# Cereal Landraces

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Cereal landraces are still cultivated on marginal lands due to their adaptability to unfavourable conditions, constituting an important source of genetic diversity usable in modern plant breeding to improve the adaptation to abiotic or biotic stresses, yield performance and quality traits in limiting environments. Traditional agricultural production systems have played an important role in the evolution and conservation of wide variability in gene pools within species. Today, on-farm and ex situ conservation in gene bank collections, together with data sharing among researchers and breeders, will greatly benefit cereal improvement. Many efforts are usually made to collect, organize and phenotypically and genotypically analyse cereal landrace collections, which also utilize genomic approaches. Their use in breeding programs based on genomic selection, and the discovery of beneficial untapped QTL/genes/alleles which could be introgressed into modern varieties by MAS, pyramiding or biotechnological tools, increase the potential for their better deployment and exploitation in breeding for a more sustainable agricultural production, particularly enhancing adaptation and productivity in stress-prone environments to cope with current climate changes.

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## 1. Exploration of Genetic Diversity and Population Structure

Selection activities in the frame of the ongoing breeding programs led to a reduction of the diversity in genetic materials and are considered as a bottleneck in crop evolution after the domestication process. This assumption is accompanied by the idea that many alleles useful for breeding could have been lost in the selection process. Therefore, in the last few years a growing interest has focused on analysing genetic diversity in landrace collections in cereal crops.

In some cases, these studies were aimed at characterizing a limited number of important genotypes, such as those traditionally grown by farmers in particular areas. The genetic analyses, carried out on a proper number of individuals for each accession, often showed a certain degree of heterogeneity in each landrace. As an example, Mangini et al. [1] carried out a phenotypic and molecular analysis of three durum and one common wheat Italian landrace population, and the SNP characterization revealed different haplotypes within each landrace, indicating a genetic structure based on a mixture of genotypes. In other cases, landraces were maintained as inbred lines, and analysis on very large collections became possible. These analyses were often focused on panels of landraces with a specific geographical origin, as in the case of durum or common wheat landraces from Ethiopia [2][3], Sicily

[4], Morocco [5], Iran [6], Palestine and Israel [7], Pakistan [8], Turkey [9] and Mexico [10]; barley from Nepal [11], the Canary Islands [12], Tunisia [13][14] and Jordan [15]; oat from Poland [16] and Spain [17]; rice from Pakistan [18] and India [19] and millets from Senegal [20] and China [21][22]. If focusing on specific geographic areas has the advantage of exploring within a range of genotypes well adapted to that environment, examining wider collections opens the possibility of investigating the genetic relationship across landraces spread around the world, and having a more precise estimation of the genetic diversity within the group of landraces and with respect to advanced breeding lines or modern cultivars. To quote some examples, studies carried out on panels of hundreds of landraces have been considered in durum and common wheat [23][24][25], barley [26][27] and rye [28]. In general, a higher genetic diversity has been observed in the group of landraces compared to the groups of advanced breeding lines and modern cultivars, indicating landraces as a useful source of variation for breeding. Additionally, when clustering and population structure analyses have been considered, the total genetic variation was higher within than between groups, and the groups were in general consistent with the geographical origin of the lines, except in a few cases. Mzid et al. [29] assessed genetic diversity in a panel of 53 Lebanese barley landraces through the electrophoretic pattern of the seed storage proteins, hordeins. In this case, the absence of correlation between the genetic variability and the geographic origin of sample provenance was explained by the fact that Lebanon is a small country where seeds are easily exchanged between farmers' communities in the different regions. Similarly, Yadav et al. [11] phenotypically evaluated 25 naked barley landraces from different regions of Nepal. The UPGMA cluster analysis, carried out with qualitative phenotypic descriptors and quantitative traits, categorized the landraces in five clusters with no distinct regional grouping patterns. In this case, principal component analysis revealed the quantitative traits, such as grain yield, plant height and earliness, and qualitative traits, such as grain colour, lemma awn/hood and lemma awn barbs, to be the principal discriminatory characteristics of the Nepalese naked barley landrace collection.

