Review

Landrace Germplasm for Improving Yield and Abiotic Stress Adaptation

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Plant landraces represent heterogeneous, local adaptations of domesticated species, and thereby provide genetic resources that meet current and new challenges for farming in stressful environments. These local ecotypes can show variable phenology and low-to-moderate edible yield, but are often highly nutritious. The main contributions of landraces to plant breeding have been traits for more efficient nutrient uptake and utilization, as well as useful genes for adaptation to stressful environments such as water stress, salinity, and high temperatures. We propose that a systematic landrace evaluation may define patterns of diversity, which will facilitate identifying alleles for enhancing yield and abiotic stress adaptation, thus raising the productivity and stability of staple crops in vulnerable environments.

Modern Agriculture: A Threat to Landrace Diversity

The current industrial agriculture system may be the single most important threat to **biodiversity** (see Glossary) [1,2]. A serious consequence of biodiversity loss is the displacement of locally adapted **landraces** with adaptation traits to future climates [3–6] by mono-cropping with genetically uniform hybrids and improved cultivars [7]. Modern agriculture has contributed to decreasing agricultural biodiversity; most of humankind lives now on only 12 crops, with wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), and potato (*Solanum tuberosum* L.) accounting for 60% of diets [8]. For example, 74% of rice cultivars in Indonesia are derived from the same stock, while 50% of wheat, 75% of potato, and 50% of soybeans in USA trace back to 9, 4, and 6 cultivars, respectively [9]. Likewise, there was a significant loss of genetic variability when analyzing data of collecting missions in Albania in 1941 and 1993, and in southern Italy in 1950 and the late 1980s. The **genetic erosion** was estimated at 72.4% and 72.8%, respectively [10]. Furthermore, the number of rice cultivars declined in Indian farms from about 400 000 before colonialism to 30 000 in the mid-19th century, with unknown thousands more being lost after the **Green Revolution**. Greece also lost 95% of its wheat landraces after being encouraged to replace them with modern cultivars [11].

The evolution of plant breeding may explain genetic erosion and the gradual shift towards a model of agriculture based on uniformity. For millennia, plant breeding was carried out by farmers who selected for specific adaptations leading to the formation of landraces. By contrast, modern plant breeding has emphasized wide adaptation, which has resulted in modern agriculture depending on a small number of cultivars for major crops. Hence, the main sources of food are more genetically vulnerable than ever before. The importance of diversity loss is becoming more important today as we face the need to adapt crops to climate change [12,13]. However, there are no unanimous views on whether and where diversity has been lost [14].

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Landraces have long been recognized as source of traits for local adaptation, stress tolerance, yield stability, and seed nutrition. This review is focused on identifying and deploying gene(s) for yield and **abiotic stress** adaptation from landraces to modern cultivars in cereal and legume grain crops. The use of **haplotype** diversity for identifying superior alleles and **genomic signatures** of environmental adaptation is also discussed, in addition to stressing the greater use of landrace diversity (Figure 1) in developing climate-smart crops.

Underuse of Exotic Germplasm Including Landraces in Plant Breeding Programs

Improvement in crop plants is occurring in breeding cycle after breeding cycle, and plant breeders are optimistic about future improvements. While optimism appears justified, there is an important consequence associated with this genetic gain that has significant implications for the future. As favorable alleles are selected and fixed, genetic variability is reduced, thus presumably reducing the potential for future progress. The obvious remedy is to augment improved plant populations with a continuing infusion of genetic diversity. It appears, however, that programs for adding genetic diversity have had relatively low priority, or have had only limited success, compared to programs that develop cultivars using already improved elite germplasm [15].

