
The Role of Host Plant Resistance in Management of Wheat Rusts: A Review

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Abstract

Wheat is the world's most important crop and rusts are present wherever wheat is grown. Rust diseases of wheat are among the oldest known diseases and are important worldwide. Use of resistant cultivars is the most important, economical, effective and practical method of managing rusts in wheat. It is also the most environmentally friendly and profitable strategy for commercial farmers if they grow genetically resistant varieties using different resistance genes. Wheat rust diseases can successfully be controlled through genetic resistance. For example, wheat stem rust was controlled for about three decades using sr31 resistance gene. Breakdown of resistant cultivars due to new races of rust pathogens is a common occurrence in wheat production of the world. Similarly, in Ethiopia, wheat rusts are major threats for wheat production causing frequent and widespread epidemic largely due to fast breakdown of resistant cultivars. Thus the susceptible cultivars should be replaced by resistant cultivars to minimize rust epidemics and so yield loss. The problem of fast breakdown of resistant genes in cultivars can largely be elevated by continual development of new cultivars with a combination of different types of resistance. This review discusses information on the role of host plant resistance in management of rust diseases in wheat, types of host plant resistance in wheat against rust diseases and sources of host plant resistance in wheat against rusts diseases.

Key words: resistance; host plant; wheat; rusts; diseases; management.

1. Introduction

Wheat is one of the most important and significant cereal staple food crops in the world, both in terms of food production and for providing the total amount of food calories and protein in the human diet [44].

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In Ethiopia, wheat is among the most important staple food crops, cultivated in a wide range of agro-ecologies and produced at 1.69 million ha of land with an annual yield approximated to 4.64 million metric ton [3]. Nevertheless, wheat production is affected by biotic and abiotic stresses; of which biotic stresses are major constraints for wheat production. Even though many biotic stresses hinder wheat production, the wheat rust diseases are best known for their devastating and widespread nature causing major crop losses globally [37,131]. For example, stem rust and stripe rust can cause 100% loss, whereas leaf rust can cause yield loss up to 75% [4]. The rust fungi are highly specialised pathogens with significant variation for avirulence/virulence to specific host resistance genes. New virulent pathotypes develop through a range of mechanisms like mutation and recombination, allowing the pathogens to overcome resistance genes and continue posing a constant and ongoing threat to global wheat production [7,114]. The Rust fungi are biotrophic, obligate, parasitic organisms that takes nutrition from their host plants [25]. They hinder the photosynthetic ability of the plant and thus reduce plant height, floret set and grain yield. The impact of rust fungi also results in slow growth and low forage quality, poor seedling germination, foliar injury and shrivelling of the grain [23,101]. The above features of the rust fungi make them major biotic production constraints for wheat [108]. They are highly productive and their spores can spread over long distances. The rust fungi can grow anywhere; where they get suitable host and favourable environmental conditions and can pose a persistent threat to all the sustainable wheat producing areas [108]. Historically, it is well known that rust epidemics caused famine in different parts of the world and about US \$5 billion losses occur due to cereal rusts including wheat around the globe every year [73]. The occurrence of widespread epidemics of wheat rusts at the beginning of the 20th century initiated the need for in-depth studies in genetics of disease resistance in plants, life cycle of plant pathogens, and genetics of host-parasite interactions [22, 76]. Effective control of wheat rust diseases is possible mainly through utilisation of genetic resistance to the pathogen, and fungicides [18]. However, using genetic resistance is efficient, economical, environmental friendly and effective means of managing rust diseases [2,143]. It is also the most profitable strategy for commercial farmers if they grow genetically resistant varieties using different resistance genes [14,80]. Both race-specific and non-race-specific resistances are utilized to manage all three wheat rust diseases [35]. However, the value of non-race-specific resistance genes is highly recognized because of their durability and protection against multiple pathogens or races. To date, breeding programmes have favoured the use of either gene stacking or pyramiding in order to achieve resistance durability, and often generate combinations of race-specific and non-race-specific resistance genes with additive effects to optimize protection [109].

2. Advantages of using host plant resistance compared to other methods of rust management in wheat

The major advantages of using genetic resistance includes: reduction or avoidance of the dependence on chemical control, non-detrimental effect on the environment and demanding no action by farmers once the cultivar is selected [101]. The use of rust resistant cultivars can reduce the negative impact of fungicides on the environment and may also be economically beneficial to wheat producers [20,117]. Sometimes, planting a rust resistant cultivar with a lower yield potential may result in higher profits compared to planting a higher yielding rust susceptible cultivar that will require several fungicide applications in the season [23]. Use of resistant cultivars can also avoid fungicide-resistance development by the rust pathogens [5]. Moreover, regular chemical applications pose a potential risk of the reduction or loss of fungicide sensitivity [91]. Zwer and his colleagues [143] reported that deployment of stem rust resistant cultivars provided an annual protection estimated at \$ 124

million in Australia. Similar estimation provided an annual protection of \$ 217 million per year in Canada due to the use of resistance cultivars against wheat stem rust disease. Similarly, Brennan and Murray [17] reported that losses from rust diseases in Australia at between AUD \$2–11 million per annum, whereas rust control using genetic resistance returned savings of AUD \$99, \$85 and \$161 million per annum, for stem rust, leaf rust and stripe rust, respectively. Brennan and Murray [17] also reported that the value to the Australian wheat industry in preventing loss of production and crop processing quality from the investment in breeding for stem rust resistance is AU\$ 128 million per annum in 1988 value. In the same way, Brennan and Murray [17] also reported that the benefit of breeding for resistance to all species of rust in Australia is estimated at AU\$ 289 million per annum. It is also estimated that the Australian wheat industry spent between AU\$ 40 and 90 million between 2003 and 2005 on spraying to control stripe rust [135]. Yield losses due to leaf and stripe in Western Australia for susceptible varieties have been estimated as high as 80% [13]. Similar losses have been estimated in the USA [36]. In Australia, during the period 2003–2005, approximately AU\$ 40–90 million per year was spent on chemical control to prevent stripe rust epidemics [13]. Generally, management of wheat rusts through host by the application of resistance genes is the most effective, economical, environment friendly and practical approach [23].

