the avirulence allele is not present in the pathogen. Then, the host is unable to recognize the presence of the pathogen, which allows for disease to emerge. Most of the R genes encode nucleotide-binding and leucine-rich repeat (NB-LRR) proteins that interact with the pathogen effectors, thereby inducing the defense responses (Ellis et al., 2014). Coiled coil (CC), nucleotide-binding-site (NBS), and leucine-rich-repeat (LRR) motif (Wang et al., 2011) have been identified in the *Lr1* (Cloutier et al., 2007), *Lr10* (Feuillet et al., 2003) and *Lr21* (Huang et al., 2003) leaf rust resistance genes. Also, the *Yr10* stripe rust resistance gene have been shown to encode proteins containing nucleotide binding sites and leucine-rich repeats (Fu et al., 2009).

The NBS-LRR-type R-genes, which are present in both monocot and dicot plant species, tend to be present as multi-genic families along with resistance gene analogs (RGAs) (Hammond-

Kosack and Jones 1997; Meyers et al., 1999; Ellis et al., 2000; Zhang & Gassmann, 2007; Miller et al., 2008). Several ASR genes have been characterized by using molecular assisted approaches (Anderson et al., 2018).

3.1.2 Adult plant resistance

Adult plant resistance (APR), also called quantitative and non-race specific resistance, is governed by minor genes. APR is considered as a durable type of resistance, and the level of resistance is mostly partial, while it often provides resistance against a wide range of pathogen races (Krattinger et al., 2009; Moore et al., 2015). This kind of resistance is mainly observed in the adult stage, and specifically during field conditions. Fu et al. (2009) identified cytoplasmic resistance proteins in the stripe rust resistance gene, *Yr36*, although, ATP-binding cassette transporter and hexose transporter were characterized in the leaf rust resistance genes *Lr34* and *Lr67* (Rajagopalan et al., 2016; Moore et al., 2015).

Normally, the APR genes influence the size of the pustule, the rate of the infection, and the dormancy period, so that the negative effect of the pathogen on the plant is decreased. Therefore, when it comes to rusts diseases, APR genes are often called “slow rusting” genes. Due to the fact that APR genes are not hindering pathogen sporulation, they do not contribute such a strong selection pressure on the pathogen as seedling resistance genes, and therefore, the speed of the genetic changes of the pathogen is reduced, leading to more durable resistance of APR genes compared to for seedling resistance genes (Visioni et al., 2020). Thus, the *Sr2* is an APR stem rust resistant gene that has been in use for 100 years in wheat breeding programs (Moore et al., 2015).

APR can be pleiotropic (i.e. the gene complex consists of resistance to several different rusts pathogens such as stem, stripe and leaf rust), as exemplified by the *Sr2*/*Yr30*/*Lr27*, *Sr55/Yr46*/*Lr67/Ltn3*, *Sr57/Yr18*/*Lr34/Ltn1* and *Sr58/Yr29*/*Lr46* APR genes (McFadden 1930; Fu et al. 2009; Yang et al., 2013; Lan et al., 2014). Furthermore, APR of stem rust has been conferred by the *Sr12* gene (Rouse et al., 2014).

The APR genes have been associated with a number of morphological/physiological traits in wheat. One such example is the *Lr34* gene which is correlated with leaf tip necrosis (LTN), which is a post-flowering morphological trait (William et al., 2003; Singh et al., 2011; Herrera-Foessel et al., 2014). The pseudo-black chaff (PBC) phenotype is also associated with the pleiotropic *Sr2*/*Yr30*/*Lr27* as "slow rusting” APR genes (Singh et al., 2005; Singh et al., 2008; Mago et al., 2011). The *Sr2* gene is derived from the cultivar Hope and provided durable resistance to stem rust in the CIMMYT-Mexican spring wheat germplasm (Borlaug et al.,

1949). The effects of the APR genes might be moderate if they are used solely, although, when used in combination with other major genes and/or multiple QTLs contributing additive effects, durable resistance may be the result. High temperature adult-plant resistance (HTAP) is a type of race non-specific stripe rust resistance expressed only at high temperature during the adult plant stage (Line and Chen, 1995). At present, a few ASR genes (all stage resistance or seedling resistance), such as *Yr5* and *Yr15*, and APR genes, such as *Yr18* and *YrZH22* (Wang and Chen, 2017), have kept an effective resistance to *Puccinia striiformis* races.