Phenotypic evaluation of landraces is important to identify sources of useful loci for traits of interest in breeding and pre-breeding programs, in relation to traits with a simple genetic basis as the resistance to diseases, but also to complex traits such as grain yield (reviewed by Dwiwedi et al. [30]). Nevertheless, a clearer picture, in terms of genetic diversity, can be achieved using molecular markers. Markers based on polymorphisms at the level of seed storage proteins have been used in different cereal species such as Ethiopian emmer accessions [13], durum wheat and barley landraces [29][31]. Molecular markers based on DNA have been developed, both at the chromosome and the DNA sequence level. Polymorphisms were identified at the level of chromosome banding, through cytofluorometry [32][33]. The analysis of 58 varieties and landraces demonstrated a remarkable reproducibility and sensitivity of flow cytometry for the detection of numerical and structural chromosome changes [34]. In this regard, the dissection of complex genomes by flow cytometric sorting into the individual chromosomes reduces its complexity in a lossless manner, having a significant impact in many areas of research and giving a strong impulse to the sequencing of complex plant genomes [35][36][37]. At sequence level, DNA-based molecular markers have become the most suitable tool in this kind of study, thanks to their informativeness and to the great reduction in time processing and costs observed in the last few years. Random Amplified Polymorphic DNA (RAPD) markers were initially used for assessing genetic diversity in cereal landraces [13], but they were characterized by a low reproducibility, therefore Simple Sequence Repeat (SSR) markers became the method of choice thanks to their reproducibility and informativeness with a high number of alleles detected per locus. As an example, 8.1 alleles per locus were detected in a panel of 66 barley landraces from Tunisia [14], and 14.6 alleles per locus were identified in a collection including 36 oat commercial varieties and 141 landraces from Spain [17]. In more recent times, high-throughput methods have been developed, such as those based on fixed markers arrays, which include Diversity Array Technology (DArT) markers and SNP arrays. These methods have been shown to be suitable for genetic studies on cereal landraces and can assess a large number of entries, as in the case of panels with several hundreds of durum wheat landraces from Spain, assessed with DArT markers, or from Ethiopia and different countries worldwide, tested with SNP arrays [23][3]. An important aspect is that a certain ascertainment bias should be considered, as these platforms were mainly developed starting from cultivars [38]. For this reason, methods based on Genotyping by sequencing, including DArTseq, are also used in this kind of study [10][39]. The use of high-throughput markers allowed, in particular, the collection of more precise information on decay of linkage disequilibrium in landrace panels, which showed a higher resolution compared to commercial cultivars, for their use in association mapping analysis [15][40]. Moreover, the availability of a large number of markers with a good coverage of the genome is important to identify rare and private alleles, which are present only in a defined group of genotypes [23][41][1][2][3][4][5][6][7][8][9][10][11][12][13][14][15][16][17][18][19][20][21][22][24][25]. This kind of knowledge is very important for breeding, as landraces can be chosen not only based on their diversity per se, but also for specific alleles of interest in a particular breeding program.

# 2. Landraces as a Genetic Resource to Identify the Genetic Factors Responsible for Resistance to Biotic and Abiotic Stresses

The evolution of plant breeding with the consequent genetic erosion and the gradual shift towards a model of agriculture based on genetic uniformity results in the need to re-gain genetic variability to adapt crops to climate changes [42]. The importance of keeping diversity in breeding programmes has been well established. The possibility of accessing the information present in the gene banks offers a significant contribution to the identification of genes/alleles useful in the populations of landraces preserved in the various ex situ collections.