3. The role of host plant resistance in management of wheat rusts

The evolution of new virulence through migration, mutation, recombination of existing avirulence genes in the pathogen, and the selection of virulence has been common in the fungi that cause wheat rust diseases. To tackle these diseases, the use of genetic resistance is very important. Moreover, management of wheat rusts through host plant by the application of resistance genes is the most effective, economical, environment friendly and practical approach [2,23,44,50,104,113,143]. Furthermore, it is the principal mechanism of controlling wheat rusts [23,101] and is the best strategy for resource poor farmers in the developing world [14,80]. It is also the most profitable strategy for commercial farmers if they grow genetically resistant cultivars using different resistance genes [14,80]. Genetic basis of resistance to wheat rusts was described, for the first time, by Biffen in the early 1900s' [15]. Since then, the discovery of genetic variation for rust resistance has been an on-going component of wheat breeding programs.

3.1. The role of host plant resistance in management of wheat stem rust disease

The use of resistant cultivars to stem rust is the most important in protecting the yield loss due to this disease [101]. Reports indicated that the use of resistant cultivars provide sufficient protection against yield losses due to wheat stem rust disease. For example, in Australia, deployment of stem rust resistant cultivars provided an annual protection estimated at \$ 124 million in Australia [143]. Similar estimation provided an annual protection of \$ 217 million per year in Canada due to the use of resistance cultivars against wheat stem rust disease. Hence, use of resistant cultivars against currently aggressive stem rust races, such as Ug99 and Diglu race is crucial to minimize yield losses due to the disease [112]. Emergence and spread of new races of stem rust pose an imminent threat to wheat production worldwide and this requires the rapid development of wheat cultivars with durable resistance to stem rust [101]. The durability of effective resistance genes can be enhanced by deploying them as pyramids in cultivars [110]. To date, about fifty eight stem rust resistance genes have been identified

and some of them have been mapped on different chromosomes in wheat and its relatives [77]. All these genes are race specific except Sr2 that has provided durable non-race-specific slow-rusting adult plant resistance [76,111]. Among these resistance genes, some genes deployed in commercial cultivars worldwide remained effective individually or in combination with other Sr genes until recently [119]. Moreover, the Sr2 complex in combination with other resistance genes showed effective protection against Ug99 [110]. Resistance gene Sr26 provides resistance to current stem rust races of wheat in Australia [69]. Most deployed resistance genes are susceptible to Ug99 except few genes such as Sr2. In Ethiopia, the use of resistant cultivars has been the major strategy to control stem rust. Several rust resistant cultivars have been developed since the beginning of wheat research in the country [125]. Under large-scale production, resistance to stem rust became ineffective, limiting the duration of cultivation despite wide adaptability and high productivity of the cultivars. These rapid breakdowns of resistance genes of Ethiopian wheat cultivars are associated with inadequate knowledge of the virulence present in the pathogen population and the disease screening protocol, which is inadequate to identify and select the resistant wheat lines [27]. In addition, continuous release and wide cultivation of CIMMYT originated bread wheat genotypes with common parentage could be the most important factor for fast evolution of rust pathogens in Ethiopia [6].

3.1.1. Types of host plant resistance to stem rust

Studies of the interaction between cereal rusts and their hosts show a very close relationship between the genetics of the pathogen and of the host in the expression of disease [121]. Host-pathogen interaction could be specific or non-specific [101]. Commonly plant pathologists divide resistance in to two major categories [121]. These are race-specific and race non-specific.

3.1.1.1. Race-specific resistance to stem rust disease

Race-specific resistance is also termed as qualitative, vertical, seeding stage, all stage, monogenic, major gene, hypersensitive etc., resistance [107]. Race-specific resistance is effective only against some pathotypes of the pathogen population and it often “breakdown” easily with the occurrence of new pathotypes of a pathogen [59]. Because cultivars with race-specific resistance usually do not remain resistant long-term, research focus has been on using non-race-specific resistance that is controlled by many genes in recent years [94].

3.1.1.2. Race non-specific resistance to stem rust disease

Race non-specific resistance is also termed as quantitative, horizontal, adult plant resistance, slow rusting, polygenic (minor gene) and durable. Race non-specific resistance is based on the additive interaction of a few or several genes having minor to intermediate effects. This type of resistance is characterised by a non-differential interaction. Non-specificity is only recognised by the absence of specificity and, because all tests are of limited size, the presence of race-non specificity can never be proved [55]. It is not possible to define pathotypes based on this type of resistance, and it generally allows low level of rust sporulation [94]. Deployment of resistance genes at various stages of a plant development in different years and regions resulted in a durable non-race-specific, field resistance of adult plants [16]. According to Parlevliet [93], durable resistance is a quantitative

term that indicates a relatively long period of effectiveness of the resistance when exposed to the pathogen under investigation. The components of the durable resistance include infection frequency, infectious period, latency period and the size of the colony and lesion [92]. Slow rusting resistance is a type of resistance whereby the rate of pathogen development is retarded without much chlorosis like that of the hypersensitive type [90]. Cultivars with slow rusting resistance usually exhibit low terminal severity, reduced size of pustules, longer latency period, low sporulation and small number of pustules [137].