Plant breeders are always under pressure to fulfill short-term breeding goals, and to achieve this they use elite germplasm with which they are familiar and that is reasonably adapted to the target population of environments, versus exotic germplasm which may require lengthy pre-adaptation or pre-breeding [16]. The reluctance of plant breeders to use exotic germplasm is largely due to fear of loss of co-adapted gene complexes, linkage drag, and the protracted time needed to develop cultivars. In addition, the potential value of such germplasm for the stress environments was neither fully appreciated nor appropriately documented until recently, when advances in plant phenotyping and genomics facilitated access to the discovery and deployment of allelic diversity into improved genetic backgrounds, which resulted in large-scale adoption of abiotic stress-tolerant cultivars, and phosphorous deficiency- and submergence-tolerant rice [17], in some parts of the world. Today, agricultural production worldwide is affected by climate change. Landraces, given their past evolutionary history and adaptation to stress environments, often out-yield modern cultivars under low-input production systems. A paradigm shift in breeding program is needed to ensure greater use of landraces as a resource for improving edible yield, nutrition content, and abiotic stress adaptation of locally adapted cultivars for sustaining global food and nutritional security. A pre-breeding program should be carried out by public-sector breeders and, to achieve this, the private sector should support pre-breeding programs, and the product with required characteristics should be shared globally. This two-way interaction is expected to facilitate greater use of unadapted germplasm, including landraces, in the development of climate-smart crops.

Value and Impact of Landraces in Crop Improvement
Landraces Enhance Adaptation and Trait Variability

Cultivars with increased tolerance to abiotic stress are necessary to enhance food and nutritional security. Landraces provide a source for discovering novel alleles for enhancing crop adaptation to abiotic stress. Maize landraces from Mexico show immense diversity, growing from arid to humid environments and from temperate to tropical environments, while observed climatic adaptability ranged from 0 to 2900 m altitude, 12 to 29.1 °C growing season mean temperature, 426 to 4245 mm annual rainfall, and 12.46 to 12.98 h growing season day-length [18]. Mexican maize landraces are known for high-altitude adaptation and tolerance to abiotic stresses [19], while the naturally occurring mutant *Opaque-2* – which gives a chalky appearance to the kernel and improves protein quality – was found in a Peruvian maize landrace. This trait was thereafter used to breed quality-protein maize lines and cultivars, which today grow in Africa, Asia, and Latin America, because it improves the diets of those depending on maize as a staple. Recent

Glossary

Abiotic stress: climatic or edaphic conditions that affect cellular homeostasis adversely impacting on growth and fitness. The major abiotic stresses include water surplus (leading to flood) or deficit (resulting in drought), extreme variation in temperature (cold and heat), salinity, nutrient deficiency, ion deficiency, and ion toxicity.

Biodiversity: entire diversity of genes, species, cultivars, and ecosystems in agriculture, including taxonomic, ecological, morphological, and molecular diversity.

Fertile Crescent: region of the Middle East extending from the Persian Gulf, through modern-day southern Iraq, Syria, Lebanon, Jordan, Israel, and northern Egypt. Considered to be the birthplace of agriculture, urbanization, writing, trade, science, history, and organized religion, the area was first populated 13 000–11 000 BCE when animal and plant domestication began in this region, signing the start of agriculture.

Genetic erosion: loss of variation which may occur at the level of crop, cultivar, and allele. Reduction in allelic evenness and richness is the greatest concern in the agriculture of today.

Genome-wide association: assessing marker–trait association (MTA) by studying a large number of germplasms. This approach takes advantage of historic linkage disequilibrium to link phenotypes with genotypes to find MTAs underlying complex traits.

Genomic signature: a characteristic frequency of oligonucleotide sequences in a genome or sequence.

Green Revolution: a suite of agricultural technologies including irrigation, synthetic nitrogen fertilizer, pesticides, and improved cultivars that revolutionized maize, rice, and wheat production in many parts of the world.

Haplotype and haplotype map: a set of alleles in cluster of tightly linked genes on a chromosome that are inherited together. The haplotype map is a catalogue of common genetic variants describing what these variants are, where they occur in the DNA, and how they are distributed among individuals within a population or between populations.