3.1.3 Breeding for rust resistance

Bread wheat is vulnerable to attacks from many pathogens but none as devastating as the stripe, stem and leaf rusts. The rust pathogens have plagued wheat since ancient times, but widely virulent races emerge and spread around the globe every year. To overcome this challenge, it is very important to protect wheat from rust attack by using genetic resources. Therefore, new genetic resources have been developed to diversify the current narrow genetic base of wheat using closely related species to wheat, such as rye, *Thinopyrum, Aegilops*, etc.

Resistant wheat cultivars have been developed by using Neuzucht germplasm with fragment of rye chromosomes e.g., Kavkaz, Avrora, Bezostaya 2, Skorospelka 35 and Predgornaya 2 and grown in various European countries (Lukyanenko, 1973). In early 1970s, the wheat cultivars Kavkaz and Avrora become susceptible to powdery mildew. However, these cultivars have many valuable disease resistant traits and became good sources for developing new genotypes i.e. cultivar Lukyanenko has *Pm8, Lr26, Sr31* and *Yr9* resistant genes originating from the rye genome. Furthermore, the Kavkaz and Avrora wheat cultivars were used in Hungary due to their high yield and resistance to stem rust. Wheat wild relatives i.e., *Aegilops* and *Thinopyrum* species have played an important role to transfer resistance genes to common wheat, e.g. *Lr9 — Ae. umbellulata; Lr24* and *Lr29 — Thinopyrum ponticum; Lr37* and *Yr17 — Ae. ventricosa; Lr38, Yr50, Sr44 — Th. intermedium; Sr32, Sr39, Sr47, Lr28, Lr35, Lr36, Lr51* and *Lr66 — Ae. speltoides; Sr33, Sr45, Lr21 , Lr22a , Lr32 , Lr39 , Lr40 , Lr41* and *Yr28 — Ae. tauschii; Sr53, Lr57* and *Yr40 — Ae. geniculata; Lr58 — Ae. triuncialis; Lr53 ,Lr64, Yr15 , Yr35* and *Yr36 — Ae. longissima* and *T. dicoccoides* (Riar et al., 2012).

Researchers of International Maize and Wheat Improvement Center (CIMMYT) have been using single back cross methods from several years to produce rust resistance cultivars (Singh et al., 2014). Hence, different approaches have been used to develop durable resistant cultivars by using genetic resources.

4.0 Molecular-assisted breeding (MAB)

During recent years, the DNA sequencing technologies have been developed into next-generation sequencing (NGS), where DNA are massively processed through high-thoughput operations (Mosele et al., 2020). NGS technologies have been widely used for whole genome sequencing (WGS), whole genome resequencing (WGRS), *de novo* sequencing, genotyping by sequencing (GBS), and transcriptome and epigenetic analysis (Varshney et al., 2009; Poland et al., 2012). One major challenge with the use of this technology is the requirement of sufficient knowledge about bioinformatics, to obtain the accurate information from the sequence data in a short period of time (Doyle et al., 2020).

The availability of a large amount of sequencing data, and opportunities to connect DNA and phenotypic data, have opened the field to link phenotypic characters to specific regions of the DNA, to which markers can be produced (Ritchie et al., 2015). Thus, marker-assisted selection (MAS) is a technology that have emerged and which provides effective and speedy selection in breeding programs using a large array of DNA markers linked to desired traits, e.g. abiotic/biotic stresses, agronomic characters, end-use qualities (Gantait et al., 2019). With MAS, molecular markers are used to detect genomic regions that are specifically linked to traits of interest and by using these markers as a proxy for the trait the selection process is more effective than using traditional plant breeding methods.

The MAB (use of MAS in plant breeding) started by the use of Restriction Fragment Length Polymorphisms (RFLPs), which was soon followed by other and improved types of markers such as Randomly Amplified Polymorphic DNAs (RAPDs), Amplified Fragment Length Polymorphisms (AFLPs) and Simple Sequence Repeats (SSR) (Amom & Nongdam, 2017).

Some of the above-mentioned markers are still in use both by researchers and breeders, although most of them have limited impact in practical plant breeding. Currently, high-density molecular marker systems like SNP-chip and DArT, etc. are overtaking the space as most useful markers within practical plant breeding and they are boosting the plant breeding selection cycles. The high-throughput and large-scale genotyping of SNPs has become a routine tool in plant breeding in all major crop species including cereals (Rasheed et al., 2017). SNP genotyping has almost completely replaced other genotyping technologies due to their high-throughput, high-speed data generation, repeatability, and cost effectiveness.

