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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.**

## Trends

Global climate change emphasizes the need to use better-adapted cultivars of the main crops and landraces as potential donors of useful genes.

The contribution of modern agriculture to total human-made greenhouse gas emissions is approximately 30%, and a shift to agro-ecological modes of production is increasingly seen as urgent, with landraces playing an important role in breeding programs.

During the past few decades interest in landrace conservation has been growing, with much research focusing on the maintenance of on-farm crop genetic diversity.

There is increasing consumer concern worldwide about food safety and nutrition. Landraces or old crop cultivars may provide solutions as sources of healthy and nutritious food.

## 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