Landrace: a dynamic population(s) of a cultivated species that has a historic origin and distinct identity that

Key Figure

Cereal and Legume Landraces: Showing Various Plant and Grain Types, where They Are Still Grown

Trends in Plant Science

Figure 1. (A) Diversity in cob and seeds among maize landraces. (B) Variation for seed characteristics in barley landraces. (C) Maldandi 35-1, a popular landrace of sorghum from India. (D) ICTP 8203, an open pollen pearl millet cultivar derived from the '*Iniadi*' landrace. (E) Mixture of bush-type or climbing-type red mottled common bean landraces grown between or on dry corn stalks in Colombia. (F) Tepary bean landraces from Mexico differ in leaf size and shape, or seed color ranging from black to yellow and white.

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was locally adapted in association with traditional farming systems.

Linkage disequilibrium: nonrandom association of alleles at different loci.

Near-isogenic lines (NILs): introgression lines containing a single fragment or a small number of genomic introgression fragments from a donor parent into an otherwise homogeneous genetic background.

Pleiotropic effect: genes that control more than one trait.

Quantitative trait loci (QTLs): DNA segments carrying genes controlling quantitative traits.

Recombination: the production of offspring with a combination of traits that differ from either parent.

Seed dormancy: seeds unable to germinate in a specific period of time under optimal environmental conditions that are suitable for the germination of the non-dormant seed.

Vernalization: a process of prolonged exposure of plants to low temperatures that is a prerequisite for the plants to flower.

work on introgression of alleles from diverse landraces into adapted maize cultivars led to populations producing more grains than recurrent parents, thereby demonstrating that improved populations are valuable sources for developing cultivars and parental lines of hybrids combining drought adaptation and high grain yield [19–21].

Post-rainy sorghum [*Sorghum bicolor* (L.) Moench] in India is a predominant crop grown on 5.7 million ha in the Deccan Plateau of India under receding soil moisture, with highly variable production environments and low productivity [22]. 'M35-1' (Figure 1C) – a selection from a local landrace 'Maldandi' nearly 75 years ago – is the most popular cultivar largely because of its earliness, high grain and stover yields, bold and lustrous grains, and drought adaptation. Several Maldandi variants collected from farmers' fields showed immense phenotypic variation and molecular diversity, and such phenotypically diverse and molecularly distinct variants may be used to enrich the Maldandi race genepool [23]. Improving grain yield but retaining grain quality and adaptive capacity of M35-1 was the major challenge. The use of Maldandi variants in crosses led to the development of several restorer lines (ICSR#) and cultivars (ICSV#) which, when tested separately across six locations during the 2014 postrainy season in India, six restorer lines and two cultivars, respectively, outyielded M35-1 (grain yield: restorer trial, 1.54 t ha^{-1}; variety trial, 2.25 t ha^{-1}) by 83–128% and 33–37%, with some having the same grain quality as M35-1.

'*Iniadi*' pearl millets [*Pennisetum glaucum* (L.) R.Br] from West Africa are widely adapted, drought-tolerant, relatively photoperiod-insensitive, and are known for early maturity, and have a conical head shape with large globular bluish-grey colored grains [24]. Some of the open pollinated cultivars (OPV) bred in the 1980s are still grown on large acreages in India, for example, 'ICTP 8203' [25] (Figure 1D) grown on about 0.65 million ha despite stiff competition from hybrid cultivars [26]. The composite cultivar 'CZP 9802' – bred from the landrace-based early Rajasthan population – recorded 24% and 56% higher grain and stover yields than ICTP 8203 (675 kg ha^{-1} and 1903 kg ha^{-1}, respectively) in drought-prone environments [27].

Mediterranean Landraces Are the Source of Variability for Abiotic Stress Tolerance in Barley and Wheat

The domestication of wheat and barley took place before 7000 BC in the **Fertile Crescent**, which includes parts of Jordan, Lebanon, Palestine, Syria, southeastern Turkey, Iraq, and western Iran. Evidence suggests that the most important of the early cereals was barley, and that the first barleys were two-rowed [28]. The wild progenitor of cultivated barley, *Hordeum vulgare* ssp. *spontaneum*, is still widely distributed along the Fertile Crescent where, particularly in the driest areas, it can be identified within fields of cultivated barley from a distance because of its height. It is likely that *H. spontaneum* contributes to the evolutionary processes of barley landraces through continuous gene introgression [29].

