Chapter 11
Contribution of Landraces in Wheat Breeding

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11.1 Introduction of Landraces

Agriculture is one of the oldest livelihood sources of mankind. Humans remained actively involved in the selection of favorable traits which resulted in significant changes in the phenotype and genotype of wild plants. In addition to man's

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selection activities, environmental factors also played a significant contribution in the selection of various favorable traits suitable for man-made land and gardens. Combination of these activities resulted in the development of distinctive populations called “landraces” (Zeven 1998). Landraces are dynamic populations of cultivated plants having a historical background, genetically diverse and distinct identity, and good adaptation to local environment and that are associated with traditional farming systems (Villa et al. 2005). Dwivedi et al. (2016) stated that landraces are heterogeneous populations of domesticated species having great adaptation to local environment and can serve as a source of genetic variations that can be very helpful to combat the current and new challenges for farming in changing environments. Landraces are found phenotypically diverse and less productive compared to their cultivated types (Mir et al. 2020). However, regarding their quality attributes, landraces have been found highly nutritious compared to their cultivated ones (Azeez et al. 2018). Landraces played a major role in plant breeding by providing novel genes for various agronomic, quality, mineral, biotic, and abiotic traits (Azeez et al. 2018; Lopes et al. 2015). An impressive increase in yields per hectare was the result of the “Green Revolution” due the inclusion of high-yielding varieties (HYVs) having better response to inputs (Mir et al. 2020). After the inclusion of these high-yielding varieties, it was supposed that landraces will inevitably disappear with time (Frankel and Bennett 1970; Zeven 1998). However, these breeding activities led to genetic erosion and emergence of various modern cultivars that are prone to various biotic and abiotic stresses. It is estimated that approximately 75% loss of genetic diversity is observed in the last 100 years (Hammer et al. 1996). Globally, loss of genetic diversity is very alarming because it can be used to combat food scarcity problems in the long term. Therefore, it is very important to pay attention to collect, preserve, and grow these landraces as they guarantee the existence of variations that can be used for breeding of crops for the production of more quantity of food with high quality. Besides the inclusion of HYVs, landraces maintained their position by playing a key role in agricultural production, specifically in those environments where commercial cultivars failed their competitive advantage (Casañas et al. 2017).

11.2 Origin of Wheat Landraces

Wheat is one of the domesticated food crops cultivated in mild temperature and consumed as a staple crop by millions of people (Lodhi et al. 2020). Domestication of wheat is considered a key reason behind increased human population, thereby participating in the emergence of the human civilization (Jaradat 2011). Domestication of wild emmer (*Triticum dicoccoides*), which is the progenitor of all polyploid cultivated wheats, is considered an important event in the emergence of agriculture in Southwest Asia. Domestication of wild emmer occurs in the Fertile Crescent, and it acted as a prerequisite for the evolution of tetraploid durum and hexaploid bread wheat (Jaradat 2011). However, the domestication and the subsequent breeding activities drastically reduced wheat genetic diversity (Dvorak et al. 1998).

Ancient farmers planted diverse assemblages of wheat genotypes (i.e., landraces) aiming to decrease the risk of crop failure and to improve food security because they had limited capacity to control the spatially heterogeneous and temporally unpredictable environment (Jaradat 2006; Peng et al., 2011a, b). This exercise resulted in the development of wheat landrace meta-populations and the evolution of farmers' seed systems through which they accessed and exchanged diverse genetic material. A meta-population structure can be defined as a group of subpopulations that is interconnected through gene flow and seed exchange and favors the evolution of diversity (Jaradat 2011). It is believed that natural interference, human skills, and years of continuous cultivation resulted in great diversity in wheat genotypes (Lodhi et al. 2020). Zeven (2000) stated that previously many farmers used wheat crops to develop new cultivars. Archaeological evidence are present revealing the cultivation of wheat in Iberian Peninsula, since the fifth millennium BC, and the development of wild wheats, traditional wheat varieties, and other crops happened in the Fertile Crescent (Diamond 2002).

Wheat landraces were developed from their older ones having the ability to grow in such conditions which are not feasible for the growth of the regular wheat (Witcombe et al. 1996). Zeven (1999) stated that wheat landraces are crop varieties developed by farmers through human and natural selection and reflect adaptation to local management practices and environmental conditions. Combination of both human and natural selection resulted in changes in the architecture of genotypes having better attributes like drought, salt, cold, or heat tolerance, quality traits, time to heading and maturity, and seed filling duration (Masood et al. 2005). Due to genetically distinct plant populations, wheat landraces are conserved, and some specific names were given by the traditional farmers in order to meet their environmental, cultural, social, and economic needs. Therefore, landraces are also known as farmer's varieties or folk varieties (Belay et al. 1995).

11.3 How Landraces Contributed in Wheat Breeding

Landraces played a significant role in wheat breeding by gaining focus from breeding community. Wheat landraces served as genetic resource for the development of climate-resilient cultivars with high yield (Abu-Zaitoun et al. 2018). An increasing interest has been observed for the usage of landraces as source of nutritional traits and flavor repertoire and landrace cultivation for niche markets (Roselló et al. 2018). Wheat landraces contain higher genetic diversity compared to most modern wheat landraces, and this diversity includes their adaptation to environmental conditions according to the place of origin. Some countries used this characteristic in the development of first improved cultivars through the selection of local landraces. For example, "Aragon 03" was the leading variety in Spain during the period 1960–1976. It was developed from indigenous landrace population "Catalan de Monte" (Gadea

1958) and showed high ability to drought resistance (Royo and Briceño-Félix 2011a; b). Similarly, "Turkey" (syn. "Turkey Red"), a hard red winter wheat having better adaption for cold regions, showed marvelous impact on wheat cultivation in the United States at the turn of the last century due to decreased winterkill, among other traits (Olmstead and Rhode 2002). A Japanese landrace "Akakomugi," containing Rht8c and Ppd-D1, was used by Italian breeder Nazareno Strampelli to improve Italian wheat gene pool (Salvi et al. 2013). The sensational varieties "Ardito and Mentana" developed from the crosses of Strampelli, including Akakomugi, became the basis of most of the new varieties developed in Mediterranean countries, South American countries, and several distant countries such as Russia and China. In Argentina, "Ardito" was used as parent to develop the variety Klein-33, which became the backbone of the former USSR breeding program, generating the variety Bezostaja-1 (Borojevic and Borojevic 2005). Contribution of landraces in wheat breeding for various traits is discussed comprehensively.

11.3.1 Role of Landraces in Adaptive Traits

Adaptive traits suited to target the environment have acted a decisive role during domestication and the spread out of domesticated wheat. Fitting flowering time to the current conditions in the target environments is presumably one of the main important factors during dispersal (Peng et al. 2011a; b; Royo et al. 2020). The first domesticated cereals/old landraces had most probably response to day length and cold temperatures like their wild relatives/progenitors. Motzo and Giunta (2007) hypothesized that old cultivars/landraces had the greatest day-length sensitivity and vernalization in comparison to intermediate and modern ones. However, novel adaptive traits for each target environment were naturally or artificially selected during the domestication and spreading process from the Fertile Crescent to new agricultural areas (Kilian et al. 2009). Especially other yield-related traits such as plant height, waxiness, number of spikes, and weight of spikes and grains were also co-selected by ancient farmers, and many botanical variants have been developed in this process (Peng et al. 2011a; b). Wheat landraces arising from the migration from the Fertile Crescent to the other regions of the world had been grown extensively until the Green Revolution in the early 1970s (Harlan 1975). As a result of the Green Revolution, more productive semidwarf wheat cultivar shaving better response to inputs replaced the landraces/local populations which are generally identified as tall, tended to lodge, sensitive to the foliar diseases, and low yielded (Reynolds and Borlaug 2006a; b; Lopes et al. 2015). Nevertheless, their cultivation has continued in marginal environments and they currently support subsistence farming in many regions of the world (Newton et al. 2010).