## 2.1. Abiotic Stresses and Traits of Agronomic Importance in Limiting Environments

The identification of abiotic stress tolerant alleles in landraces of cereal crops through mapping and GWAS approaches is of great importance to improve cereal crop adaptation to stress-prone environments. Two types of studies have been carried out in this regard: on one hand, traits directly associated to tolerance to abiotic stresses have been analysed by assuming their importance in improving the agronomic performance of crops in stress-prone environments. On the other hand, landraces have been evaluated for grain yield and quality, or related traits in limited environments. For the first kind of investigation, in rice, the discovery of submergence-tolerant landrace ‘FR13A’ led to the identification of the locus *SUBMERGENCE 1* (*SUB1*) located on chromosome 9, which codes for ethylene response factor [43]. The positional cloning of *SUB1* locus revealed three genes: *SUB1A*, found in tolerant lines, and *SUB1B* and *SUB1C*, found only in intolerant lines [44][45]. In turn, it was found that *SUB1A* has two allelic forms, *SUB1A-1*, associated with tolerant lines, and *SUB1A-2*, associated with intolerant line. Two QTLs for drought tolerance, based on leaf wilting, were recently identified on chromosomes 2H and 5H in the Chinese barley landrace ‘TX9425’ [46], which account for 42% and 14% of phenotypic variation, respectively. The QTL on 2H was closely linked with a gene controlling ear emergency, while the candidate gene underlying the QTL on 5H was suggested to be *9-cis-epoxycarotenoid dioxygenase 2* (*HvNCED2*), which is involved in the synthesis of abscisic acid. In another study of GWAS, two candidate genes, *HvCBF10B* and *HvCBF10A*, underlying this QTL were identified, which have regulatory function under drought condition [47]. Attempts to apply GWAS to drought resistance are limited due to the intrinsic complexities of investigating drought stress and its associated responses. Using 645 wheat landraces collected from 10 Chinese agroecological zones, Lin et al. [48] identified 26 QTLs associated with drought through the evaluation of 16 seedling traits related to root and shoot growth and water content under normal and drought (induced by polyethylene glycol) conditions. Extremely resistant and sensitive accessions were identified for future drought resistance breeding and further genetic analyses.

Rice productivity in both rain-fed and irrigated agro-ecosystems is also affected by salt stress. Rice landraces ‘Nona Bokra’ and ‘Pokkali’ are excellent sources of salt tolerance. Nona Bokra contributed a major QTL for shoot $K^+$ concentration on chromosome 1 (SKC-1) [49], and additive QTLs with small effects, mainly affecting $Na^+/K^+$ ratio [50][51]. The SKC-1 gene, isolated by map-based cloning, encodes a sodium transporter that control $K^+/Na^+$ homeostasis under salt stress [49]. Pokkali contributed a major QTL, *Saltol1*, associated with $Na^+/K^+$ ratio and salinity tolerance [52] and additive QTLs associated with $Na^+$ and $K^+$ concentration and with salt injury score [53]. Further researches revealed that Saltol1 is a complex locus, mapped on chromosome 1, with multiple Pokkali alleles regulating shoot $Na^+/K^+$ homeostasis [54][55]. Similarly, the barley landrace ‘TX9425’ contributed a major QTL for salinity tolerance on chromosome 7H, explaining 28% of phenotypic variation estimated by plant survival under salt stress [46], and a significant QTL on chromosome 2H that explains 45% of phenotypic variation in the potting mixture trials, using plant survival and leaf chlorosis as evaluation criteria [56]. Finally, another salt tolerant locus, *HvNax4*, was identified on chromosome 1HL in the Algerian landrace ‘Sahara 3771’ [57].

Another trait, potentially limiting crop production, is boron toxicity. Tolerance to toxicity is associated with the ability to maintain low boron concentrations in the shoot [58]. The *Bot1* gene, responsible for the high boron-toxicity tolerance of the Algerian barley landrace ‘Sahara 3771’, was identified [59]. In bread wheat, the boron tolerant landrace ‘G61450’ contributed the boron toxicity gene, *Bo4*, which was mapped on chromosome 4AL [60].