The main contributions of landraces to plant breeding are useful traits for more-efficient nutrient uptake and utilization, and genes associated with adaptation to water stress, salinity, and high temperatures [30]. Several comparisons between barley landraces and modern cultivars have shown that landraces consistently outyield modern cultivars under stress by as much as 20% maximum grain yield. Furthermore, in contrast to modern cultivars, landraces rarely fail in the most extremely stressed environments [31]. The yield advantages of landraces over modern cultivars that were observed under stress conditions in barley cannot be necessarily extrapolated to other crops with a different range of adaptation: for example, an environment defined as stressful for wheat or maize may be moderately favorable for barley or sorghum. Hence, comparisons between crops must consider carefully what is defined as a stress environment in each case.

Traits associated with grain yield under stress of landraces were early growth vigor, earliness, growth habit, plant height under drought, long peduncle, and a short grain-filling duration [32].

Landrace analysis has identified and mapped **quantitative trait loci** (QTLs) that control these traits [33]. The strength of the correlation between each of these traits and grain yield under stress varied from year to year, suggesting that all these traits are important, but their relative importance depends on the timing, duration, and intensity of drought [34]. Hence, at least for the abiotic stresses predominant in the Fertile Crescent, what seems to be important is not the individual trait but the trait complex.

When barley landraces were used in a breeding program based on direct selection in the target environment, an interesting pattern emerged: lines derived from crosses with landraces not only outyielded lines derived from crosses without landraces under drought conditions, but the grain yield of lines derived from crosses with specific landrace lines, such as 'Tadmor', a pure line cultivar selected from a Syrian landrace [35], was twice (1237 kg ha^{-1}) that of lines lacking Tadmor in their pedigree (604 kg ha^{-1}). This result could suggest that there are blocks of genes in chromosomal regions with a low frequency of **recombination** that can confer specific adaptation to stress environments [2].

It is very likely that landraces possess useful genes for adaptation to future climates. Farmer-based programs exploiting landrace gene pools may reconcile an increase in available and accessible food production with an increase in agro-biodiversity [12]. The evidence in wheat also supports the view that landraces can provide sources for increased biomass and thousand-kernel weight, both important traits for adaptation to tolerate drought and heat stress [36]. More recently landraces have also been acknowledged as potential sources of nutritious and healthy food [37–40].

Common Bean Landraces and Relatives Enhance Abiotic Stress Tolerance

Common bean (*Phaseolus vulgaris* L.) is a New World domesticate that is arguably the most diverse of the pulses based on its multiple domestications in the Andes and Mesoamerica [41]. In conjunction, Andean, Mesoamerican, and inter-genepool landraces have been selected for growth in disparate environments ranging from lowlands to high altitude mountains, and ranging from equatorial regions to temperate climates up to 50°N [42–46]. As a result, landraces of common bean are extremely diverse in their adaptation to different soils and weather regimes both as dry grain and vegetable types. Because many common bean landraces were selected on marginal lands, they contain traits of importance for adaptation to soil problems such as nutrient deficiencies and ion toxicities. This is true of the 'Chaucha Chuga' landrace G 19833 from Perú that was the subject of QTL analysis for its aluminum (Al) toxicity tolerance as well as its tolerance of phosphorus (P) deficiency [47–49]. These traits seem to be correlated given the **pleiotropic effects** of organic acid exudation, a trait that is widespread and inducible in many landraces of common beans grown in acid soils that are high in Al or poor in P. G 19833 was selected as the reference genome for a whole-genome sequencing effort in common bean [50] because of its status as a multiple abiotic stress resistant landrace.