The wide range adaptability of wheat is mainly based on three genetic groups such as vernalization (*Vrn*) genes, photoperiod (*Ppd*) genes, and genes controlling "narrow-sense earliness" or "earliness per se" (*Eps*). Vernalization, which is inducting flowering by exposure to cold, basically determines plant growth habit types as winter (strong vernalization requirement) and spring (no vernalization requirement). Vernalization in wheat has very allelic complex and previous studies have presented that *Vrn* allele combinations or frequencies with an adaptive value in target growing areas are varied geographically (Stelmakh 1990; Damania et al. 1996; Iwaki et al. 2001; Zhang et al. 2008; Sun et al. 2009). Kato and Yokoyama (1992) observed the main adaptive traits in 158 bread wheat landraces collected from various climatic regions including Asian and European countries, and they claimed that nearly half of the variation for observed traits was accounted by geographical differences of their origin centers. Kato et al. (1997) also studied geographical variation of wild emmer (*Triticum dicoccoides*) accessions for vernalization response and earliness in comparison to other tetraploid relatives such as cultivated emmer (*T. dicoccum*), durum wheat (*T. durum*), and *T. turgidum*. They concluded that spring growth habit in *T. dicoccoides* could have evolved from a winter type especially in temperate conditions.

Many studies presented that the vernalization requirement in wheat is considered to be genetically controlled by at least three loci, *Vrn-A1* (*Vrn-1*), *Vrn-B1* (*Vrn-2*), and *Vrn-D1* (*Vrn-3*), located in chromosomes 5A, 5B, and 5D, respectively (Pugsley 1971, 1972; Law et al. 1976; Galiba et al. 1995; Dubcovsky et al. 1998; Yan et al. 2003). While *Vrn-A1* has the major impact on transition from vegetative to generative phase, recessive mutants of *Vrn-B1* trigger flowering. While a dominant allele of any *Vrn* genes causes spring growth habit, wheats classified as winter type must have recessive alleles at all *Vrn* loci (Turner et al. 2013). On the other hand, photoperiodic response in wheat is primarily controlled by three major genes, *Ppd-D1* (*Ppd1*), *Ppd-B1* (*Ppd2*), and *Ppd-A1* (*Ppd3*), located in 2DS, 2BS, and 2AS chromosomes, respectively. It is known that *Ppd-D1* plays an important role in regulation of photoperiodic response. In addition, "earliness per se" or "narrow-sense earliness" is the difference in flowering times of genotypes whose vernalization and day-length requirements have been completed (Kato et al. 2001). Earliness per se genes can also affect flowering time independently, but these genes have not been studied in detail because of major effects of vernalization and photoperiod genes on flowering time. Moreover, this trait is highly heritable and can be effectively used in breeding programs (Kato and Wada 1999). Many QTLs have been identified for earliness per se in all three genomes with previous studies (Bullrich et al. 2002; Hanocq et al. 2004; Kamran et al. 2013).

Previous studies with a marker-assisted selection approach have clarified that landraces/accessions have a huge genetic diversity and very allelic complex for vernalization and photoperiod genes. Jiang et al. (2010) found that the frequencies of the dominant *Vrn* genes in 153 Chinese wheat landraces were 60.78% (*Vrn-D1*), 5.88% (*Vrn-A1a*), 5.23% (*Vrn-B1*), and 0 (*Vrn-B3*), respectively. Andeden et al. (2011) determined that Turkish wheat germplasm has mostly the dominant *Vrn-B1* allele followed by *Vrn-D1* and *Vrn-A1*. Derakhshan et al. (2013) reported that the frequencies of dominant *Vrn-D1* and *Vrn-B1* alleles in 395 Iranian wheat landraces were 67.35% and 38.48%, respectively. Manickavelu et al. (2014) characterized 400 wheat landraces genetically collected from different agroecological zones of Afghanistan for adaptive and other yield-related traits, and they reported that 53%

of all landraces were winter types, 43% had one or more dominant *Vrn* alleles, and 4% were either unknown or had *Vrn-A1c* – a rare spring allele. Guo et al. (2015) also studied distribution of the *Vrn-D1b* allele in Chinese wheat accessions and determined that the frequencies of *Vrn-D1a*, *Vrn-D1b*, and *Vrn-D1* alleles were 27.3, 20.6, and 52.1%, respectively, of 689 accessions. They also claimed that *Vrn-D1b* allele originated from Chinese landraces as a result of pedigree analysis. Goncharov (1998) claimed that there is a high rate of the *Vrn-D1* allele in countries near the equator in addition to Pakistan, Afghanistan, and China.

Other important genetic factors like dwarfing genes (*Rht*) are critical against environmental stresses to guarantee both adaptability and grain yield in addition to vernalization, photoperiod, and earliness. It is known that over 30 height-reducing genes have been identified so far (McIntosh et al. 2013). The major dwarfing genes "*Rht-B1*" and "*Rht-D1*" known as the *Reduced height* (*Rht*) loci were introduced during the "Green Revolution" that achieved to improve harvest index by reducing plant height. These genes are known as gibberellic acid (GA)-insensitive dwarfing genes and located on chromosomes 4BS and 4DS, respectively. Another important height-reducing gene is *Rht8* classified as GA-sensitive. *Rht8* is located in chromosome 2D close to *Ppd-D1* and previous studies clarified that *Rht8* and *Ppd-D1a* alleles are often derived together (Worland et al. 1998), but *Ppd-D1a* has pleiotropic effects independently on plant height, grain yield, and yield-related traits (Börner et al. 2002; Chebotar et al. 2013; Zhang et al. 2019a, b). Zhang et al. (2006) determined that *Rht-B1b*, *Rht-D1b*, and *Rht8* are common in autumn-sown Chinese wheat germplasm, while the frequencies of alleles vary from between regions. Kolev et al. (2011) also reported the most frequent alleles as *Ppd-D1b*, *vrn-A1*, *vrn-B1*, *vrn*-D1, and *Rht-B1a* in Bulgarian germplasm including old cultivars and landraces. Rasheed et al. (2016) studied the allelic variation of economically important traits such as *Vrn*, *Ppd* and *Rht*, in 107 wheat landraces collected from different geographic zones of Pakistan. They determined that less than half of the landraces has *Ppd-D1a*, *Rht-B1b*, *Rht-D1b*, and spring-type alleles of *Vrn-A1* and *Vrn-D1*. The studies explained above highlight how these genes from landraces have geographically evolved in the target areas.

11.3.1.1 Success Stories of Wheat Landraces for Adaptive and Yield-Related Traits

There are many successful reports in the development of new wheat varieties with the use of landraces containing different dwarfing genes. A Japanese landrace "Akakomugi," containing *Rht8c* and *Ppd-D1*, was used by Italian breeder Nazareno Strampelli to improve Italian wheat gene pool (Salvi et al. 2013). The crosses between Italian genotypes and Akakomugi resulted into the introgression of new alleles such as *Ppd-D1* and *Rht8c*. The sensational varieties "Ardito and Mentana" developed from the crosses of Strampelli, including Akakomugi, became the basis of most of the new varieties developed in Mediterranean countries, South American countries, and several distant countries such as Russia and China. In Argentina, "Ardito" was used as parent to develop the variety Klein-33, which became the backbone of the former USSR breeding program, generating the variety Bezostaja-1 (Borojevic and Borojevic 2005). Another variety, Frontana, derived from a cross with Mentana, was part of the pedigree of the varieties Penjamo 62, Yaqui 48, Lerma 50, Escobar, and Supremo. Similarly, many genotypes derived from Mentana were developed in breeding programs of Canada and Australia (Salvi et al. 2013; Tadesse et al. 2016).

A similar success story from the Nobel laureate Norman Borlaug in the mid-20th century was recorded with the Norin 10/Brevor cross containing *Rht-B1* and *Rht-D1*. The lineage of Norin-10, developed by a Japanese breeder G. Inazuka, is tracked back to a Japanese short-straw landrace "Shiro Daruma" containing *Rht-B1* and *Rht-D1* crossed with the American high-yielding varieties Fultz and later Turkey Red (Reitz and Salmon 1968). Norin 10-Brevor 14 cross was sent to N. Borlaug at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico, and this cross and new crosses with Norin/Brevor 14 variants were tested for adaptation in tropical and subtropical climates in the center (Hedden 2003). Wheat varieties developed from semidwarf wheats developed by N. Borlaug and his colleagues in CIMMYT are grown in millions of hectares in many regions of the world.

The story of the Turkey Red brought to America is also very interesting. This bread wheat landrace, which was firstly grown in the USA around Kansas in the 1870s, was introduced to this region by German Mennonites who migrated from Crimea to the USA (Quisenberry and Reitz 1974; Smale 1996). The landrace has thin stem, high plant height, tended to lodging, narrow and dark green leaves, resistance to harsh climate conditions, white grain, high biomass, resistance to rust diseases, and tolerance to other foliar diseases (Quisenberry and Reitz 1974; Lopes et al. 2015). In addition, the landrace "Crimean," introduced at the same time as Turkey Red, was directly included into the Nebraska gene pool. The effects of these two landraces on wheat improvement were indirectly reported with previous studies (Ali et al. 2011; Mengistu et al. 2012). Previous reports reported the investigation of major quantitative trait locus (QTL) related to grain yield on chromosome 3A originated from the cultivar "Wichita" which was obtained from these landraces.