Cereal landraces are also important sources of beneficial alleles for grain yield and quality in low-producing environments. For this reason, collections of landraces have been assessed in mapping studies to identify genetic determinants for these traits. As grain yield is a trait with a very complex genetic basis and a strong genotype x environment interaction, in some cases traits which are strongly correlated with yield have been considered. As an example, different leaf traits were assessed in a panel of 180 Vietnamese rice landraces in controlled conditions, such as leaf dry matter percentage, which can be considered a proxy for the photosynthetic efficiency per unit leaf area, contributing to yield [61]. Genetic analysis with more than 21,000 SNP markers led to identified QTLs, some of which were in a position where genes with a known function in leaf development or physiology were located. Similarly, Ta et al. [62] analysed several traits related to panicle architecture, one of the key components of rice yield, in a panel of Vietnamese landraces.

Numerous studies have focused on the evaluation of grain yield and yield components directly. Huang et al. [63] identified ~3.6 million SNPs by sequencing 517 rice landraces and performed GWAS for 14 agronomic traits based on a high-density haplotype map of the rice genome. Many chromosomal regions were mapped in this study, as the overall genetic variation observed in this panel represented at least 80% of the world's rice cultivars. In this case, characterizing a large panel of cereal landraces with a high-density marker system, based on genome re-sequencing, provided useful information not only on genetic determinants of traits of agronomic importance, but also on genetic relationships across groups of genotypes adapted to various agro-climatic conditions. A panel of 150 Jordanian landraces was evaluated for yield and yield components in Jordan under rain-fed conditions [15]. The GWAS analysis allowed the identification of three significant QTLs located at 1H, 2H and 7H, important for grain yield in dry environments. Moreover, three accessions with high yield and stability across environments were identified [15]. Studies in which favourable and limiting environments were compared allowed the identification of genomic regions specifically involved in sustaining grain yield and quality in difficult conditions. Alleles that were adaptive under drought stress conditions for a number of agronomic traits, including yield, were identified in a collection of 298 Iranian bread wheat varieties and landraces [64] (Rahimi et al. 2019). Fourteen large-effect QTLs for grain yield associated with drought adaptation were identified in rice landraces, six of which were effective in multiple genetic backgrounds and environments [65]. A set of 472 rice genotypes comprising landraces and breeding lines was evaluated under field conditions with low and recommended nitrogen to identify genotypes with relative higher yield under low nitrogen, together with 12 genomic regions for yield and yield associated traits and three candidate genes from QTL regions showing enhanced expression in the genotypes with promising yield under low N [66]. As regards phosphorus deficiency, widespread in tropical soils, the well-known gene *Phosphate uptake 1* (*Pup1*), identified in the rice landrace 'Kasalath' and located on chromosome 12, increases phosphorus uptake and confers significant grain yield advantage in phosphorus deficient soils [67][68]. *Pup1* is found in landraces or cultivars adapted to drought-prone environments [69] and it is effective in different genetic backgrounds and environments [70]. A study on the functional mechanism of *Pup1* revealed the presence of a Pup1-specific protein kinase gene, named *Phosphorus starvation tolerance 1* (*PSTOL1*), which is absent in intolerant cultivars. The overexpression of *POSTL1* significantly enhances grain yield in phosphorus deficient soils, promoting early root growth, thereby enabling plants to acquire more phosphorus and other nutrients [71].

For a good agronomic performance in stress-prone environments, it is important to sustain not only grain yield but also quality. A good variation has been found in landraces as an example for storage proteins in wheat grain [72]. In the last few years in particular, a great interest has arisen for traits related to the nutritional quality of cereal grain for human nutrition. A core set of 190 rice landraces was used to decipher the genetic structure and to discover the chromosomal regions containing QTLs affecting the grain micro-nutrients and fatty acids, as well as yield-related traits [73]. A total of 22 significant QTLs were identified, comprising those involved in the control of content of Zn, oleic acid and Fe. Landraces with a strong expression of the traits analysed in this study and the closely linked molecular markers represent a valid tool for the use of these QTLs in rice breeding for developing new varieties with high yield and nutritional value.