Particular common bean genotypes share the ability to tolerate the acid soil complex while others adapt to high temperatures or drought. Al tolerance is found among Andean genotypes and some lowland landraces from Brazil and Mexico [51]. Al tolerance ranges from high to extremely low and is often worst in recently bred advanced lines selected on neutral pH soils at centralized breeding stations. Populations generated from crosses of abiotic stress tolerant landraces × improved but abiotic stress susceptible cultivars have even been the subject of various QTL analyses, for example, offspring with G 122 and Indeterminate Jamaica Red that are landraces with reproductive heat-tolerance [52]. Drought adaptation, based on deep-rooted-ness or other traits, has been found in specific Mexican landraces of the Durango–Jalisco germplasm group, but generally breeder-selected advanced lines are used for breeding and QTL analysis [53–56].

In addition to common bean, two of its relatives have been sources of abiotic stress adaptation for the major cultigen. In this case, these secondary and tertiary genepool relatives are also cultivated, but have not been subject to breeding programs and are therefore represented entirely by landraces or wild accessions. These relatives include scarlet runner beans (*P. coccineus* L.) from Central and northern South America, that have tolerance to high Al soils and P acquisition efficiency, and cultivated tepary beans (*P. acutifolius* Gray) (Figure 1F) from Mexico and the southwestern USA that show heat- and drought-tolerance. While scarlet runner bean are easily crossed with common bean, their progeny are rarely useful in breeding programs because of dominance of the aggressive climbing growth habit. Tepary beans have been, however, successfully used for breeding advanced lines of common bean with some level of drought adaptation in congruity backcross lines, although genomic introgression levels are low [57]. Empirical results indicate that tepary bean landraces may contribute to heat tolerance, and their characteristic water use efficiency under high temperatures may give them a clear advantage. Salt tolerance was noticed in tepary bean landraces but not in common bean.

Identifying Genomic Signatures of Environmental Adaptation

Improving environmental adaptation in crops is essential for food and nutrition security under global climate change. Single nucleotide polymorphism (SNP) variants associated with environment origin in crop landraces are likely to reflect adaptations that could then be used to predict phenotypic variation for adaptive traits. A study using 404 627 SNPs on 1943 georeferenced sorghum landraces found that environment explained a substantial portion of SNP variation, independently of geographical distance, and genic SNPs were enriched for environmental (drought and Al toxicity) associations [58]. Thus, genomic signatures of environmental adaptation may be useful for crop improvement, enhancing germplasm identification and marker-assisted selection.

Haplotype Diversity and Identifying Superior Alleles in Landraces

Maize was domesticated in southern Mexico between 6000 and 9000 years ago, but its landraces are found where farmers have grown this crop for many centuries [59], thus selecting germplasm with better adaptability; for example, Al tolerance in 'Cateto' landraces from South America and their use in local maize hybrid breeding [60]. Maize inbred lines capture less than 80% of landrace alleles, suggesting that landraces have significant value as sources of genetic diversity for further maize breeding [61]. **Linkage disequilibrium**, which has increased as a result of domestication, declines to below 1 kb in maize landraces [62], which provides more opportunity for selection. A DNA survey of maize landraces may reveal functional alleles existing before modern industrial agriculture, thereby facilitating the understanding of the frequency distributions of haplotypes among MesoAmerican landraces [19]. Such an undertaking will also determine the extent of allelic variation in available maize genetic resources. The genome sequence of the highland popcorn 'Palomero Toluqueño' landrace provided a means to identify genes related to abiotic stress response or heavy-metal detoxification [63]. The re-sequencing of maize landrace core subsets [64] will give further insights about the distribution of SNP allelic variants in the genome, thus facilitating both gene discovery and establishing their distinct haplotypes. For example, the resequencing of 517 rice landraces led to the identification of about 3.6 million SNPs that were further used in developing a high-density **haplotype map** and for **genome-wide association** research to unravel the genetic basis of 14 agronomic traits [65].