4.1 Single Nucleotide Polymorphism (SNP)

Single nucleotide polymorphism (SNP) is the designation for variation in a single base pair at a corresponding locus in the genome, and is the most frequent reason for variation among different individuals of a species (Brookes, 1999). Based on the character of the nucleotide substitution, the SNP is categorized into different types, e.g. transitions (C/T or G/A) or transversions (C/G, A/T, C/A, or T/G) (Edwards et al., 2007), and also insertions and deletions (InDels) are called SNPs. Moreover, SNPs are extremely useful for plant breeders, as they are robust with relatively low mutation rates (one SNP every 100-300 base pair of plant genomes) and easily recorded.

Several SNP genotyping and next generation sequencing platforms are used to facilitate MAS, and these platforms are generally highly efficient with a high throughput and a low cost per data point. Kavanagh et al. (2013) developed an Illumina iSelect array with 9K SNPs. Later a 90K SNP array was developed and used to characterize both hexaploid and tetraploid wheat populations (Wang et al., 2014). Additionally, the Affymetrix Axiom® 820K SNP array, containing 820 000 SNP markers, have been utilized to screen 475 accessions of hexaploid wheat and related species including putative progenitor species, in order to differentiate SNPs useful to genotype, monitor and map introgressions to hexaploid wheat (Winfield et al., 2016). In a recent study, SNP markers were selected from the above described Affymetrix Axiom® 820K SNP array, based on their suitability in wheat breeding, a wheat breeders array was developed and the utility of the selected markers was also confirmed (Allen et al., 2017).

Bread wheat is an allohexaploid species, which means that the genes are present in multiple copies. In addition, the wheat genome is complex with more inter-chromosomal duplications than related grass species, i.e., 20 to 30% of the genes have been duplicated (Choulet et al., 2014; Glover et al., 2015). Hence, the presence of homoeologous and paralogous loci makes the genotyping complicated (Wang et al., 2014; Akhunov et al., 2009). The SNP arrays development has opened novel opportunities to uncover variation in agriculturally relevant wheat populations (Robbins et al., 2011; Shirasawa et al., 2010). Till now, the SNP arrays have been of relevance in the characterization of several stem, stripe and leaf rust resistance genes (Zhang et al., 2018; Liu et al., 2020; Leonova et al., 2020)

4.2 Genomic selection (GS) or Genome-wide selection (GWS)

Not all traits are governed by only a few genes and the difficulty of using markers for more complex traits like grain yield has made it necessary to further develop the use of markers in

plant breeding. One method that simultaneously can predict complex traits from high density marker information is genomic selection (GS). This method is not only effective in predicting complex traits but the use of it often shortens the breeding cycle (Crossa et al., 2011; Jannink 2010). GS may be a more reasonable option as compared to high cost phenotyping (Jannink 2010). In GS, a Genomic estimated breeding value (GEBV) is estimated from molecular marker information and this (GEBV) is used for eugenic traits selection (Nakaya and Isobe, 2012).

To predict the GEBV, the GS models applied are important. If GS is successful, QTL mapping, using populations obtained from particular crosses, can be skipped (Desta and Ortiz, 2014). To carry out GS, a training population is first developed where both the genotypic and the phenotypic information is known. This data is used to develop prediction models that then subsequently is used on a data set where only genotypic information is available. The GEBV for different desired traits is calculated using the models developed with the help of the training set, and thereafter, selections are made by the plant breeders based on this information (Jiang, 2013).

4.2.1 The role of genomic selection in wheat breeding

GS has been significantly used in breeding of hybrid and pure lines e.g. in wheat, rye and other cereal crops (Bernardo, 2016; Crossa et al., 2017). GS is applicable in breeding for increased yield (Belamkar et al., 2018), disease resistance (Juliana et al., 2017) and end-use quality (Hayes et al., 2017) of wheat, but can also be used to predict breeding value of genetic resources. Recently, GS has been applied to produce synthetic-derived introgression lines that have higher GEBVs values (gives high grain yield in heat-stress conditions) as compared to both the synthetic and the bread wheat parent (Jafarzadeh et al., 2016).

When GS is used for; i) domestication of new crops such as *Th. intermedium* (Zhang et al., 2016), ii) using landraces in breeding for rust resistance (Daetwyler et al., 2014; Pasam et al., 2017) and iii) breeding for heat and drought stress adaptations (Mwadzingeni et al., 2016), iv) breeding for malting quality in barley (Schmidt et al., 2016) or v) baking quality in wheat (Michel et al., 2018), optimization of the procedure is a necessity.