Another important landrace "Chinese Spring" (CS) has also affected the wheat improvement and genetics in depth. This variety is known to be a Sichuan landrace, and Yen et al. (1988) claimed that CS is similar to a Sichuan white landrace "Cheng-du-guang-tou" (CDGT) in terms of morphology, physiology, and cytogenetics-based comparison. The similarity of these two landraces was also presented with RFLP profiling by Ward et al. (1998). CDGT has still been used widely in Sichuan breeding programs because of its high tillering potential, high number of spikelets, and high level of floret fertility (Liu et al. 2018). In addition, the landrace has been widely used to develop wheat-rye translocation lines because of its ready crossability, and therefore, many cultivars and pre-/breeding lines have been developed using CS as parent both in China and many different regions of the world. However, the main important impact of CS is on genetics and molecular breeding of wheat in which CS (IWGSC RefSeq v2.0) was sequenced at genome and single chromosome level and released the genomic data for public access (http://www.wheatgenome.org/News2/IWGSC-RefSeq-v2.0-now-available-at-URGI).

In addition to important wheat landraces mentioned above, several landraces with important adaptive and yield-related traits used by plant breeders in the early twentieth century have intensely been used in pedigrees of modern wheats such as Zeeuwse Witte in the Netherlands, Blount's Lambrigg and Purple Straw in Australia, Marquis and Red Fife in Canada, Kunduru in Turkey, Saragolla in Italy, and Turkey Red in USA, which actually originated from Turkey (Gökgöl 1935; Quisenberry and Reitz 1974; Ozberk et al. 2016; Alsaleh et al. 2016) and became a cornerstone of the early European and indirectly world breeding programs (Smale 1996; Braun et al. 2001). In addition to these examples, wild progenitors/relatives and transition forms of wheat have formed the evolution and distribution of modern wheat landraces and (indirectly) cultivars. Especially, many unique alleles that provide resistance to different diseases and pests, including rust diseases, powdery mildew, *Septoria tritici* blotch, *Septoria nodorum* blotch, tan spot, cyst nematode, root knot nematode, Hessian fly, greenbug, Russian wheat aphid, wheat curl mite, and soil-borne cereal mosaic virus, have been introgressed to modern wheat cultivars (Kishii 2019).

Introgression of new alleles from the locally adapted landraces to modern wheat cultivars should be one of the main breeding targets. Unfortunately, most of landraces have not still been identified both genetically and agronomically. However, the efficient use of landraces in breeding programs requires understanding their genetic diversity and population structure. Baloch et al. (2017) evaluated the genetic diversity of 92 durum wheat landraces from the Central Fertile Crescent including Turkey and Syria with 39,568 DArT-seq and 20,661 SNP markers. As a result of the study, Turkish and Syrian landraces complexly clustered into three groups, and the results illustrated that farmer-mediated selection and lack of the commercial varieties might have concluded in the exchange of genetic materials between two neighboring regions. Soriano et al. (2016) classified 172 durum wheat landraces, using molecular markers, into four genetic populations in relation to their geographic origin: eastern Mediterranean (EM), eastern Balkans and Turkey, western Balkans and Egypt, and western Mediterranean (WM). They determined that the genetic diversity among landraces increased during migration to West Mediterranean basin due to lower genetic diversity in the eastern Mediterranean population. Soriano et al. (2018) also support the theory with an association mapping study that 23 marker alleles in relation to important agronomic traits with different frequencies from east and west regions of Mediterranean basin were identified. With a similar approach, Liu et al. (2017a; b; c) reported a genome-wide association study with 52,303 DArT-seq markers that 723 wheat landraces collected from ten different agroecological zones of China were investigated for 23 agronomic traits in six environments. As a result of the study, all landraces were classified into five clusters based on phenotypic data, and 25 candidate genes associated with significant markers were characterized.

Unveiling the genetic basis of yield-related traits in wheat landraces is vital to ensure global food security because of their higher genetic diversity, large number of alleles, and potency of unique variants of alleles compared to modern wheat varieties. The advent of new technologies about sequencing, mapping, and other related technologies has been facilitating high-quality sequences of wheat and its relatives. The sequences will likely stimulate many new studies on evolution, genetics, and genomics of wheat, and accelerate characterization of novel genes controlling important adaptive and yield-related traits from landraces and wild relatives of wheat.

11.3.2 Role of Landraces in Abiotic Stress

Resistance to abiotic and biotic stresses, productivity, seed quality, seed mineral content, and many other traits will be future breeding aims to meet the world's rapidly increasing food demand. Availability of higher natural genetic diversity to increase selection efficiency is one of the most critical and significant objectives of breeding programs. The abiotic stress factors (salinity, heat, drought, etc.) adversely affect crop production and yield (Jaleel et al. 2009; Thakur et al. 2010; Mantri et al. 2012). Traditional plant breeding is a long-term process that has been used effectively for many years, and molecular tools can be employed to overcome complications and to ensure the improvement of speed breeding strategies (Nadeem et al. 2018; Baloch et al. 2016). In this part, we discussed the role of landraces in different abiotic stress conditions such as salinity, heat, and drought to provide a significant resource for wheat breeders.

11.3.2.1 Wheat Landraces' Role in Salinity Tolerance

Salinity is a major feature that reduces crop production and affects nearly 1 billion hectares of land worldwide (Fageria et al. 2012). Therefore, developing crops providing a satisfactory amount of product in salty soils or different climatic conditions is important to meet the growing food demand. Screening of wheat germplasm for salt tolerance has been conducted by various researchers (Kumar et al. 2017; Arabbeigi et al., 2018). For example, Shahzad et al. (2012) evaluated wheat landrace genotypes using morphological and molecular markers for salinity tolerance at the vegetative stage. The authors proposed that accessions 10793 (Pakistan), 10790 (Pakistan), 10821 (Pakistan), and 11526 (Pakistan) are found salt-tolerant at 200 mM NaCl stress. At 250 mM NaCl stress, accession 11299 (Pakistan) was the most salt-tolerant followed by accessions 11335 (Pakistan), 11370 (Italy), and 11214 (Pakistan). Additionally, accessions 10790 (Pakistan), 10828 (Pakistan), 10823 (Pakistan), and 4098805 (4098805) performed better at both 200 and 250 mM NaCl stresses. In another study, Chaparzadeh et al. (2014) determined the effects of NaCl (control, 75, and 150 mM) on the plant leaves of 18 bread wheat (*Triticum aestivum* L.) landraces from the west area of the Urmia Saline Lake. While accessions 12194 (from Piranshahr), 11199 (from Urmia), and 11488 (from Salmas) were found as the most tolerant with combined salt tolerance indexes for all biochemical and physiological parameters, accessions 11479 (from Mahabad) and 11492 (from Urmia) were determined as the least tolerant. It was suggested that these parameters could be used together as powerful biomarkers to screen for salt-tolerant landraces using the cluster analysis method. Al-maskri et al. (2014) investigated specific stem and leaf structural traits for water conservation. Based on the results of the study, cultivars/landraces were rated according to their degree of drought and salt tolerance as S-24 (from Pakistan) > J-305 (from Oman) > Sarraya (from Northern Asia, Africa, Middle East, Asia Minor) > Senain (from Oman) > Cooley (from Chile and Mongolia) > MH-97 (from Pakistan) > Missani (from the Mediterranean, Middle East Asia, and North Africa) > Hamira (from Oman) > Shwairaa (from Oman). Two of them (S-24 and J-305) are rated as highly tolerant, five moderately tolerant (Sarraya, Senain, Cooley, MH-97, and Missani), and two sensitive (Hamira and Shwairaa). The recent advances in genomic information and technology have opened new horizons and foundations for genetic breeding of salt tolerance. Various QTL mapping studies for salt tolerance in wheat were conducted by Quarrie et al. (2005), Ma et al. (2007), Genc et al. (2010), Hussain et al. (2017), Shamaya et al. (2017), Ren et al. (2018), Devi et al. (2019), and Ilyas et al. (2020). On the other hand, Yu et al. (2020) analyzed in a GWAS using 307 wheat accessions including local landraces and exotic cultivars. Researchers found that some Chinese landraces such as Baihuamai, Youzimai, Beijing 10, Jimai 1, and Zaosui 30 displayed superior salt tolerance. According to kinship analysis, Chinese landraces revealed a source of rare favorable genetic variation. Moreover, many of these landraces have already adapted to the different environments in China (Liu et al. 2017c; Zhou et al. 2018). In addition to these examples, wild relatives of wheat are also potential sources of important genetic materials such as salinity tolerance for wheat breeding. The use of wild relatives of *Triticum* species is one of the main breeding targets and may offer an opportunity to improve salinity tolerance by presenting availability to more variable germplasm (Shavrukov et al. 2009). For this content, researchers investigated the salinity tolerance of various accessions of *Aegilops tauschii*, and determined that the accessions studied are found similar to bread wheat. On the other hand, it was presented that accessions of *Aegilops tauschii* had a much lower Na^+ ratio but higher K^+/Na^+ ratios in their leaves than did durum wheat (Gorham et al. 1987, 1990). Another important wild relative of wheat is jointed goatgrass, *Aegilops cylindrica* Host. ($2n = 4x = 28$; CCDD) species, which was formed through amphidiploidization of a hybrid or hybrids between *Ae. tauschii Coss*. ($2n = 2x = 14$; DD) and *Ae. markgrafii* (Greuter) Hammer ($2n = 2x = 14$; CC). Farooq et al. (1989) screened *Ae. cylindrica* accessions obtained from inland Pakistan and oversea, and determined that some of salinity-tolerant accessions survived at 300 mM NaCl and 400 mM NaCl in treatments using Hoagland solution. Another researcher reviewed the use of wild relatives of wheat for salinity tolerance (Colmer et al. 2006). Arabbeigi et al. (2014) evaluated the physiological response of the highly salinity-tolerant *Ae. cylindrica* genotypes and the SSR and EST-SSR markers linked to the salinity tolerance. As a result of the study, ten most salinity-tolerant genotypes of *Ae. cylindrical* were identified. In addition, Xgwm312, Xwmc170, Xgwm291, and