Landraces Contribute Yield and Abiotic Stress Adaptation Alleles to Modern Cultivars

Abiotic Stress Adaptation Alleles

About 29% of the 135 million ha of rainfed lowland rice area in Asia experiences one or two weeks of prolonged flood, leading to substantial production loss. The discovery of submergence-tolerant landrace 'FR13A' led to the identification of *SUBMERGENCE 1* (*SUB1*) located

on chromosome 9, which is associated with submergence tolerance [66]. *SUB1* was further mapped to a 0.16 cM region [67] and fine-mapped to 0.075 cM on chromosome 9 [68]. The positional cloning of *SUB1* locus reveals three genes, *SUB1A*, *SUB1B*, and *SUB1C*, the former being found in tolerant lines and the latter two only in intolerant lines. *SUB1A* has two allelic forms, *SUB1A-1* being associated with tolerant lines and *SUB1A-2* with intolerant lines [68]. *SUB1A-1* allele has been introgressed using marker-aided backcrossing into locally adapted and widely grown rice cultivars in Asia, which were released as 'Swarna-Sub1' in India, Indonesia, and Bangladesh; 'BR11-Sub1' in Bangladesh; and 'IR64-Sub1' in the Philippines and Indonesia [69]. These cultivars had significant impact on rice growing in Asia; for example, Swarna-Sub1 submerged for 7 to 14 days across 128 villages of Odisha offers a 45% increase in yields over the popular cultivar 'Swarna', with no yield penalty under non-flooding [70].

Upland rice is one of the major rice production systems worldwide, and drought stress during the crop season often adversely impact on rice production. The landraces 'Aus 257', 'Aus Bak Tulsi', 'Azucena', 'Basmati 370', 'Dular', 'Kalia', 'Kali Aus', 'Lal Aus', and 'N22' were the source for grain yield under drought stress, which led to the development and release of 17 high-yielding drought-tolerant rice cultivars in Asia and Africa. Moreover, landraces contributed 14 large-effect QTLs associated with drought adaptation, of which six QTLs were effective in multiple genetic backgrounds and production environments. Pyramiding of large-effect QTLs improved drought adaptation of widely grown rice cultivars such as Swarna (India, Nepal and Bangladesh), 'IR64' (many countries in South and Southeast Asia), 'Sabitri' (Nepal), 'TDK1' (Laos), and 'BR11' (Bangladesh). Furthermore, introgressed offspring bearing *SUB1* and drought-tolerant QTL alleles on Swarna, TDK1, and IR64 backgrounds are being agronomically evaluated in some countries in Asia [71].

Phosphorus (P) deficiency is widespread in tropical soils [72]. The rice landrace 'Kasalath' is highly tolerant to P deficiency [73]. *Phosphate uptake 1* (*Pup1*) on chromosome 12 increases P uptake [74], which confers significant grain yield advantage in P-deficient soils. It is found in landraces or cultivars adapted to drought-prone environments [75]. *Pup1* is effective in different genetic backgrounds and environments, and introgressed lines containing *Pup1* allele significantly increased grain yield on P-deficient soils [76]. A study on the functional mechanism revealed the presence of a Pup1-specific protein kinase gene, named *phosphorus starvation tolerance 1* (*PSTOL1*), which is absent from the rice reference genome and P-starvation-intolerant cultivars. The overexpression of *POSTL1* in such cultivars significantly enhances grain yield in P-deficient soils. *POSTL1* promotes early root growth, thereby enabling plants to acquire more P and other nutrients [77].