3.1.2. Sources of host plant resistance to stem rust

The deployment of single genes for resistance can lead to profound changes in the population structure of *Puccinia graminis tritici*. The large scale cultivation of wheat lines carrying single genes for resistance deployed on a large scale places tremendous directional selection pressure on stem rust pathogen populations towards the predominance of pathotypes virulent to the resistance gene [129]. The large scale deployment of a highly resistant single gene effective against a large fraction of the pathogen population and the subsequent evolution of the pathogen population towards virulence is known as the "boom and bust cycle" [122]. The inefficacy of the resistance gene is not due to changes in the gene itself but to the proliferation of mutants in the pathogen population with an aberrant avirulence gene [101]. These individuals are able to proliferate on hosts carrying the cognate resistance gene for the avirulence gene that was mutated. The aberrant pathogens come to predominate the population, as they are the only individuals able to proliferate on the widely deployed host carrying the defeated gene. The opportunity for sexual reproduction by *Puccinia graminis tritici* is strictly dependent on its alternate host, the plant barberry. However, without the opportunity for sexual union of mating types and recombination during meiosis, most common genotypes of *Puccinia graminis tritici* have adapted to strictly asexual reproduction [141]. In this adaptation they have lost the ability to produce teliospores and induce recombination through meiosis. In asexual reproduction, the main source of variation is mutation [74]. Resistance to *Puccinia graminis tritici* is conferred by genes that interact with pathogen virulence genes in a gene-for-gene manner [38]. It is in this relationship a particular stem rust resistance gene present in the host is cognate to an avirulence gene in the stem rust pathogen. In many cases, a single resistance gene can effectively control one or more strains of particular pathogen, and breeders have used resistance genes in conventional resistance breeding programs for decades [110]. These stem rust resistance genes came from common wheat or wheat relatives. Twenty resistance genes including Sr6, Sr28, Sr29 and SrTmp were identified in common wheat, *T. aestivum*; seven including Sr2 were from *T. turgidum*; three Sr genes (Sr21, Sr22, and Sr35) were from *T. monococcum*; four Sr genes including Sr24, Sr25, and Sr26 were from *Agropyron elongatum*; Sr31 and Sr1A.1R were from *Secale cereale*; Sr36 and Sr37 were from *T. timopheevi*; one each was from *T. ventricosum* (Sr38) and *T. araraticum* (Sr40), respectively [110]. All these catalogued Sr genes are race specific, except gene Sr2. At present, 58 Sr genes have been designated, with three gene loci having multiple alleles [76] and other stem rust resistance genes exist with temporary designation status. Several of the genes derived from wild relatives present on small chromosomal introgression segments have been relied upon breeding programs and have been deployed commercially. Some of the Sr genes have been widely deployed in commercial wheat cultivars, Sr2, derived from *T. turgidum* is on chromosome 3BS, and has conferred durable rust resistance against all virulent races of *P. Graminis* worldwide for more than 50 years. It has been deployed in many wheat cultivars worldwide [76]. Sr2 as a slow rust resistance gene shows partial resistance with variable levels of disease on adult plants

grown in the field when it is used alone [110]. The effect of Sr2 can be enhanced by adding race-specific Sr genes [61]. Pseudo-black chaff, a dark pigmentation around the stem internodes and glumes is closely associated with Sr2 and has been used as a morphological marker to select for the gene [45]. Sr24 was originally derived from *A. elongatum* and has been integrated into many wheat lines in South America, Australia and CIMMYT [110]. The stem rust resistant variety Agent has a spontaneous translocation between chromosomes 3Ag of *A. elongatum* and 3DL of bread wheat [118]. Amigo, another wheat variety that has a 1AL.1RS translocation from *Insave rye*, has two Sr genes: one on rye chromosome 1RS and the other, Sr24, on 1BS [69]. Sr26 is translocated from *A. Elongatum* to chromosome 6AL of wheat [61]. Sr26 has not been widely deployed in commercial wheat varieties due to the yield penalty associated with the gene [126]. Sr31, a strong resistance gene derived from *Secale cereale* introduced to bread wheat through a 1B/1RS translocation, has been deployed in winter and spring wheat varieties in China, Europe, India, and USA [76]. Enhanced stem rust resistance was reported when it was stacked with Sr25 [127]. Sr36, derived from *T. Timopheevi* was originally transferred into two hard red spring wheat lines, CI12632 and CI12633 [128]. Sr36 is located on chromosome 2BS, and has been deployed in many Australian wheat cultivars [10] and some soft winter wheat cultivars in the USA [110]. The unique virulence profile of Ug99 (*Pgt* race TTKSK and derivatives) makes it a tremendous threat to wheat production worldwide. For many years Sr31 provided seemingly durable resistance globally but inevitably selection pressures led to the development of virulence in Ug99. Developing lines with adequate and durable resistance to Ug99 has presented unique and challenging problem to wheat scientists worldwide with the majority of genes conferring resistance coming from wild relatives. Many of the effective resistance genes are present on large translocations and are associated with linkage drag. Field evaluations in 2006 and 2007 in Kenya and greenhouse evaluations at the USDA Cereal Disease Laboratory have elucidated Sr genes effective against Ug99 [112]. These include Sr22, Sr25, Sr26, Sr27, Sr28, Sr32, Sr33, Sr35, Sr37, Sr39, Sr40, Sr44 and SrTmp and have been transferred into wheat backgrounds. However, deployment of these genes in commercial cultivars is still in its infancy due to their presence on large alien translocations that have deleterious effects on important agronomic characteristics [112]. At the present time, the research of stem rust in wheat is focusing on identifying more resistance genes to control Ug99 [26]. In general, identification and deployment of new genes for rust resistance must be the on-going requirements of world wheat breeding programs, as the existing genes become ineffective due to rapid and dangerous evolution of new races or pathotypes [112]. New resistance genes to wheat rusts can be found among the wild relatives of cultivated wheat that have evolved with their parasites and have grown along with cultivated wheat during the last several thousand years [70]. Generally, cultivated wheat and closely related grasses can be sources of specific and nonspecific resistance genes against wheat stem rust pathogen [101,112].