Xgwm410 microsatellite markers produced a distinguished banding pattern in the ten most salinity-tolerant genotypes in the study. These markers can play important role in wheat breeding programs. Very recently, Ahmadi et al. (2020) investigated the domesticated and ancestral wheat genotypes, including *Ae. triuncialis*, *Ae. neglecta*, *Ae. umbellulata*, *Ae. caudata*, *Ae. speltoides*, *Ae. tauschii*, *T. boeoticum*, *T. durum*, *T. urartu*, and *T. aestivum*, under control and salinity stress to evaluate the mechanisms involved in salinity tolerance. It was found that two neglected (*Ae. triuncialis*) and ancestral (*Ae. tauschii*) wheat genotypes responded better to salinity tolerance than other genotypes. The studies explained above revealed that variation among the wild relatives and landraces of wheat is available for salinity tolerance, and they can be used to develop modern wheat cultivars in breeding studies.

11.3.2.2 Drought and Heat Stress Tolerance in Wheat

Drought and heat stress are important climatic factors that occur in almost all climatic areas of wheat-growing areas and cause a significant crop loss of up to 40% and 60% by drought and heat stresses in fields, respectively (Zampieri et al. 2017; Thirumalaikumar et al. 2018). These factors affect crops at the physiological, morphological, and biochemical levels (Guo et al. 2020); reduce photosynthesis (McKay et al. 2003), cell turgor (Taiz and Zeiger 2006), and chlorophyll fluorescence with a critical reduction of the Fv/Fm ratio (Mohammed and Tarpley, 2009; Izanloo et al. 2008), and impair cell division and elongation (Bal et al. 2010) in sensitive wheat lines compared with tolerant lines. Wheat yield is particularly sensitive to drought and heat stress factors that reduce spikelet productivity, individual grain weight, grain number, and grain filling time during the breeding season (Mahrookashani et al. 2017). The lack of water is not invincible (Ballesta et al. 2019). The adverse effects of drought and heat factors can be overcome by using drought- and heat-resistant cultivars (Van Oosten et al. 2016). The global scenario consists of having a genetic balance of major/minor genes suitable key for these stress factors and developing stress-resistant varieties (Mujeeb-Kazi et al. 2009). Success in plant development commonly depends on the size of genetic variability and the extent to which the beneficial traits are inherited (Kahrizi et al. 2010). Information from the germplasm evaluation will be of great importance for drought- and heat-tolerant genotype selection (Okechukwu et al. 2016). Breeding wheat varieties that tolerate these stressors is currently a major challenge for wheat breeders (Mwadzingeni et al. 2016). Exotic wheat landraces have been shown to be an excellent source of various genes and to function better under stressful conditions (Reynolds et al. 2007). Various studies were conducted to evaluate genetic resources in terms of drought and heat resistance (Hede et al. 1999; Sareen et al. 2014; Pinto et al. 2017; Al Khateeb et al. 2017; Ullah et al. 2018; Korkut et al. 2019). Hede et al. (1999) used a group of 2255 accessions from a Mexican landrace collection in which three landrace accessions (CWI 60155, CWI 59788, and CWI 60391) were determined as having superior and stable leaf chlorophyll content in both environments in 1997. In a study conducted by Sareen et al. (2014), six wheat genotypes (IC 28661, IC 57586, IC 78856, IC 28938B, IC 36761A, and IC 78869A) were identified as tolerant to drought and heat stresses. Al-maskri et al. (2014) rated cultivars/landraces according to their degree of drought and salt tolerance as S-24 (from Pakistan) > J-305 (from Oman) > Sarraya (from Northern Asia, Africa, Middle East, Asia Minor) > Senain (from Oman) > Cooley (from Chile, Mongolia) > MH-97 (from Pakistan) > Missani (from Mediterranean, Middle East Asia, North Africa) > Hamira (from Oman) > Shwairaa (from Oman). Aktaş (2016) determined the most tolerant genotypes (SEN-DER genotypes G7, G10, landrace group genotype G11 (Sorık)) to be used to improve drought-tolerant varieties. Al Khateeb et al. (2017) used four wheat landraces collected from Jordan and indicated that Karak landrace may be selected as the most tolerant wheat capable of adapting to drought-prone environments. Chaichi et al. (2019) screened 123 Iranian wheat (*Triticum aestivum* L.) landraces (spring and winter genotype) for drought tolerance using morphological and physiological features. They determined L-82 and Marvdasht genotypes as drought-tolerant and sensitive genotypes, respectively. Korkut et al. (2019) determined that some genotypes (Nota, Dropia, CIMMYT-HTN 2014/15-6, CIMMYT-HTN 2014/15-2, CIMMYT HTN 2014/15-10) could be evaluated as genitor(s)/progenitor(s) in the wheat breeding programs for heat tolerance.

Landraces, wild relatives, and traditional varieties are potential reservoirs of novel alleles for improving abiotic stress tolerance (Karan and Subudhi 2012). In this context, a deeper understanding of the genetic mechanisms of drought and heat resistance is important to maintain and further develop the efficiency of wheat breeding programs (Arriagada et al. 2017). The initial genetic investigations of wheat under both drought and heat stress in controlled conditions were conducted in durum wheat and bread wheat by Aprile et al. (2013) and Qaseem et al. (2018), respectively. Merchuk-Ovnat et al. (2016) revealed that introgression of QTLs on chromosomes 1B and 2B of *T. turgidum* into *T. aestivum* can improve drought tolerance in domesticated wheat. B genome has been identified carrying loci controlling water utilization efficiency, associated traits, and grain yield under water stress conditions (Mohammadi et al. 2012; Poersch-Bortolon et al. 2016). In another study conducted by Touzy et al. (2019), a panel of 210 elite European wheat varieties in 35 field trials was evaluated, and GWAS (genome-wide association study) was done with six characters in four different environment types to confirm 590 QTLs, some of which were specific to the different water stress patterns. Schmidt et al. (2020) used 315 spring bread wheat accessions to evaluate in pots with semi-controlled environmental conditions that combined drought and heat stress in 2016 and 2017. Australian and Mexican varieties were rated as having great productivity potential under both stresses, which have been selected for their yield performance and made up about 70% of the spring wheat panels. Nearly one-fifth of the tolerant wheat came from varieties of various origins such as the Middle East, the USA, Central Africa, India, and Canada. In the study, QTLs were determined on all chromosomes, most of which were on chromosomes 3B, 5A, 5B, and 6B. Drought and heat stress factors, which together can lead to significant yield losses, have restricted wheat yields in various wheat-growing areas worldwide, and their combined impact could result in critical yield losses (Toreti et al. 2019). Information about QTLs can help breeders to improve new cultivars tolerant to drought and heat stress in marginal environments in future global margins.