These results confirm that landraces, thanks to their long evolutionary history and adaptation to stressful environments, are ideal genetic resources to explore novel genetic variation for responses to environmental constraints. In particular, landraces are an effective source of useful alleles to sustain grain yield and quality in both favourable and limiting environments. In some cases, the loci involved in the control of yield in good conditions can still maintain a good level of production when stresses are mild [74]. In other cases, alleles which specifically express in environments with more pronounced stress conditions have been identified in landraces, which can help in breeding for improved lines well adapted to specific areas.

## 2.2. Biotic Stresses

Plant diseases are serious constraints to the production of cereal crops. During the vegetation period, the largest infections are caused by pathogenic fungi. Powdery mildew and rusts of cereals and grasses are the most dangerous diseases of wheat and barley. Head blight caused by different fungi of the genus Fusarium also affect wheat, rye, triticale, barley and oat crops, but also maize. Genetic improvement of resistance to pathogens through breeding represents the best economical and eco-friendly alternative to minimize yield losses. Many studies aimed at identifying resistance genes/loci against various diseases are available for cereals. Most of these studies were based on the analysis of biparental populations and, more recently, GWAS has been employed. Landraces may carry new sources of resistance that can be exploited to enrich the narrow resistance spectrum currently found in adapted cultivars. Studies that have reported screening with molecular markers linked to specific resistance genes of panels including landraces grown in a particular geographic area are available, such as the collection of rice landraces and breeding lines from India evaluated for 22 genes against the fungus *Magnaporthe oryzae*, from which two landraces emerged for high resistance to blast, and were therefore useful in breeding programs [75]. In particular, the landrace Tetep was the donor of the *Pi54* gene for broad-spectrum blast resistance, which has been cloned, and transgenic lines harboring *Pi54* showed a high degree of resistance to diverse strains of blast pathogen [76].

Many studies that have focused on landraces as a good reservoir of resistance genes against rusts are available for wheat [77][78][79][80][81][82][83][84][85][86][87][88][89]. The Portuguese durum wheat landrace PI 192051 has been used to map leaf and stem rust resistance QTLs on chromosomes 4A and 7A, respectively, and to develop SNP markers tightly linked to the identified loci [90]. A GWAS was performed using 152 wheat landraces from China to identify effective stripe rust resistance loci, which resulted in 19 accessions displaying stable and high degrees of resistance to stripe rust development when exposed to mixed races of Pst at the adult-plant stage in multi-environment field assessments, and 40 QTL regions for adult-plant resistance [91]. A multi-pathogen resistance gene, *Lr67*, which confers partial resistance to all three wheat rust pathogen species (*Pt*, *Pst*, *Pgt*) and powdery mildew (*Bgt*), as demonstrated by using a combination of comparative genomics, mutagenesis and transformation studies, was isolated from a bread wheat landrace (PI250413) [92]. Wheat landraces have also been studied for other diseases, including Fusarium Head Blight [93], barley yellow dwarf (BYD) [94], powdery mildew [95][96][97] and stem sawfly [98]. A recombinant inbred line (RIL) population derived from Haiyanzhong, a Chinese wheat landrace showing a high level of resistance to FHB spread within a spike (type II resistance), has been used to map six QTLs (one major and five minor) and obtain KASP markers useful for MAS [93]. In particular, it is known that Germplasm from East Asia harbours highly resistant genotypes, including landraces (e.g., Wangshuibai, Nobeokabozukomugi) [99]. Indeed, Wangshuibai is an FHB-resistant Chinese landrace unrelated to cv. Sumai 3, the most commonly used FHB-resistant source, and it was the source of two major type I resistance FHB resistance QTLs, named *Fhb4* and *Fhb5*, that were fine mapped by using NIL populations [100][101].