3.2. The role of host plant resistance in management of wheat yellow rust disease

The fungal disease yellow rust (caused by *Puccinia striiformis* Westend. f. sp. tritici Eriks), results in significant yield losses to wheat production world-wide [60,49,123]. Yellow e rust can cause up to 100% yield losses in susceptible wheat cultivars [23,116]. Several epidemics and outbreaks of yellow rust significantly threatened the food security and livelihoods of poor farmers in many wheat growing regions of the worldwide [136]. Deployment of host plant resistance is the most economical and environmentally safe approach to reduce losses due to rust diseases in wheat [20,117]. Thus, use of new cultivars which are proven resistant to yellow rust and

cultivation of these resistant cultivars is the best approach to control wheat losses to yellow rust [100,132]. Due to the ability of yellow rust to accelerate quickly, to cause significant losses, early and regular scouting is recommended for making decisions to combat the disease [32]. Once the disease is established in a stand of susceptible hosts, given a conducive environment, yellow rust will rapidly accelerate if not managed. Use of HTAP cultivars is another approach in fighting with yellow rust. A combination of HTAP resistance and effective all-stage resistance is the best approach to develop durable and high-level resistance [14]. Incorporation of resistance based on additive slow rusting genes by the use of single backcross approach has shown 5-15% of higher yield potential than the original cultivar and many cultivars have also been developed by this methodology [109]. So far, 82 Yr genes have been formally designated; about 25 of these confer adult plant resistance or high temperature adult plant resistance while the remainder provide all stage resistance [82,83,133]. An effective deployment of resistance genes for the management of yellow rust in wheat requires knowledge about the resistance status and the diversity of resistance genes in cultivars under consideration as well as knowledge on the prevailing pathogen races is crucial as pathogens evolve their virulence frequently, thereby compromising the durability of resistance [95,54]. Periodic outbreaks of yellow rust occur in Ethiopia due to lack of knowledge regarding the genetic resistance present in commercial cultivars and breeding populations, and inadequate monitoring of the pathogen race population [6]. In Ethiopia, breeding for resistance is solely based on field observations at naturally infected trial sites. There is only limited information on the genetic composition of current cultivars and even less on materials undergoing selection [29]. Identification and development of slow rusting resistant cultivars can reduce the cost of production and frequency of serious epidemics. Wheat genetic materials with related parentage and largely carrying race-specific major gene resistance have been the backbone of the wheat improvement programs of Ethiopia [6]. However, most of the released varieties in the country do not possess durable resistance, became susceptible shortly after their introduction and release. In most cases, the failures were due to new virulent pathotypes and deployment of the same resistance gene(s) in wide array of wheat cultivars [1]. Slow rusting wheat varieties are the simple solution for disease management, thus replacing susceptible cultivars with slow rusting ones is important in resistance diversity and to create an opportunity for further improvement of resistance level of wheat [124]. For such rapid evolution and spread of new virulent races of yellow rust, and frequent failure of new cultivars with major gene yellow rust resistance in wheat improvement programs require to identify durable sources of resistance [46]. Therefore, achievement of slow rust resistance against wheat yellow rust requires constant characterization and identification for deployment of new resistant genotypes that resist the prevailing virulent races.

3.2.1. Types of host plant resistance to yellow rust disease

The genetic resistance to yellow rust can be characterized as qualitative and quantitative resistances. The qualitative resistance is named as race-specific or vertical, seedling resistance, monogenic (major genes), hypersensitive and the quantitative resistance is also named as race-nonspecific or horizontal, adult plant resistance, slow rusting, polygenic (minor gene), durable [56,75,76,23,66].

3.2.1.1. Race-specific resistance to yellow rust disease

There is an obvious differential reaction, pathotypes can be determined, and race-specific resistance genes are

recognised by the presence of low infection types [34]. Major genes are at risk due to pathogen plasticity [110]. Gene-for-gene resistance is called major gene resistance or race-specific resistance because it is effective only against some pathotypes of the pathogen population and it often “breaks down” easily with the occurrence of new pathotypes of a pathogen [59,74,]. Because cultivars with major genes usually do not remain resistant long-term, research focus has been on using non-race-specific resistance that is controlled by many genes in recent years [64]. Furthermore, the gene-for-gene relationship states that for every resistance gene in the host plant there is a corresponding avirulence gene in the pathogen. However, the ability of an avirulent gene to mutate to a virulent gene, no longer recognizable by the corresponding resistance gene, implies a type of resistance termed race-specific resistance [40]. According to Dyck and Kerber [34], a race-specific or vertical resistance signifies that the resistance to some pathogens is relatively simply inherited. The race-specific resistance is virulent only to particular races of a pathogen. Race-specific resistance is often based on genes that are effective at the seedling stage and remain effective at all post-seedling stages of the plants. Most of the yellow rust resistance genes are determined at seedling stages, and thus interact with specific races of the pathogen to confer resistance in a gene-for-gene relationship [40]. Race specific resistance is usually governed by a hypersensitive response, controlled by major genes. The race-specific resistance is determined by a single gene, often led by a boom and bust cycle [34,96]. Yellow rust resistance genes are postulated or characterized based on seedling resistance test. The seedling resistance (race-specific resistance) genes can be detected and are effective at the seedling stages, and they are characterized by the gene-for-gene interaction model [40]. The race-specific resistance (seedling resistance) genes are also active during the adult plant stage [23,63]. So far, above sixty yellow rust race-specific resistance genes have been identified [81,115]. However, the seedling resistance genes are often broken down due to new and various races of the rusts pathogen [115].