Salt stress adversely impact on rice productivity in rainfed and irrigated agro-ecosystems. Rice landraces 'Nona Bokra' and 'Pokkali' are excellent source of salt tolerance. Nona Bokra contributed major QTLs for shoot K^+ concentration on chromosome 1 (*qSKC-1*) and for shoot Na^+ concentration on chromosome 7 (*qSNC-7*); *qSKC-1* encodes a sodium transporter that control K^+ homeostasis under salt stress [78]. Pokali contributed another major QTL, *Saltol1*, associated with Na/K ratio and salinity tolerance [79]. Further research revealed that *Saltol1* is a complex locus, with multiple Pokkali alleles regulating shoot Na^+/K^+ homeostasis [80]. The *Saltol1* region was recently mapped with a SNP set on chromosome 1. The SNPs associated with Na^+/K^+ ratio were in complete linkage disequilibrium [81]. Another rice landrace 'Hasawi' contributed many QTL alleles, some with major effects associated with increased grain yield and salinity tolerance (at reproductive stage) across different genetic backgrounds [82]. Pyramiding of *Sub1* and *Saltol1* is in progress to develop flood- and salinity-tolerant rice cultivars [17]. Similarly, the barley landrace 'TX9425' contributed two QTLs for drought tolerance (accounting for 42% and 14% of variation) and one QTL for salinity tolerance (explaining 29% of variation) [83].

Boron (B) toxicity has potential to limit crop production, and tolerance to toxicity is associated with the ability to maintain low B concentrations in the shoot [84]. Barley landrace 'Sahara 3763' is highly tolerant to B toxicity [85]. A gene associated with tolerance to boron toxicity, *Bot1*, a *BOR1* ortholog, was delimited to a 0.15 cM interval between markers *xBM178* and *xBM162* which encodes Bot1 protein [86]. *Bot1* was introgressed into commercial barley cultivars using linked markers. The introgressed lines show lower yield than the recipient cultivars, which have been further tailored to develop lines carrying recombination events directly adjacent to *Bot1* for use in barley breeding [86]. A B-tolerant landrace 'G61450' contributed the B toxicity gene *Bo4*, which was mapped on chromosome 4AL in bread wheat [87]. Preharvest sprouting (PHS) often reduces grain yield and end-use quality of wheat flour [88]. Landraces from China showed strong **seed dormancy** and resistance to PHS. 'Wanxianbaimaizi' contributed two major QTLs that could be used as source alleles to incorporate strong seed dormancy and resistance to PHS in new cultivars [89].

The discovery of abiotic stress tolerant alleles in landraces of barley, maize, rice, and wheat clearly shows the importance of conserving and exploring landrace germplasm as a means to identify agronomically beneficial alleles for enhancing adaptation and productivity in stress-prone environments.

Grain Yield-Enhancing Alleles in Rice

The productivity of many food crops has stagnated or is not keeping pace with the growing global food demand. Rice is the most important staple. To date, genetic resources have contributed to the identification and isolation of at least nine genes associated with grain yield-enhancing traits in rice [90]. The discovery and deployment of new grain yield-enhancing genes together with known yield-enhancing alleles are expected to provide additional sources for raising cereal productivity. *SPIKELET NUMBER* (*SPIKE*), identical to *NARROW LEAF1* (*NAL1*), was identified in the tropical *japonica* rice landrace 'Daringan' [90]. *SPIKE* enhances grain productivity in *indica* cultivars through pleiotropic effects on plant architecture. **Near-isogenic lines** (NILs) derived from 'IR64' and including *SPIKE* showed increased spikelet number, leaf size, root system, and number of vascular bundles, and achieved 13–36% grain yield increase without any negative effect on grain appearance. Uniform expression of *SPIKE* in panicles, leaves, roots, and culms support its pleiotropic effect on plant architecture. Furthermore, *SPIKE* increased grain yield by 18% in the recently released *indica* cultivar 'IRRI146', and increased spikelet number in the genetic background of other popular *indica* cultivars. Grain weight is a major determining factor for rice yield. *THOUSAND-GRAIN WEIGHT 6* (*TGW6*) was isolated from landrace 'Kasalath' [91]. *TGW6* encodes a novel protein with indole-3-acetic acid (IAA)-glucose hydrolase activity. A loss of function Kasalath allele enhances grain weight through pleiotropic effects on source organs and leads to significant grain yield increase.