11.3.3 Role of Wheat Landraces in Quality Traits

11.3.3.1 Landraces for Biofortification

"Biofortification" or "biological fortification" is the process of improving the nutritional status of staple crops such as minerals, vitamins, and proteins through traditional breeding, modern biotechnological methods, and agronomic approaches (Garg et al. 2018; Yeken et al. 2018; Saini et al. 2020). It is a long-term and sustainable approach, and a cost-effective way to overcome hidden hunger, which is a progressively severe universal challenge for humanity around the world (De Valença et al. 2017). In low-income countries, micronutrient deficiencies have largely increased in the last decades. Zn and Fe deficiencies in particular are a serious public health problem that negatively affects people's lifespan, health, and productivity (WHO 2009; Khan et al. 2008). People need cereals for their dietary requirements; hence, biofortification of cereals is important worldwide (Saini et al. 2020). Wheat is one of the world's most important crops for global food grain production, which was adversely affected by several biotic and abiotic stresses (Ozer et al. 2020). Annual wheat production is expected to increase in the coming years depending on increases of population (Iizumi et al. 2017). Biofortification can be divided into two categories as agronomic biofortification and genetic biofortification (Saini et al. 2020). The first step of biofortification in food crops for plant breeders is to understand the current genetic diversity in germplasm collections (Baloch et al. 2014). Wheat has a large number of wild relatives that can lead to its genetic development (Dempewolf et al. 2017; Ahmadi et al. 2018; Saini et al. 2020). The most frequently required mineral elements in the human diet can be obtained from genetic variations, which improve the levels of nutrients in crops (White and Broadley 2005; Bouis and Saltzman 2017). Agronomical biofortification techniques include fertilizing crops with different fertilizers containing elements such as zinc, iron, and selenium, while genetic biofortification includes traditional and molecular breeding approaches. These techniques have the potential to increase the levels of these minerals in grains (Saini et al. 2020). Monasterio and Graham (2000) claimed that iron and zinc concentrations especially in some bread wheat genotypes were negatively correlated with *Rht* genes. They also reported that the high-yielding wheat cultivars developed after Green Revolution contained less iron and zinc compared to old cultivars/landraces. Heidari et al. (2016) reported that landraces had higher Fe and Zn concentrations compared with commercial cultivars. Ram and Govindan (2020) clarified that genetic diversity in wheat landraces and wild relatives provides novel alleles for genetic enhancement of Zn and Fe. Lyons et al. (2005) examined 665 wheats (ancestral and wild relatives, landrace accessions, and registered cultivars) in Australia and Mexico for Se concentration in grain. They found that Se concentrations of grains changed between 5 and 720 microgr/kg. Khokhar et al. (2020) studied 245 bread wheat genotypes derived from crosses with landraces and the modern wheat cultivar Paragon to detect grain Zn concentration, and they reached promising results for high level of grain Zn where Zn concentration in wholegrain was positively correlated with Fe concentration and grain protein content. They claimed that landraces have a huge potential to increase the concentration of Zn in whole grain and flour of modern high-yielding bread wheat cultivars.

11.3.3.2 Landraces for Some Important Quality Traits

It is generally known that old landraces or cultivars have a huge diversity for some quality traits such as grain protein content, grain texture (hardness), and gluten strength and quality (glutenin and gliadin subunits) than modern wheat cultivars (Aguiriano et al. 2006; Moragues et al. 2006; Ruiz et al. 2012). The grain protein content (GPC) is a crucial trait in determining the quality of wheat (Veraverbeke and Delcour 2002), and modern wheat grains include inherently low protein levels. Hence, breeding for an increase in the protein levels of grain wheat is required to alleviate hunger and nutrient deficiencies. However, the grain protein content was negatively related to grain yield (Blanco et al. 2006; Iqbal et al. 2007; Klindworth et al. 2009). Avivi (1978) claimed that wild emmer wheat (*T. turgidum* ssp. *dicoccoides*) can be a potential gene source to improve grain protein content in modern wheat. Joppa and Cantrell (1990) also studied this hypothesis that they crossed wild emmer wheat and durum wheat, and obtained substitution lines with high GPC. Joppa et al. (1997) reported that a QTL explained 66% of total variation in these substitution lines for GPC. The QTL was named as *Gpc-B1* (Distelfeld et al. 2004), and Uauy et al. (2006a) also positionally cloned the locus and renamed as *NAM-B1*. Hagenblad et al. (2012) studied 367 bread wheat germplasm with worldwide origin and determined that five accessions had wild-type *NAM-B1* allele where it confers high levels of protein and microelements. They also indicated that several accessions with wild-type *NAM-B1* were traced back to Fennoscandian origin. In addition to landraces, cultivated transitional forms of wheat such as einkorn (*T. monococcum* ssp. *monococcum*), emmer (*T. turgidum* ssp. *dicoccum*), and spelt (*T. aestivum* ssp. *spelta*) and wild relatives have the possibility to contain the wild-type *NAM-B1* allele. Uauy et al. (Uauy et al. 2006a; b) reported that wild emmer accessions and most of cultivated emmer accessions studied had wild-type *NAM-B1* allele. Asplund et al. (2010) also determined that only two spelts had a wild-type *NAM-B1* allele among 62 wheat germplasm displayed at the International Exhibition in London in 1862. It's likely that unique variants for grain protein content can be uncovered due to higher genetic diversity of landraces.

As another important trait, endosperm texture is mainly controlled by the *Hardness* (*Ha*) locus located in 5DS, and it's simply inherited despite the fact that softness is the dominant trait. The lipid binding proteins, puroindoline genes (*Pina-D1* and *Pinb-D1*), which are tightly linked to *Ha* locus, have been used to determine the differences between hard- and soft-textured wheats, and landraces that originated from different geographic regions had different *Puroindoline* allele combinations. As an example of this situation, Ayala et al. (2013) studied 102 lines selected from 15 Mexican landraces and determined that while 16 lines had hard texture, 86 lines were soft-textured. Ten out of 16 lines had presence of both *Pina-D1* and *Pinb-D1* alleles. They concluded that the Mexican old landraces are potential sources for important quality traits to develop new wheat varieties with hard grain texture. Li et al. (2019) also studied 107 Chinese wheat cultivars and landraces in terms of diversity of *Puroindoline* genes and their association with kernel hardness. The most frequent combinations were *Pina-D1a/Pinb-D1a* and *PinaD1a/Pinb-D1b* with 39.3% and 34.6% ratios, respectively. They indicated that Chinese landraces had more allelic than do cultivars and are a valuable source of genetic variability in *Puroindoline* genes. Gluten strength and quality are other important quality traits of wheat. Many studies were conducted to determine the genetic variability of old durum wheat cultivars or landraces for glutenin and gliadin profiles, which affected viscoelastic properties of dough, especially in Mediterranean basin (Melnikova et al. 2010; Xynias et al. 2011; Ribeiro et al. 2011; Ruiz et al. 2012; Janni et al. 2018). Nazco et al. (2012) studied the variability of some quality traits such as protein content, SDS sedimentation, and yellow color index and gluten strength in 154 durum wheat landraces from 20 Mediterranean countries with 18 modern wheat cultivars. They determined that the largest variability for quality traits was observed in landraces from eastern Mediterranean basin followed by landraces from western Mediterranean basin, and identified landraces could be used to improve quality traits especially for gluten strength and grain weight in durum wheat breeding programs. While *Glu-A1c* was the most frequent allele in almost all genetic materials studied for *Glu-A1* locus, but *Glu-A1a* was found at low frequency in Mediterranean basin (Mir Ali et al. 1999; Moragues et al. 2006; Naghavi et al. 2009). In addition to *Glu-A1a*, *Glu-A1b*, and *Glu-A1VI*, encoding the subunits 2* and 2*** were determined at very low frequency. However, Henkrar et al. (2017) reported that in Moroccan genotypes, *Glu-A1a* and *Glu-A1b* were the predominant alleles. On the other hand, at the *Glu-B1* locus, there were more genetic variation between genotypes with *Glu-B1b*, *Glu-B1d*, and *Glu-B1e* alleles encoding the subunits 7+8, 6+8, and 20, respectively. Moreover, the variation varied geographically that while *Glu-B1d* allele was predominant in Algerian, Syrian, and Spanish germplasm (Mir Ali et al. 1999; Moragues et al. 2006; Hamdi et al. 2010), the allele was not present in Iranian landraces that they had more *Glu-B1a*, *Glu-B1e*, and *Glu-B1i* alleles (Naghavi et al. 2009). Similar genetic variation was determined for low molecular weight glutenin subunits (LMW-GS). Li et al. (2009) studied 615 Chinese wheat germplasm including 390 landraces and 225 varieties, for HMW-GS, LMW-GS, Zeleny sedimentation, volume, dough development time, stability time, and strength, and reported that genetic materials with good gluten strength and quality were identified in landraces that did not contain wheat-rye translocation. Wheat-rye (the 1BL/1RS) translocation has been used widely in breeding programs because of its disease resistance genes especially for foliar diseases and increased grain yield in some environments, but it negatively affects bread-making quality of wheat at the same time (Zhao et al. 2012; Oak and Tamhankar 2017).