3.2.1.2. Race non-specific resistance to yellow rust disease

The genetic nature of this type of rust resistance is usually complex and is based on the additive interaction of a few or several genes having minor to intermediate effects. This type of resistance is characterised by a non-differential interaction. Non-specificity is only recognised by the absence of specificity and, because all tests are of limited size, the presence of race-non-specificity can never be proved [55]. It is not possible to define pathotypes based on this type of resistance, and it generally allows low level of rust sporulation [94]. Deployment of resistance genes at various stages of a plant development in different years and regions resulted in a durable non-race-specific, field resistance of adult plants [16]. Van der Plank [129], described race non-specific resistance to be characterized by reduced apparent infection rate. Thus, resistances that varied in a quantitative way and resulted in slow rusting were accepted to be supported by race non-specific resistance genes [94]. Most of the race non-specific resistance tests have been carried out in adult plants [101]. Thus, adult plant resistance genes are considered to control race non-specific resistance, thereby contributing with partial resistance and being associated with a slow rusting resistance [96]. The stem rust resistance gene Sr2 is considered to be one example of a gene contributing to partial or slow rusting resistance [8,76]. The race non-specific resistance is governed by minor genes and is therefore considered as a polygenetic resistance. This type of resistance is often considered as durable and the genes are pyramided. Most commonly, race non-specific resistance is characterized by durability, having a partially resistant phenotype, and being effective to a broad range of races with optimal level of expression at the adult plant stages [76,94]. Wheat breeders and

pathologists have always been concentrating on adult plant resistance genes in order to identify and improve the level of resistances [8]. The detection of adult plant resistance is usually conducted at the post-seedling stage, and is often characterized as field resistance [63,130]. Adult plant resistance genes are effective only in adult plant resistance stages, but have been shown to be an important part of durable rust resistance [49,96]. The principle of adult plant resistance may derive at any time during the post-seedling stage and environmental factors (i.e. high and low temperature, climate change etc.) may interact for the adult plant resistance gene expression [11].

3.2.2. Sources of Resistance to Yellow Rust Disease

Since, new races of yellow rust are spreading throughout the world, where wheat is produced, identification and transfer of novel sources of resistance genes is necessary. A number of wheat lines with transferred genetic material from related species are available such as wheat-rye, wheat-leymus and wheat-thinopyrum translocations. The incorporation of genetic material from related species leads to wheat varieties adapted to the environment of interest, and to greater sustainability of the wheat production. New sources of resistance genes can be obtained from various sources in the primary, secondary and tertiary gene pools of wheat. One promising source of new genes for wheat is the tertiary gene pool, which includes *Secale cereale*, *Agropyron spp.*, *Leymus spp.*, *Thinopyrum spp.* and *Hordeum vulgare*[33,86]. Rye has been among the most successfully used alien resources contributing against biotic and abiotic stresses for wheat [53,120]. Moreover, genes Yr8, Yr9, Yr15, Yr17, Yr24/26, Yr35, Yr36, Yr53, Yr64 and Yr65 were obtained from diploid and tetraploid wild and cultivated relatives, e.g., Yr15 derived from *Tritium dicoccoides*[41,142], Yr8 from *Aegilops comosa*[99], Yr9 from *Secale cereale*[67], Yr17 from *Ae. Ventricosa*[66], Yr28 and Yr48 from *Ae. ventricosa* [66,142], Yr37 from *Ae. Kotschyi*[47], Yr38 from *Ae. Sharonensis*[72], Yr40 from *Ae. Genuculata*[62], Yr42 from *Ae. genuculata*[71]. Yr50 from *Thinopyrum intermedium*[65], Yr70 from *Ae. umbellulata*[9]. Other genes came from hexaploid wheat landraces [82,142]. Among the permanently designated ASR genes, Yr5, Yr15, Yr53, Yr61, Yr65 and Yr69 are still widely effective and can be used in breeding for stripe rust resistance [140] provided they are not associated with detrimental linkage drag. Following the discovery of the gene-for-gene interaction between plant hosts and their pathogens [40], host resistance genes and their corresponding pathogen avirulence genes could be postulated. Dawit and his colleagues [29] tested 22 Ethiopian bread wheat cultivars and 24 differential lines with 20 *Puccinia striiformis tritici* races collected from Ethiopia, France and Germany. They postulated different combinations of Yr2, Yr3a, Yr4a, Yr6, Yr7, Yr8, Yr9, Yr27, Yr32 and YrSU in tested materials. Hovmøller [48] reported Yr1, Yr2, Yr3, Yr4, Yr6, Yr9, Yr15, Yr17, Yr25 and Yr32 in 98 Danish wheat cultivars; Xia and his colleagues [139]; Zeraf and his colleagues [142], detected Yr2, Yr3a, Yr4a, Yr6, Yr7, Yr9, Yr26, Yr27, YrSel and YrSd in 72 Chinese wheat cultivars and advanced lines; and Sharma and his colleagues [106] reported Yr2, Yr6, Yr8, Yr9, Yr10, Yr15, YrA and YrSu in tests of 52 wild emmer derivatives and advanced bread wheat lines from Nepal. The drawback of this method of gene postulation is that while it is the most effective for identifying race-specific single resistance genes or simple gene combinations at the seedling stage, it cannot be easily used to identify adult-plant, often non-specific resistance genes that tend to be more common in the case of yellow rust [133,142]. Breeding for yellow rust resistance always requires a constant inflow of novel sources of resistance genes, due to the appearance of new virulent pathogen races [66,115]. Resistance breeding might utilize novel yellow rust resistance genes by means of wheat-rye, wheat-