Lessons from Barley Landraces for Breeding in Stress-Prone Environments

Landraces have been grown continuously since domestication, often without inputs. After the adoption of modern cultivars, landraces of several crops moved into unfavorable and stress-prone environments [92]. Hence, their evaluation could teach a few lessons about adaptation to low-input and stressful environments [93]. Such lesson(s) may be useful where landraces are still predominant [94]. This hypothesis was tested with barley grown in the dry areas of the Fertile Crescent.

The evaluation of pure lines extracted from Syrian and Jordanian barley landraces [95] revealed a high degree of seed dormancy and variability in the requirement for **vernalization**. Genetic variation was further found for seed color (Figure 1B), growth habit, days to heading, culm length, leaf width, awn length, early growth vigor, lodging, and powdery mildew resistance [34]. Thus, these landraces showed adaptive traits such as vernalization and seed dormancy. They harbor

considerable functional diversity. Additional findings were related to within-landrace genetic variation noted in stress-prone sites, and most landraces outyielded modern cultivars in stressful environments, as confirmed recently in Spain and Iran [96,97], although modern cultivars outyielded landraces, though not always significantly, under non-stress conditions. There was also a large and significant variability for almost all traits both between and within collection sites.

Heterogeneity did not decrease in most adapted landraces after thousands of years of natural and human selection in a stressful environment. Therefore, the variability available within the population appears itself to be an important adaptive trait in stressful environments and under low inputs. The concept of using cultivar mixtures as a means to increase stability and maintain evolutionary potential is increasing because it seems to be a sound strategy to cope with climate change [98]. Given that the major strength of landraces is their adaptation to the area where they evolved, a strategy to increase their yield potential is to consider them as recipients, rather than as donors, of genes which improve their performance without altering their adaptation.

Landraces fit into the farming systems of their area of adaptation, and are often essential components in the diet: using their genes in formal breeding programs addressing either nutritional or adaptation issues, and maintaining them through on-farm management, is an obligation toward the many farmers who have maintained landraces over millennia [3].

Concluding Remarks and Future Perspectives

About 70% additional food production from the same arable lands currently used for agriculture will be necessary to feed 9 billion people by 2050. This land-use intensification will occur mostly in the developing world[i]. Drought, salinity, low soil fertility, and heat stress rank among the most important abiotic constraints, which together have a significant negative impact on agricultural productivity [99]. Plant breeding for adaptation to abiotic stress-prone environments remains a challenging task. Genetic enhancement of crops needs to identify genetic variation that would permit plants to tolerate the expected levels of abiotic stress beyond those experienced by the present-day agriculture; adopt new tools to dissect the genetic, physiological and molecular basis of stress tolerance; identify genetic tags associated with enhanced tolerance; and integrate these genetic tags in applied breeding to develop 'smart' crop cultivars that yield more with low inputs.

Landraces, given their more than a millennium of evolutionary history and adaptation to stressful environments, are ideal genetic resources to explore novel genetic variation that overcomes challenges to crop production. Landraces are heterogeneous with variable phenology, low to moderate but stable edible yield, and are often nutritionally superior. The genebanks of the CGIAR (Consortium of International Agricultural Research Centers) and the World Vegetable Center hold over 791 565 cereal and legume germplasm accessions, of which about 35% are landraces (accessed on March 6, 2015[ii]). Traditional agricultural production systems in the past have played a vital role in the evolution and conservation of on-farm diversity, allowing farmers to circumvent crop failure by reducing vulnerability to environmental stresses. A systematic evaluation of landraces for assessing the pattern of diversity is urgently needed to identify alleles for enhancing yield and adaptation to abiotic stress for raising the productivity of the staple food crops in stressful environments.

Outstanding Questions

Why do global public or private breeding programs not use landraces extensively?

To what extent will modern plant breeding be able to adapt crops to climate change by pursuing genetic uniformity? Or do we need a return to diversity?

What are the thresholds between food safety and food security?

Will an agro-ecological mode of production be able to feed the 9 billion people projected for 2050?

How can we provide healthy food at a price affordable to all people?

Resources

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