As breeders implement GS to decrease the breeding cycle time and increase the overall gain rate, a continuous selection for the whole suite of traits that compose a successful cultivar will also be carried out (Pasam et al., 2017). Compared with QTL mapping and GWAS, GS shows a higher promise in harnessing gains from genetic resources for quantitative traits and is seen

as a more reliable and useful approach (Bernardo, 2016). Key challenges for successful practice of GS are the development of cost-effectiveness and less biased approaches for genotyping, software for handling, quality control and joint analysis of genotypic, phenotypic and environment data.

Thus, GS was proven as a successful procedure, using GS models on two CIMMYT bread wheat screening nurseries against three major necrotrophic foliar diseases of wheat: *Septoria tritici* blotch (STB), *Stagonospora nodorum* blotch (SNB), and tan spot (TS). Prediction accuracy from GS for disease resistance traits is increased by the use of resistant gene markers and association mapping (Arruda et al., 2016; Daetwyler et al., 2014; Rutkoski et al., 2014). However, low prediction accuracies might be obtained if GS is applied with untested parents, because of a deficiency of accuracy of prediction as a result of multiple breeding generations (Arruda et al., 2016). Furthermore, the size required for the training population and marker set is affected by the trait under evaluation and the relationship of individuals and should thus be considered independently before the implementation of GS in a breeding program (Robertsen et al., 2019).

5.0 Utilization of alien-germplasm

Many stem, stripe and leaf rust resistance genes have been characterized that originates from wheat wild relatives but also from cultivated wheats. Furthermore, a range of resistance/tolerance genes against several biotic and abiotic stresses have been characterized that originates from the *Triticeae* (Colmer et al., 2006; Nevo and Chen 2010; recent examples are given in Yudina et al., 2016). Moreover, bread wheat nutritional properties, such as the zinc and iron content, have been improved by the use of genes from *Triticum* ssp. and *Aegilops* spp. (Rawat et al., 2009; Khlestkina et al., 2011; Tereshchenko et al., 2012). Below, resistance genes available from cultivated and wild relatives of wheat for the three rusts are summarized (Table 1-3).

Table 1. *Puccinia striiformis f.*sp. *tritici*. resistance genes from cultivated and wild relatives of wheat (Source), chromosomal location and linked genes.

Genes	Source	Chromosome Location	Linked Genes
Yr5	*Triticum spelta album*	2BL	-
Yr7	*Triticum turgidum*	2B, 2BL	-
Yr8	*Aegilops comosa*	2D = T2DS-2M#1L.2M#1S	***Sr34***
Yr9	*Secale cereale*	1B=1BL.1RS	***Pm8, Lr26, Sr31***

Yr15	*Triticum dicoccoides*	1BS	-
Yr17	*Aegilops ventricosa*	2AS	***Lr37, Sr38***
Yr26	*Haynaldia 23illosa*	1 BS, 1BL	-
Yr28	*Ae. tauschii*	4DS	-
Yr35	*Triticum dicoccoides*	6BS	-
Yr36	*Triticum dicoccoides*	6BS	-
Yr37	*Ae. kotschyi*	2DL	***Lr54***
Yr38	*Ae. sharonensis*	6AL	***Lr56***
Yr40	*Ae. geniculata*	5DS	***Lr57***
Yr42	*Ae. neglecta*	6AL (6L.6S)	***Lr62***
Yr50	*Thinopyrum intermedium*	4BL	-
Yr53	*Triticum turgidum ssp. durum*	2BL	-
Yr56	*Triticum turgidum ssp. durum*	2AS	-
Yr64	*Triticum turgidum ssp. durum*	1BS	-
Yr65	*Triticum turgidum ssp. durum*	1BS	-
Yr83	*Secale cereal*	6RL	-
6R^{afr}	*Secale africanum*	6R	-

Table 2. *Puccinia graminis tritici* resistance genes from cultivated and wild relatives of wheat (source), chromosomal location and linked genes.