On the other hand, the new technologies such as sequencing, mapping, and other related technologies have been recently used to reveal genetic diversity and novel variants/alleles among landraces related to quality traits of wheat. For instance, Giraldo et al. (2016) performed an association mapping study with 183 Spanish wheat landraces using 749 DArT markers for 18 agromorphological and grain quality traits including protein content, gluten strength, vitreousness, yellow color index, thousand kernel weight, and test weight. They identified 85 stable MTAs (marker-trait associations) with more than 10% explained phenotypic variation, and claimed that novel MTAs were identified and can provide new information to understand genetic control of complex traits. Roselló et al. (2018) also performed an association mapping study with 165 durum wheat landraces from 21 Mediterranean countries using 1149 DArT markers. Landraces had generally higher GPC than modern ones in this study but lower gluten strength. In addition to this, while eastern landraces showed the highest yellow color index, Balkan landraces had the lowest test weight. They also identified 15 meta-QTL (MQTL) for grain quality traits of wheat.

Various studies about landraces conducted in different countries have been briefly summarized and discussed above. We hope that improving the grain quality via agronomic/genetic biofortification and quality breeding studies and producing wheat genotypes with better quality will be beneficial to prevent hidden hunger and to live healthy. In this regard, collaboration among various specialists from public and private research institutes and universities can accelerate the improvement of wheat varieties with high bread- and pasta-making quality. This section will be helpful for wheat breeders, providing knowledge of the advancement made so far in wheat biofortification and quality.

11.4 Role of Landraces in Biotic Stress

There are many studies conducted to discover resistance properties of wheat landraces for different biotic stresses. Since in the wild the host and the pathogen have co-lived in mutual habitats for long periods of time, they co-evolved together. Thus, the sources of resistance can be found most often at these centers of origin, among the wild relatives and landraces of wheat (McIntosh et al. 1995). Pinpointing the resistance factors and genes in the genome and development of molecular markers to test their presence are of great importance.

11.4.1 Role of Wheat Landraces in Disease Resistance

11.4.1.1 Role of Wheat Landraces in Rust Diseases

11.4.1.1.1 Yellow Rust or Stripe Rust

Rust diseases of wheat are among most important and economically devastating diseases of wheat. Rust diseases of wheat consist of yellow (stripe) rust (YR) caused by *Puccinia striiformis* f. sp. *tritici*, leaf rust (LR) caused by *Puccinia triticina*, and stem rust (SR) caused by *Puccinia graminis* f. sp. *tritici* (Reynolds and Borlaug 2006a; b). Genes that confer resistance to the rust diseases are generally designated as *Yr*, *Lr*, and *Sr* for the effectiveness against yellow rust, leaf rust, and stem rust, respectively. Resistances against rust diseases are the most studied resistance properties in wheat landraces. To date, some genes against rust diseases have been identified from landraces and wild relatives of wheat. Among them, *Sr2* gene, which provides resistance against stem rust, has been incorporated from an emmer wheat landrace (McIntosh et al. 1995). Race-nonspecific resistance genes *Yr52*, *Yr56*, *Yr57*, and *Yr62*, which provide adult plant resistance (APR) against yellow rust, have been also incorporated from landraces (Mondal et al. 2016).

Yellow rust or stripe rust is one of the most prevalent and devastating wheat foliar diseases worldwide (Kumar et al. 2016). It is observed mostly on cool and moist regions and causes lower kernel quality and massive yield losses (Chen et al. 2013). Recently, there are many studies on YR done by genome wide association studies (GWAS) using bread and durum wheat landraces (Tehseen et al. 2020; Long et al. 2019; Liu et al. 2017a; b; c; Manickavelu et al. 2016). Wu et al. (2016) used simple sequence repeats (SSR), sequence-related amplified polymorphism (SRAP), and resistance gene analog polymorphism (RGAP) markers, Ma et al. (2015) used SSR and SRAP markers, while Wang et al. (2010) used SSR markers to find the source of resistance in a known resistant wheat landrace. Kandel et al. (2017) used microsatelite markers to pinpoint the resistance in the genome of known resistant wheat landrace. Wu et al. (2015) used molecular markers to screen wheat landraces to find a suppressor gene of the known resistance gene *Yr18*. Li et al. (2015) used DArT-seq genotyping-by-sequencing (GBS) on 8416 Mexican Creole landrace wheats and found seven accessions from them with less than 20% disease severity after YR inoculation. Gessese et al. (2019) screened resistant landrace Aus27430 with 90K wheat SNP chip array by selective genotyping to locate a new resistance gene "*Yr81*." Yuan et al. (2018), Wang et al. (2019), and Liu et al. (2020) used also wheat SNP chip to locate resistance characteristics of wheat landraces. Bux et al. (2012) evaluated Pakistani wheat landraces phenotypically against the disease; on the other hand Akar et al. (2009) used durum wheat landraces from Turkey to evaluate their resistance against the yellow rust disease. Rola et al. (2019) have found two Lebanese wheat landraces that are resistant to different yellow rust pathogen races, including the devastating Warrior pathotype. Wamalwa et al. (2020) found that Kenyan Kenya Tai landrace shows resistance against many YR races. Mohammadi et al. (2015) screened 380 durum wheat landraces and found 46 accessions to be resistant against YR.

11.4.1.1.2 Leaf Rust

Leaf rust is one of the main wheat diseases seen worldwide, which can affect kernel weight and wheat biomass, causing major yield losses (Herrera-Foessel et al. 2006). There are many studies done on leaf rust resistance. Qureshi et al. (2018) identified a novel resistance gene "*Lr79*," from genotyping analysis of resistant durum wheat by using DArT-seq and 90K chip array, and also developed a Kompetitive Allele Specific Polymerase (KASP) marker to locate the gene. Kolmer et al. (2018) used DArT-seq technology to genotype Uruguayan wheat landrace Americano 44. Qureshi et al. (2017) used DArT-seq markers to locate disease resistance in the genome of two wheat landraces from Portugal. Zhang et al. (2019a), b) screened 46 Chinese wheat landraces for resistance against LR and used molecular markers to find out the presence of known resistance genes in those accessions. Akcura et al. (2017) used Turkish wheat landraces, while Riaz et al. (2017) used 136 wheat landraces from Vavilov Institute of Plant Genetic Resources in Russia to test against YR phenotypically. Andenow et al. (1997) used ten Ethiopian tetraploid wheat (*Triticum turgidum* L.) landraces and found some degree of resistance toward the YR disease.

11.4.1.1.3 Stem Rust

Stem rust is one of the major diseases of wheat which hinders with the nutrient flow to developing ears and result in shriveling of the grain and the breakage of the stem that can cause total yield loss (Roelfs et al. 1992; Leonard and Szabo 2005). Studies on SR have been conducted by Babiker et al. (2015) and Zurn et al. (2014), which used quantitative trait loci (QTL) and linkage map, respectively, to locate the resistance region in the known resistant landrace against stem rust pathogen. Haile et al. (2013) used molecular markers for genotyping the Ethiopian durum wheat landraces. Newcomb et al. (2013) and Toor et al. (2013) have screened the landrace collection phenotypically against the SR disease and genotyped using molecular markers. Denbel and Badebo (2012) screened Ethiopian durum wheat landraces against SR race Ug99. On the other hand, Endresen et al. (2011) used ecogeographic data of landrace accessions to predict the resistance against SR according to climatic factors of their location of origin, while Bonman et al. (2007) studied the geographic origin or the resistant accessions. There are also studies conducted to find multiple rust resistance in wheat landraces. Studies which include resistance against all three rust diseases were conducted by DArT and molecular markers (Rahmatov et al. 2019; Bansal et al. 2013) by GWAS and resistance gene prediction (Kankwatsa et al. 2017; Pasam et al. 2017; Jordan et al. 2015; Daetwyler et al. 2014). Kertho et al. (2015) studied YR and SR resistance traits with GWAS technique, Sthapit et al. (2014) used simple sequence repeat (SSR) markers to study YR and SR resistance, and Aoun et al. (2019) used QTL in durum wheat to locate the resistance region against LR and SR in the known resistant durum wheat landrace.