leymus and wheat-thinopyrum introgression lines. Ultimately, these identified genes will be used to develop high yielding wheat cultivars, keeping in mind food security, environmental issues and human health. Bread wheat (*Triticum aestivum* L.) is a hexaploid species constituted of the AABBDD genome. The donors of the wheat genome are: AA *Tritium urartu*, BB *Aegilops speltoides* and DD *Aegilops tauschii*[31]. Wheat belongs to the tribe Triticeae of the family Poaceae. According to crossability with hexaploid wheat, other related species are divided into three major gene pools: The primary gene pool; the secondary gene pool; and the tertiary gene pool [86,115]. These gene pools can play an important role for present day wheat breeding when introducing novel sources of resistance to develop resistant cultivars toward yellow rust [76,115]. The primary gene pool of bread wheat consist of species that have genomes homologues, with bread wheat, *Triticum aestivum* (AABBDD), e.g. hexaploid spelt (*Triticum spelta* AABBDD), tetraploid *Triticum turgidum* (AABB), diploid *Triticum monococcum* (AA), *Triticum dicoccoides*, *Aegilops tauschii* (DD), as well as landraces of hexaploid and tetraploid wheat [86,115]. The desired genes within this group are possible to transfer via direct hybridization, homologous recombination, backcrossing, and selection. The secondary gene pool of hexaploid wheat contains *polyploid Aegilops* and *Triticum species* that have one genome in common with *Triticum aestivum* e.g. *Triticum timopheevii* (AAGG) and *Triticum araraticum* (AAGG). Some *Aegilops species* share the evolution of wheat and have played an important role in wheat domestication. Examples of such *Aegilops species* include the Sitopsis section related to the B genome of hexaploid wheat, e.g. *Aegilops speltoides* and *Aegilops longissima* ($2n=2x=14$). Thus, the genus *Aegilops* represents the largest part of the secondary gene pool of wheat, and several species have been used by direct crossing, backcrossing, selection via chromosome recombination, embryo rescue and cytogenetic manipulations to enhance the recombination in wheat improvement programs [57,84]. Diploid and polyploid species, which are members of the tertiary gene pool of hexaploid wheat, have non-homologous genomes with hexaploid wheat. One promising source of novel genes for wheat is wheat grasses and wild rye both being included in the tertiary gene pool. This gene pool has been successfully hybridized with wheat and genes have been incorporated into the bread wheat genome, representatives are from *Agropyron*, *Pseudoroegneria*, *Psathyrostachys*, *Thinopyrum*, *Elymus*, *Secale cereale*, *Hordeum vulgare* and *Leymus species*[30,85,134]. However, the tertiary gene pool species have been limitedly exploited in wheat, because the genomes of these species are non-homologous to those of wheat, and genetic transfers cannot be made by homologous recombination. In order to incorporate genome of these species, special techniques such as embryo rescue, irradiation etc., and further cytological manipulation are required [84]. Consequently, in this gene pool usually linkage drag is the effect, which could be associated with undesirable agronomic traits [35], and due to homoeology the linkage block might be inherited [97]. Despite this, some of the yellow rust resistance genes are originating from tertiary gene pool species.

3.3. The role of host plant resistance in management of wheat leaf rust disease.

Use of resistant varieties is the most practical, effective, economical and environmentally safe method of plant disease control. The use of resistant varieties cannot only ensure protection against diseases but also save the time, energy and money spent on other measures of control disease [23,101]. Resistance to leaf rust is conditioned by more than 80 Leaf rust (Lr) genes, with Lr1, Lr3, Lr10 and Lr20 being commonly used in global wheat cultivars [76].

3.3.1. Types of host plant resistance to leaf rust disease

Studies of the interaction between cereal rusts and their hosts show a very close relationship between the genetics of the pathogen and of the host in the expression of disease [121]. Host-pathogen interaction could be specific or non-specific [101]. Based on this, plant disease resistance can be classified into two major categories: race-specific and race-non-specific resistance [121].

3.3.1.1. Race-specific resistance to leaf rust disease

Race-specific resistance is conferred by a single resistance gene and is also termed as qualitative, vertical, seedling, all-stage, monogenic (major genes), and hypersensitive, etc., resistance [101,121]. It is effective against only particular races of a pathogen and often “breaks down” easily with the occurrence of new pathotypes of a pathogen, often led by a boom and bust cycle [34,59,74,96]. It is effective at the seedling stage and remains effective at adult stage [63]. However, there are a few race-specific resistance genes that express their resistance genes at adult plant stage, for example Lr12, Lr13 and Lr22a[34]. Most Lr genes are classified in this category [12,76,83].

3.3.1.2. Race non-specific resistance to leaf rust disease.

Race non-specific resistance is conferred by multiple genes or quantitative trait loci (QTLs) and is also termed as quantitative, horizontal, adult plant, slow rusting, polygenic (minor gene), durable etc. resistance with each providing a partial increase in resistance [23,39,76,]. It is effective at adult plant stages and is often detected as field resistance [49]. It is also effective against a broad range of races & is an important source for durable resistance [102]. Therefore, wheat breeders and pathologists have always been concentrating on adult plant resistance genes in order to identify and improve the level of resistances [8]. Among the Lr genes catalogued, only 14 confer race non-specific resistance [83]. These include Lr12, Lr13, Lr22 (alleles a, and b), Lr34, Lr35, Lr37, Lr46, Lr48, Lr49, Lr67, Lr68, Lr75, and Lr77 [83]. Some of them provide partial resistance, for example, Lr34. However, there are exceptions, where some race non-specific resistance genes provide race-specific resistance (i.e. Lr13) or confer a hypersensitive response (i.e. Lr48) [8]. Only a few wheat leaf rust race non-specific resistance genes confer partial resistance against multiple pathogens, and these include Lr34, Lr46, and Lr67 [103].

