Chapter 2
Plant Genetic Resources for Food and Agriculture

"If an allele is consistently rare, how likely is to be useful?"
Robert W. Allard†, Univ. of California, Davis

Agriculture began with plant domestication about 11,000 years ago in various distinct and well-defined locations mainly within world's tropics and subtropics, especially in southwest and southeast Asia and the American continent. Plant domestication, crop evolution, and further migration led to an efficient agriculture that provided the foundation of human civilization (Salamini et al. 2002). The time scale of interactions between humans and the plants they domesticated has a very short lifespan (Vaughan et al. 2007). The most ancient relics date back to about 9000 BCE in the Near East, 8000 BCE in Thailand, 7000 BCE in Mexico, and 6000 BCE in Peru. Domestication was a gradual change process. Early farmers domesticated mostly flowering plants belonging to the Brassicaceae, Poaceae, Fabaceae, Rosaceae, and Solanaceae. They noticed that some interesting plants had the ability to colonize open or disturbed habitats near human settlements but could not withstand a high level of competition with other plants. Hence, early farmers gathered and brought into cultivation these plants after learning how to grow them for their further use when it was necessary, for example, due to population pressure or changing weather patterns.

Seed agriculture (based on sexually propagated crops) became the predominant mode in dry tropics and subtropics, while vegeculture (using asexually propagated crops) was the most typical in humid lowland tropics. After instant domestication (Zohary and Spiegel-Roy 1975) and vegetative propagation of few selected high-yielding individuals, evolution was slow in asexual root, tuber and perennial fruits crops, because there was less recombination over time than in annual seed crops (Pickersgill 2007).

After plants colonized areas surrounding human settlements, seed harvesting and sowing were the next steps for seed agriculture. During this process selected plants lost their ability to survive as wild species due to mutations favoring easy seed

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handling for harvest. Most of these changes in their phenotypes and reproductive biology were determined by a few single genes—often through recessive mutations. Conscious human selection and natural selection of the traits involved in this domestication syndrome further drove crop evolution.

Wild plants evolved toward low dispersal mechanisms during domestication, for example, non-brittle rachis in cereals or non-dehiscent legumes in pulses. Humans selected plants due to the gigantism and broad variability of their edible parts such as grains, fruits, tubers, or roots. It seems that grain size and shape changed before than non-shattering ears or panicles in cereals but not in pulses (Fuller 2007). Gene flow between wild relatives and polyploidy led to broadening the physiological adaptation of some cultivated plants, for example, the A, B, and D genomes widen significantly the adaptive ability of bread wheat (Dubcovsky and Dvorak 2007) The domesticated plants also lost chemical or physical defensive mechanisms such as bitter taste or spines, thus increasing their vulnerability to pests; or their competing ability became poor against other plant species, which arose as weedy companions of various crops. Some of them are derivatives ensuing from gene flow between wild species and landraces and further disruptive selection. Other changes were associated to their reproductive biology. For example, the change from outcrossing to inbreeding led to producing adapted offspring of selfing species to distinct microclimates. Domesticated plants also favored synchronicity of flowering, increased their gynoecium volume and their seed germination became uniform. Vegetatively propagated crops reduced their sexual fertility or became completely sterile, while most seed crops changed from perennial to annual growth habit, which was often associated with a shift to synchronous tillering and ripening.

The understanding of the genetics for domestication traits has improved through the advent of saturated linkage maps based on deoxyribonucleic acid (DNA) markers, (Doebley et al. 2006) and more recently by DNA sequencing of some genes and genomes. Omics research has provided further insights into the metabolic pathways involved in particular traits. It seems that most changes brought by domestication were the result of functional damages of transcription factors rather than due to new gene functions (Pourkheirandish and Komatsuda 2007). Knowledge regarding the alleles of domestication genes and their geo-spatial distribution will facilitate breeding crops using wild relatives and landraces. This knowledge may also assist accelerating the domestication and breeding of new crops.

Crop Evolution and Plant Species Feeding the World

Plant domestication should be regarded as evolution in a human-made environment. As a result, crops depend today on humans for habitat and propagation, because some desired traits are often maladaptive in nature. For example, cereals changed their growth habit from indeterminate to determinate, their inflorescences matured evenly and produced non-shattering and non-dormant seeds, which facilitated agriculture but made them vulnerable when grown in wild ecosystems. They also

allocated a significant percentage of their net productivity to sexual structures. These changes affecting plant architecture also influence grain yield (Doust 2007). As a result of this crop history, perennial cereals are unavailable, but some advocate that artificial selection, which may be facilitated by DNA markers, may assist filling this gap (Van Tassel et al. 2010).