11.4.1.2 Role of Wheat Landraces in Powdery Mildew (PM)

Powdery mildew (PM) is a foliar fungal disease caused by *Blumeria graminis* f. sp. *tritici*, an obligate biotrophic fungus that causes yield and quality loss in wheat grains (Newton et al. 2011). Chinese wheat landraces known for their PM resistance were screened by microsatelite markers (Xue et al. 2009, Huang et al. 2000), SSR markers (Qie et al. 2019; Sun et al. 2018; Fu et al. 2017; Wang et al. 2015; Xu et al. 2015; Fu et al. 2013; Xue et al. 2012), and RNA-seq SNP markers (Li et al. 2020, Xu et al. 2018) to locate genes in the plants' genome, responsible for the resistance trait. Li et al. (2018a; b) used SSR marker to pinpoint resistance in an Afghan wheat landrace. Tan et al. (2019) and Tan et al. (2018) used single Iranian and Afghan PM-resistant wheat landrace to define new resistance genes "*Pm63*" and "*Pm59*," respectively, using SSR markers. Identification of germplasm strategy (FIGS) was used on wheat landraces in a study conducted by Wang et al. (2015), Bhullar et al. (2010), and Bhullar et al. (2009) to discover new alleles of powdery mildew resistance gene *Pm3*. Huang (1997) also used APR against powdery mildew found in the landrace accession k-15560, and monosomic and hybridological analyses were used to locate the gene (Peusha et al. 2002). Amplified fragment length polymorphism (AFLP) markers and microsatellite markers were used to locate Pm24 resistance gene in a Chinese spring wheat landrace. Li et al. (2012) used SSR markers to test the diversity of the single wheat landrace and its relation to the PM resistance. In their study, Li et al. (2016a; b) used 1,297 landraces from 57 countries to screen for the PM resistance, and molecular markers were used to check the presence of known resistance genes. Hysing et al. (2007) screened 155 Nordic wheat landraces phenotypically and with molecular markers for resistance to PM.

11.4.1.3 Role of Wheat Landraces in Fusarium Head Blight (FHB)

Fusarium head blight (FHB) is caused by the fungal pathogen *Fusarium graminearum* Schwabe and has destructive effects on cereals and especially on wheat production all over the world. Moreover, the diseased plants become contaminated with mycotoxins which are poisonous to mammals (Cetin and Bullerman 2005; Goswami and Kistler 2004). Cai et al. (2019) used meta-analysis of previous QTL studies (MQTL) of five wheat landraces to construct a consensus map, and they also developed 22 KASP markers to ease the MAS in breeding programs. Xiao et al. (2011) located a chromosomal region responsible for FHB resistance by fast-neutron induced chromosome fragment deletion, causing the resistant wheat landrace to lose its resistance and become susceptible. Li et al. (2016a, b) used SSR and sequence-tagged site (STS) markers in 195 wheat accessions to find the presence of known resistance genes, whereas Wei et al. (2005) used microsatellite markers to compare the difference between 20 resistant wheat landraces and 4 susceptible wheat lines. Xiao et al. (2013) used RNA sequencing to determine expression of a resistant wheat landrace during FHB infection. There are also studies where wheat landraces known for their resistance against Fusarium head blight have been screened with SSR markers to pinpoint the resistance source in the genome (Cai et al. 2016; Zhang et al. 2012; Li et al. 2011). Talas et al. (2011) screened 68 Syrian durum wheat landraces and Yu et al. (2008) screened 94 wheat accessions to find new sources of resistance to FHB.

11.4.1.4 Role of Wheat Landraces in Septoria Tritici Blotch (STB)

Septoria tritici blotch (STB) is major foliar wheat disease caused by the fungal pathogen *Zymoseptoria tritici* previously known as *Mycosphaerella graminicola*. It is a major threat to wheat production globally, and it is the most damaging pathogen of wheat in Europe causing loss in chlorophyll, premature death of leaves, and reduction of grain production (O'Driscoll et al. 2014; Ziv and Eyal 1977). Many European and Chinese landraces have been found to contain *Stb6* gene which provides resistance against STB (Chartrain et al. 2005a; b). Kidane et al. (2019) used 318 Ethiopian wheat landraces for GWAS analysis and found four putative loci for STB resistance. Ouaja et al. (2020) screened 304 Tunisian wheat landraces, and Ghaneie et al. (2012) screened 45 tetraploid Iranian wheat landraces to test against STB disease phenotypically and found some promising accessions.

11.4.1.5 Role of Wheat Landraces in Tan Spot

Tan spot is caused by *Pyrenophora tritici-repentis* and is an important foliar wheat disease causing severe loss in the grain yield. The disease causes large-scale chlorosis and tan necrosis on leaves and grain shriveling (Maraite et al., 1997, de Wolf et al. 1998). In their study, Gurung et al. (2011) assessed the resistance of 567 wheat landraces against *P. tritici-repentis* races 1 and 5 using DArT markers and developed association mapping.

11.4.1.6 Role of Wheat Landraces in Eyespot

Eyespot is caused by soilborne necrotrophic funguses *Oculimacula acuformis* and *Oculimacula yallundae*. The disease is seen in temperate areas and affects the stem base of the cereals including wheat, causing premature grain ripening and heavy crop losses (Crous et al. 2003, Fitt et al. 1990, Scott and Hollins 1974). Burt et al. (2014) screened all 1056 hexaploid wheat landraces of Watkins collection against both funguses and found two promising accessions with high level of resistance. They also genotyped the accessions that showed resistance to one or both funguses by SSR, STS, and QTL-linked markers.

11.4.1.7 Role of Wheat Landraces in Stagonospora Nodorum Blotch (SNB)

Stagonospora nodorum blotch (SNB) is caused by *Phaeosphaeria nodorum* and constitutes a serious disease of wheat worldwide (Eyal 1987). SNB disease infects both leaves and glumes, subsequently causing decreased grain quality and yield losses (King et al. 1983). Adhikari et al. (2011a, b) evaluated 567 spring wheat landraces of different origin for resistance to SNB and used DArT markers to genotype and develop association map of the resistance traits.

11.4.1.8 Role of Wheat Landraces in Bacterial Leaf Streak (BLS)

Bacterial leaf streak (BLS) is caused by *Xanthomonas translucens* pv. *undulosa*, the most important wheat bacterial pathogen which can cause major outbreaks in the wheat fields under favorable conditions (Adhikari et al. 2011b, Bragard et al. 1997). Adhikari et al. (2012) screened 566 spring wheat landraces for resistance against BLS and used DArT markers to generate association mapping of the resistance regions. They found five genomic regions which are associated with resistance to the BLS disease.

11.4.1.9 Role of Wheat Landraces in Spot Blotch (SB)

Spot blotch (SB) is caused by *Cochliobolus sativus* which is a fungal disease of wheat and barley, observed globally which results in severe yield losses (Kumar et al. 2002). Adhikari et al. (2012) screened 566 spring wheat landraces also for resistance against SB and used DArT markers to create association mapping of the resistance regions. They found four genomic regions which are associated with resistance to the SB disease.

11.4.1.10 Role of Wheat Landraces in Common Bunt (CB)

Common bunt (CB) is caused by the fungal pathogen *Tilletia tritici* that causes significant yield losses in spring and winter wheat production worldwide (Goates and Peterson 1999). Bonman et al. (2006) investigated 10,759 wheat accessions for resistance against the common bunt disease. Accessions from Bakhtaran province in Iran showed the most resistance.

11.4.1.11 Role of Wheat Landraces in Dwarf Bunt (DB)

Dwarf bunt (DB) is caused by the fungus *Tilletia controversa* in winter wheat in regions where snow is persistent (Goates and Peterson 1999). Bonman et al. (2006) studied 8167 wheat accessions against dwarf bunt resistance. Accessions from Hakkari province in Turkey showed the highest resistance against DB.