2.3.2. Sources of host plant resistance to leaf rust disease

Because of the evolution of new races, identification and transfer of new sources of resistance genes is necessary. New sources of resistance genes can be obtained from various sources. Leaf rust resistance genes were initially characterized in wheat *T. aestivum* (Lr1, Lr2a, Lr3, Lr10, Lr11), and later in wheat related species such as *T. tauschii* (Lr21), *Aegilops elongatum* (Lr24), *A. umbellulata* (Lr9), and common rye, *Secale cereale* (Lr26) [19]. To date, more than 80 leaf rust resistance genes have been identified and characterized in bread wheat, durum wheat and diploid wheat species [76,83]. Leaf rust resistance genes, including Lr1, Lr2, Lr2a to Lr2c, Lr3 to Lr6, Lr8, [78] Lr7 [137], Lr10 to Lr13, Lr14a, Lr15 to Lr18 [78], Lr20 [78,88], Lr22b, Lr23, Lr27, Lr30 [87], Lr31, Lr33, Lr40, [78] Lr46, [137] Lr48 [78], Lr49, Lr52, Lr67, Lr68, [105]trp1, trp29 [28], Lrac104,

and Lrac124 [52], have been derived directly from common wheat (*Triticum aestivum*) cultivars. Likewise, genes Lr14a (on 7BL) and Lr23 (on 2BS) were transferred to common wheat from the durum wheat cultivar 'Hope' and the related line 'Gaza', respectively. Similarly, wild cultivars of wheat or wild grasses can be major sources of resistance genes to leaf rust and the first introduction of leaf rust resistance genes into common wheat cultivars was from these wild accessions [42]. One gene(Lr9) was derived from the wild species *Aegilops umbellulata*, three (Lr19, Lr24, and Lr29) from *Aegilops elongatum*, five (Lr28, Lr35, Lr36, Lr47, and Lr51) from *Aegilops speltoides*, one (L37) from *Aegilops ventricosa*, one (Lr37) from *Agropyronintermedium*, seven(Lr21, Lr22a, Lr32, Lr39, Lr41, Lr42, and Lr43) from *Triticum tauschii*[51], one(Lr44) from *Triticum spelta*, three (Lr25, Lr26, and Lr45) from *Secale cereal* [78], one (Lr50) from *Triticummonococcum*[68], one (Lr33) from *Triticum dicoccoides* and one from *Aegilops kotschyi*. To date, more than half of the available Lr genes have been identified from wild relatives [83]. These include Lr9 (*Ae. umbellulata*); Lr19, Lr24, and Lr29 (*Thinopyrum ponticum*); Lr37 (*Ae. ventricosa*); Lr38 (*Thintermedium*); Lr28, Lr35, Lr36, Lr51, and Lr66 (*Ae. speltoides*); Lr21, Lr22a, Lr32, and Lr39 (*Ae. tauschii*); Lr57 (*Ae. geniculata*); Lr58 (*Ae. triuncialis*); Lr59 (*Ae. peregrina*); Lr62 (*Ae. neglecta*); Lr63 (*T. monococcum*), and Lr53, Lr64 (*T. dicoccoides*); Lr14a and Lr61 (*T. turgidum*) [78]. In the same way, because few landraces have been used in modern plant breeding, wheat landraces are important potential source of new resistance genes [98]. This might be due to the co-existence of rust pathogens and wheat may have resulted in the accumulation of diverse resistance in it [21,89].

4. Conclusion

The present study reveals that the development and deployment of resistant wheat varieties has proven to be the most economic, effective and efficient means of managing wheat rust diseases when compared to other methods of managing wheat rusts. Moreover, the use of resistant cultivars is the most environmental friendly and profitable strategy for commercial farmers if they grow genetically resistant varieties using different resistance genes. Historically, rusts of wheat have been successfully controlled through genetic resistance. For example, wheat stem rust was controlled for about three decades using Sr31 resistance gene. Therefore, it can be concluded that using resistant cultivars in management of wheat rust diseases can benefit the producers in the following ways:-

1. Reduction or avoidance of the dependence on chemical control. It may reduce or eliminate the need for chemical control and is economically beneficial to wheat producers.
2. Non-detrimental effect on the environment. The use of rust resistant cultivars can reduce the negative impact of fungicides on the environment. That is using host plant resistance is environmental friendly.
3. No action is required by farmers once the cultivar is selected. That is it requires/demands no action by farmers after cultivar selection.
4. Use of resistant cultivars can also avoid fungicide resistance development by the rust pathogens.
5. Cost of resistant cultivar development and deployment spread to all users of the cultivar. That is using host plant resistance is economical compared to using other methods of wheat rust disease

management. The use of resistant varieties cannot only ensure protection against diseases but also save the time, energy and money spent on other measures of control.

6. Resistant cultivar control can be maintained through seed supply; i.e., resistance is imbedded in the seeds.
7. Resistant varieties can be the only practical method of control of diseases such as rusts, viruses, phytoplasmas wilts etc. in which chemical control is very expensive and impractical.
8. In addition to the above benefits, though not for wheat crops, in some crops, using host plant resistance may be the only option to get a profit from the production. For example, in crops of low cash value, chemical and other methods of control are often too expensive to be applied. In such crops development of varieties resistant to important diseases can be an acceptable recommendation for the farmer. Generally, management of wheat rusts through host plant by the application of resistance genes is the most effective, economical, environment friendly and practical approach.