Genes	Chromosome Location	Source	Linked Genes
Sr2	3BS	*Triticum dicoccum*	***Yr30/Lr27/Pm48***
Sr9d	2BL	*Triticum dicoccum*	-
Sr9e	2BL	*Triticum dicoccum*	-
Sr9g	2BL	*Triticum turgidum* ssp. *durum*	-
Sr11	6BL	*Triticum turgidum* ssp. *durum*	-
Sr12	3BS	*Triticum turgidum* ssp. *durum*	-
Sr13	6AL	*Triticum turgidum* ssp. *durum*	-
Sr14	1BL	*Triticum turgidum* ssp. *durum*	-
Sr17	7BL	*Triticum dicoccum*	-
Sr21	2AL	*Triticum monococcum*	-
Sr22	7AL	*Triticum monococcum*	-
Sr24	3DL	*Thinopyrum ponticum*	***Lr24***
Sr25	7DL	*Thinopyrum ponticum*	***Lr19***
Sr26	6AL	*Thinopyrum ponticum*	-
Sr27	3A	*Secale cereale*	-
Sr28	2BL	*Triticum turgidum* ssp. *durum*	-

Sr31	1RS	*Secale cereale*	***Pm8, Lr26, Yr9***
Sr32	2B	*Aegilops speltoides*	-
Sr33	1DL	*Aegilops tauschii*	-
Sr34	2A, D	*Triticum comosum*	***Yr8***
Sr35	3AL	*Triticum monococcum*	-
Sr36	2BS	*Triticum timopheevii*	-
Sr37	4BL	*Triticum timopheevii*	-
Sr38	2AS	*Triticum ventricosum*	***Lr37, Yr17***
Sr39	2B	*Aegilops speltoides*	-
Sr40	2BS	*Triticum timopheevii* ssp. *araraticum*	-
Sr43	7DL	*Thinopyrum ponticum*	-
Sr44	7DS	*Thinopyrum intermedium*	-
Sr45	1DS	*Aegilops tauschii*	-
Sr46	2DS	*Aegilops tauschii var. meyeri*	-
Sr47	2BL	*Aegilops speltoides*	-
Sr50	1RS	*Secale cereale*	-
Sr51	3ABD	*Aegilops searsii*	-
Sr52	6AS	*Haynaldia villosa*	-
Sr53	5DL	*Aegilops geniculata*	-
Sr59	2DS.2RL	*Secale cereale*	-

Table.3. *Puccinia triticina* resistance genes from cultivated and wild relatives of wheat (Source), chromosomal location and Linked genes.

Gene	Chromosome location	*Origin*	Linked genes
Lr9	6BL	*Aegilops umbellulata*	-
Lr14a	7BL	*Triticum dicoccum*	-
Lr18	5BL	*Triticum timopheevii*	-
Lr19	7DL	*Thinopyrum ponticum*	***Sr25***
Lr21	1DL	*Aegilops tauschii*	-
Lr22a	2DS	*Aegilops tauschii*	-
Lr23	2BS	*Triticum turgidum* ssp. *durum*	-
Lr24	3DL	*Thinopyrum ponticum*	***Sr24***
Lr25	4BS	*Secale cereale*	***Pm7***
Lr26	1RS	*Secale cereale*	***Pm8, Yr9, Sr31***
Lr28	4AL	*Aegilops speltoides*	-
Lr29	7DS	*Thinopyrum ponticum*	-
Lr32	3DS	*Aegilops tauschii*	-
Lr35	2B	*Aegilops speltoides*	-

Lr36	6BS	*Aegilops speltoides*	**-**
Lr37	2AS	*Triticum ventricosum*	***Yr17, Sr38***
Lr38	2AL	*Thinopyrum intermedium*	**-**
Lr39	2DS	*Aegilops tauschii*	**-**
Lr42	1DS	*Aegilops tauschii*	**-**
Lr44	1BL	*Triticum aestivum spelta*	**-**
Lr45	2AS	*Secale cereale*	**-**
Lr47	7AS	*Aegilops speltoides*	**-**
Lr50	2BL	*Triticum timopheevii*	**-**
Lr51	1BL	*Aegilops speltoides*	**-**
Lr53	6BS	*Triticum dicoccoides*	**-**
Lr54	2DL	*Aegilops kotschyi*	**-**
Lr55	1BL.1HtS	*Elymus trachycaulis*	**-**
Lr56	6AL	*Aegilops sharonensis*	***Yr38***
Lr57	5DS	*Aegilops geniculata*	***Yr40***
Lr58	2BL	*Aegilops triuncialis*	**-**
Lr59	1AL	*Aegilops peregrina*	**-**
Lr61	6BS	*Triticum turgidum* ssp. *durum*	**-**
Lr62	6A	*Aegilops neglecta*	***Yr42***
Lr63	3AS	*Triticum monococcum*	**-**
Lr64	6AL	*Triticum dicoccoides*	**-**
Lr65	2AS	*Triticum aestivum spelta*	**-**
Lr66	3A	*Aegilops speltoides*	**-**
Lr71	1B	*Triticum aestivum spelta*	**-**
Lr72	7BS	*Triticum turgidum* ssp. *durum*	**-**

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