11.4.1.12 Role of Wheat Landraces in Wheat Blast (WB)

Wheat blast (WB) is a relatively new emerging disease (mid-1980s) caused by *Triticum* pathotype of *Pyricularia oryzae* fungus. It has immense impacts on wheat production (Inoue et al. 2017). Wang et al. (2018a, b) evaluated 520 landraces of common wheat from different regions of the world for the resistance to Br48 isolate of the fungus and found a unique accession resistant to WB. The resistance was due to combination effect of two genes "*Rmg8*" and newly found "*RmgGR119*" gene.

11.4.2 Role of Wheat Landraces in Pest Resistance

11.4.2.1 Role of Wheat Landraces in Root Lesion Nematodes

Root lesion nematodes *Pratylenchus thornei* and *Pratylenchus neglectus* are the most common root lesion parasites that grow and develop in wheat roots, causing damage and substantial losses in wheat production (Nicol et al. 2002). Thompson and Seymour (2011) analyzed the modes of inheritance of resistance to *P. thornei* in seven wheat accessions that showed resistance against the nematode. Schmidt et al. (2005) studied two resistant Middle Eastern wheat landraces with AFLP and microsatellite markers for QTL analysis of resistance to *P. thornei*. Thompson et al. (2009) screened 207 bread wheat and 102 durum wheat accessions from West Asia and North Africa for resistance against *P. thornei*. Among them, 13 bread wheat and 10 durum wheat showed significant resistance. Thompson et al. (2016) screened 78 Iranian wheat accessions for resistance against *P. thornei* and *P. neglectus*. Among them, 32 showed some degree of resistance to both nematodes.

11.4.2.2 Role of Wheat Landraces in Russian Wheat Aphid (RWA)

Russian wheat aphid (RWA) (*Diuraphis noxia*) is an important wheat pest indigenous to southern Russia and Mediterranean countries which have spread to all continents causing substantial damage to wheat fields (DuToit and Walters 1984; Hewitt et al. 1984). Valdez et al. (2012) have evaluated a resistant Iranian wheat landrace using SSR markers to identify the location of resistance trait. It was found that the trait was due to dominant gene. Similarly, Li et al. (2018a) used an Iranian wheat landrace known for its resistance to RWA to locate the trait in the genome using SSR markers.

11.4.2.3 Role of Wheat Landraces in Wheat Stem Sawfly (WSS)

Wheat stem sawfly (WSS), *Cephus cinctus* Norton, is a major pest insect of wheat observed in North America, with devastating consequences in wheat production (Michael et al. 1992). Mohammadi et al. (2015) evaluated the collection of 380 durum wheat landraces against WSS and found that 33 accessions showed resistance to the pest. Varella et al. (2017) screened 1409 accessions of wheat landraces collected from different regions to WSS. They found 204 accessions that have resistance to the disease. The resistant accessions were screened with KASP markers for QTL analysis. Varella et al. (2019) used four resistant wheat accessions and generated six recombinant inbred lines (RIL) with them and genotyped with 90K iSelect assay to find novel QTL related to WSS resistance.

11.4.2.4 Role of Wheat Landraces in Cereal Cyst Nematodes (CCN)

Cereal cyst nematodes (CCN) *(Heterodera* spp.*)* are a group of 12 known species with *H. avenae*, *H. filipjevi*, and *H. latipons* being the most important ones. The pest is observed in many regions of the world and causes major yield losses in cereals (Nicol et al. 2003). Yavuzaslanoglu et al. (2016) studied the response of 31 Iranian wheat landraces against *H. filipjevi* and found one resistant and five moderately resistant accessions.

11.4.2.5 Role of Wheat Landraces in Cereal Aphids

Cereal aphids cause important yield losses in wheat. There are 14 species of aphids that were observed causing damage to wheat. *Sitobion avenae*, *Rhopalosiphum maidis*, *R. padi*, and *Metopolophium dirhodum* are the most common of these (Popov et al. 1988). Amin et al. (2019) observed 114 wheat landraces for their resistance level against the disease and population dynamics of *R. padi*. They found promising accessions which can be used for breeding of resistant cultivars.

11.5 Landraces and the Future of Wheat Diversity

The world is confronting food scarcity problem due to rapid increase in population and climate change. Previous report showed 6–13% reduction in wheat yield for each °C rise in temperature. Continuously changing climate, extreme weather events, new pathogen strains, and pests further jeopardize linear productivity growth into the future (Mondal et al. 2016). It is believed that the world's population will cross the nine billion mark in 2050. By considering this factor, it is very important to increase wheat production by a rate of 1.6% (Lodhi et al. 2020). To feed the rapidly increasing world's population under changing climatic conditions, more pressure is put on agriculture to produce enough quantity of food. Therefore, it is very important to increase the wheat production to serve enough quantity of food. By considering these factors, it is very important to develop wheat cultivars having higher production and better adaptation to biotic and abiotic stresses (Khan et al. 2013). These targets can be achieved by harnessing wheat genetic diversity. Previous studies explored the existence of higher genetic diversity in wheat landraces compared to its commercial cultivars (Lodhi et al. 2020; Jaradat 2011; Jaradat 2013).

Genetic diversity present in wheat landraces has been successfully utilized for breeding perspectives. Wheat landraces possess a sufficient amount of diversity, including useful genes to adapt to stressful environments such as salinity, heat, and drought (Karagöz and Zencirci 2005; Özkan et al. 2011). The evaluation of genetic diversity in wheat landraces is important for the selection of the suitable landraces as donors of traits in breeding studies (Gurcan et al. 2017; Abbasov et al. 2018). Landraces represent significantly broader genetic diversity than modern varieties (Azeez et al. 2018). For this reason, they can help to increase the genetic source of modern cultivars. However, for their utilization in breeding programs, it is very important that breeders should make crosses among elite lines having the highest likelihood of developing new varieties (Baenziger and DePauw 2009). There is scarcity of information about the successful release of cultivars using wheat landraces. Gerek 79 which is a Turkish variety is developed through crosses with landraces (Smale and McBride 1996). One of the best examples of landraces serving as a source of novel genes is the identification of Rht dwarfing gene that was available through the Japanese variety "Norin 10" originating from a Japanese landrace Shiro Daruma (Reitz and Salmon 1968; Dreisigacker et al. 2005). Dr. Norman E. Borlaug utilized these genes to develop the high-yielding semidwarf wheat varieties that resulted in Green Revolution. Similarly, various wheat landraces served as a foundation in the wheat germplasm pool impotent like: "Cheyenne," a selection from landrace Crimea, founded the Nebraska wheat gene pool. Moreover, "Turkey Red" has been successfully used in winter wheat breeding in the US Great Plains (Lopes et al. 2015). Similarly, previous studies confirmed landrace diversity as a potential source for the breeding of grain yield and climate resilience, for example, the drought-tolerant variety "Aragon 03" was developed from a selection of a landrace population "Catalan de Monte" (Royo and Briceño-Félix 2011a; b). Vikram et al. (2016a; b) stated that a group of Creole wheat landraces (the landraces introduced to Mexico from Europe) has better adaptation to various abiotic stresses including drought because of the presence of rare but beneficial alleles. Further, wheat landraces reflected genetic diversity for various traits like 1000-kernel weight, biomass, and photosynthesis that can be used for cultivar development (Lopes et al. 2015). Various studies have been conducted using wheat landraces as germplasm through molecular markers and explored their potential as a source of novel variations (Sansaloni et al. 2020; Alipour et al. 2017; Lopes et al. 2015; Sofalian et al. 2008;

Alsaleh et al. 2015; Jorgensen et al. 2017; Arystanbekkyzy et al. 2019; Dababat et al. 2020; Ozer et al. 2020). As is obvious from the above-provided information, there is a need to utilize wheat landrace diversity to develop climate-resilient cultivars having high yield. Similarly, some nonbreeding efforts that should be used to promote on-farm dynamic conservation and sustainable utilization of wheat landraces include the following:

1. Awareness should be raised in the farming community about their potential in changing climate.
2. Availability of wheat landrace seeds to the farmers.
3. Development of niche market for landrace products.
4. Involvement of wheat breeders, seed producers, farmers, and end-users, as stakeholders in wheat breeding activities to develop new cultivars (Newton et al. 2011).

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