Though using host plant resistance has the above benefits to farmers, it has also its own limitations:-

1. Resistance may become ineffective after a period. Particularly race-specific resistance has short lifetime (fast breakdown of the resistance). That is it often “breaks down” easily with the occurrence of new pathotypes of a pathogen.

The use of resistant cultivars may cause a race shift in pathogen populations to races that are unaffected by the resistance present in the crop. It causes selection pressure, then overcoming of resistance genes by mutated (new) race of the pathogen population. Reports indicate that the average lifetime of the genes conferring race-specific resistance is estimated to be five years on global basis and any breakdown in resistance leads to the absence of the defence mechanism. When a host resistance gene with a large effect is spread over a vast area (boom), the pathogen adapts by evolving into a new population which overcomes the subsequent resistance (bust) in the host plant rendering some rust resistance genes ineffective. The resistance of R-genes, particularly when deployed singly, breaks down quickly, in what has been often referred to as boom and bust cycles and the use of one or more widely deployed R-genes favours the selection of new pathogen races with virulence to one or more widely deployed R-genes. To avoid the implications of boom and bust phenomenon, use of durable host resistance is advocated in several crops. Durable resistance remains effective even though it may be widely grown for a long period of time, in an environment that favours the disease.

2. It diverts effort from breeding for yield. Currently selection for resistance to rust in wheat is a major resource consuming activity in most breeding programs and prevents breeders from focusing totally on the critical issue of yield.
3. No change possible after planting. That is no chance of changing once the seeds of the resistant cultivars have been planted.

4. Requires knowledge of pathogen virulence and evolution.
5. Selection and evaluation of horizontal (non-race specific) resistance is relatively difficult. So far, there is no precise way available to identify the genetic components that are associated with durable resistance.
6. Race-specific resistance genes have limited use in breeding due to association of negative linkage drag and other problems.

Reports show that though some of the race-specific genes confer resistance to the current races, they have limited use in breeding owing to negative linkage drag, unadapted backgrounds, and their secondary and tertiary gene pool origin necessitating considerable research efforts for utilization through breeding.

5. Recommendation

Break down of resistant cultivars due to new races of rust pathogens is a common occurrence in wheat production of the world. Thus, replacing the susceptible cultivars by resistant cultivars is important to reduce the areas occupied by the susceptible cultivars. The replacement of the susceptible cultivars by resistant cultivars requires a continuous development of new resistant cultivars largely focusing on adult plant resistance. Development and use of resistant cultivars is the most effective means of control but strong seed systems and extension structures are needed to use this tool effectively. The replacement of the busted cultivars with resistant ones also requires fast track variety release, accelerated seed multiplication, popularization and promotion of the newly developed rust resistant wheat varieties. Therefore, based on these facts the following activities can be recommended:-

1. A continuous development of new resistant cultivars largely focusing on adult plant resistance. International and national agricultural research organizations and institutions should continuously develop new wheat rust disease resistant varieties to prevent yield losses due to these diseases and thus to protect the growers from risks resulted from the yield losses. Thus, strong national and international programmes are needed for breeding improved resistant cultivars.
2. Fast track variety release to replace the busted cultivars by resistant cultivars. Replacing susceptible varieties in the risk areas with resistant ones should become an immediate priority. It is highly advisable to release and promote varieties that have durable adult plant resistance or have effective race-specific resistance genes in combinations to prevent further evolution and selection of new virulence that lead to boom-and-bust cycles of production.
3. Accelerated seed multiplication and distribution. Deployment of newly developed resistant varieties in farmer fields requires rapid multiplication and distribution of seeds and farmers' access to them.
4. Popularization and promotion of newly developed rust resistant wheat varieties. Demand creation for newly released varieties through popularization and demonstration is important and it enhances the adoption of resistant varieties through improved market linkages and value chain development

activities. The links with research, seed sector, extension and farmers are critical in transferring these technologies into practice effectively

5. Regional and international collaboration in the development of rust resistant wheat varieties. Wheat rust diseases are recurrent potential global threats. Coordinated actions that reduce the risk of spread and strengthen quick response capacities for management of wheat rust diseases have to be undertaken at the national, regional and global levels. Wheat rust diseases are exemplary transboundary threats to wheat production. Wheat rust disease development in one region or country is a great concern for neighbouring countries and regions due to its airborne and transboundary nature. Therefore, coordinated efforts are essential to facilitate interactions and collaborations among the countries and regions. Regular workshops and consultations within and among the regions would facilitate exchange of experiences, developments, disease occurrence, knowledge and materials and technology transfer in general. These actions would need to be organized with an inclusive approach, ensuring engagement of all related sectors, institutions and organizations in the process. Development and deployment of resistant varieties also requires regional and international collaboration to effectively address wheat rust diseases through data sharing. There should be a need for a collective fight against rust diseases and this requires all partners, affected countries or those at risk, national plant protection services and research institutes, researchers, international centres and organizations, and investors; to be actively engaged.
6. Using modern breeding methods. It takes many years to develop new rust resistant varieties in convention breeding methods. The use of these breeding methods should be replaced by the use of high-throughput technologies to accelerate the breeding process and make available rust resistant wheat varieties in short period of time.
7. Using multidisciplinary research approach. A multidisciplinary approach involving pathologists, breeders, geneticists, physiologists, agronomists and bioinformaticians at different stages of research and development is necessary to develop an improved cultivar with stable and durable rust resistance through host plant resistance approach.

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