Landraces from China were also considered very good sources of powdery mildew resistance. For example, the Chinese wheat landrace Xuxusanyuehuang has been found by comparative genomics analysis to possess a single recessive powdery mildew resistance gene, *Pm61*, on chromosome 4A [96], whereas the landrace Duanganmang has been used to map a new gene, *PmDGM*, conferring powdery mildew resistance [102]. Resistance genes *Pm24*, *Pm24b* and *MlHLT* were identified in wheat landraces Chiyacao, Baihulu and Hulutou, respectively [103]. In particular *Pm24* was map-based cloned, and it was found to be a rare natural allele of tandem kinase protein (TKP) with putative kinase pseudokinase domains. A 6-bp deletion at the kinase domain was considered critical for the gain of powdery mildew disease resistance [103]. Finally, the gene *Pm3b*, originating from the hexaploid wheat landrace Chul, was found by positional cloning to be a member of the coiled-coil nucleotide binding site leucine-rich repeat (NBS-LRR) type of disease resistance genes [104]. Regarding barley landraces, most studies are focused on resistance against fungus *Blumeria graminis* f. sp. *Hordei* [105][106][107]. The *mlo* (Mildew resistance locus o)-based resistance is considered the most reliable weapon to protect plants from infection by this fungus [108]. Loss of function of one or more of such genes is associated with plant immunity. Ethiopian landraces of barley were the first known examples of natural *mlo* mutants [108]. Moreover, three QTLs conferring broad spectrum resistance to powdery mildew were identified on chromosomes 7HS, 7HL and 6HL in the Spanish barley landrace-derived lines SBCC097 and SBCC145 [105], whereas the barley line 2553-3, selected from a Moroccan landrace, has been reported to possess a new resistance gene, named *MlMor* [107]. QTL/genes for net blotch disease [109][110], stem rust [111], barley yellow mosaic virus (BaYMV), barley mild mosaic virus (BaMMV) [112] and barley scald [109] have also been documented.

Very recently, a genetic analysis of a worldwide barley collection, including 277 landraces, for resistance to net blotch disease (*Pyrenophora teres* f. *teres*) has been carried out, resulting in 15 QTL regions, four of which had never been described in previous studies [110]. Finally, stem rust resistance has been characterized in barley landraces, in particular against the African TTKSK race, and the *rpg4/Rpg5* locus has been indicated to be involved in conferring resistance [111].

Few genetic studies for disease resistance in maize and oat landraces are available. The well-known gene *Htn1*, reported to code a wall-associated receptor-like kinase by high-resolution map-based cloning, represents an important source of genetic resistance against northern corn leaf blight that was originally introduced from a Mexican landrace into modern maize breeding lines in the 1970s [113]. Very recently, two European maize landraces were analysed individually for *Gibberella* ear rot (GER) resistance using genome-wide association studies and genomic selection (GS) [40]. Loci with small effects were found, and for two SNPs candidate genes were proposed belonging to functional groups, including binding activity, kinase activity, response to stress/stimulation, signal transduction, catalytic activity and metabolic and biosynthetic processes. Moreover, two RIL populations were constructed to elucidate the genetic basis of resistance to Maize rough dwarf disease (MRDD), a significant viral disease caused by rice black streaked dwarf virus (RBSDV), resulting in the resistance QTL (qZD-MRDD8-1) with the largest effect (more than 23% of the phenotypic variability observed) [114]. Finally, Montilla-Bascòn et al. [115] analysed, by GWAS, a panel of 177 oat accessions, including cultivars and landraces, for crown rust and powdery mildew, providing markers as good candidates for MAS.

In conclusion, cereal landraces have a great potential as sources of novel disease resistance genes, and a good combination of these genes could help to alleviate diseases. Therefore, more efforts are needed to utilize genomic approaches in order to exploit genetic variability across landrace collections worldwide.

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