There are about 250,000 plant species known to humankind, of which more than 30,000 are edible. However, only 7000 have been used for food and about 120 plant species are still cultivated today, of which four crops—namely rice, wheat, maize, and potato—provide more than 50 % of food. The highest edible yields, which show the crop yield potential, are often achieved outside the main center of diversity due to many factors such as economic development and reduced pests.

Agriculture, a human activity, distorts the sample of genes that pass from one generation to another, thus creating a diversity "bottleneck." Genetic erosion began therefore with agriculture, because this human activity decreased allelic diversity in source population(s). Genetic erosion continued thereafter by losing crops, cultivars, and alleles. There are two other known "bottleneck" stages during the history of the crop: the replacement of landraces by modern cultivars and the result of modern breeding practices in diversity trends (van de Wouw et al. 2009). Systematic selection for desired traits may further lead to homogenization and standardization of released cultivars due to end users' demands, thus decreasing genetic diversity. This loss seems to be highest in elite open pollinated cultivars or inbred lines and lowest in landraces and crop wild relatives (Rauf et al. 2010). A meta-analysis of genetic diversity trends in twentieth century cultivars across various crops showed, however, a nonsignificant reduction in the long run of regional released cultivars, which demonstrated the lack of a further decrease of this diversity after landrace replacement by modern bred-cultivars (van de Wouw et al. 2010). This research also confirmed that genetic diversity was significantly reduced among released cultivars in the 1960s vis-à-vis the 1950s, but thereafter this diversity increased again as a result of plant breeding. The genetic betterment of edible yield could nevertheless lead inadvertently to changes in the nutritional quality of staple foods (Morris and Sands 2006). Emphasizing the role of plant breeding within a public human health strategy may solve this dilemma. For example, by genetically improving the micronutrient content of main crops that feed world population (Misra et al. 2004). This biofortification approach provides a relatively cheap and sustainable means for delivering minerals and vitamins to the poor worldwide.

Allele frequency, as measured by DNA markers, provides means for monitoring changes across samples and over time in a target area (Christiansen et al. 2002). DNA markers are therefore useful tools for assessing genetic erosion and diversity "bottlenecks." For example, they reveal a minor genome-wide reduction of crop genetic diversity due to plant breeding, while the allelic reduction at individual chromosomal segments was significant (Fu 2006), but sometimes these can be related to loci bearing undesirable traits.

Genebanks

Nations have interest on conserving plant genetic resources because of the potential uses of this germplasm. A genebank is a biodiversity reservoir that preserves plant genetic resources mostly as seeds or as in vitro plantlets. Plant genetic resources include all genes, gene combinations, or genotypes available for plant breeding (Gepts 2006). Collecting genetic resources, characterizing, evaluating, and documenting them, plus their further propagation for ex situ conservation and distribution are among the most important activities of genebanks. They are also sources of research materials for understanding plant domestication and crop evolution and of germplasm for further use in plant breeding. Their accessions are most often used for studying genetic diversity, agro-morphological and nutritional quality traits, and host plant resistance (Dulloo et al. 2013). Genebanks may hold diversity that was not used during plant domestication but with great potential for improving crops.

There are about 1300 genebanks holding about 6 million accessions worldwide. About 10 % of these genebank accessions are held in trust by the 11 CGIAR Consortium genebanks, which play a pivotal role in the global ex situ conservation and use of plant genetic resources, particularly of the main staple foods that feed the world. The costs for preserving the seeds in these genebanks vary according to the species breeding system and the storing period, for example, it costs US$0.19 and US$0.93 to keep enough seeds of a wheat and maize accessions, respectively, for more than 1 year; US$7.19 and US$30.24 for storing them throughout the genebank lifespan; and US$10.26 and US$56.85 in perpetuity (Pardey et al. 2001). In the last decade a Global Seed Vault was built in Svalbard (Norway) to consolidate the backup ex situ preservation of seeds of most important world's crops, especially those included in Annex 1 of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA). At the end of 2012, about 774,601 samples were deposited at Svalbard by 53 genebanks, of which in excess of one third were distinct accessions of 156 crop genera stored as orthodox seeds (Westengen et al. 2013).

Plant genetic resources include newly-bred and obsolete cultivars, landraces, or traditional local cultivars that evolved through natural and artificial farmer selection, breeding lines obtained as intermediate products and genetic stocks such as genic, chromosomal and genomic mutants, and crop wild relatives. Cultivars show high edible yield and are very uniform while landraces may exhibit flexibility that provide stable edible yields due to their large diversity, thus making them a useful source of genetic variation, particularly for coadapted gene complexes. Breeding lines seldom show a broad genetic base, especially when they are derived from few cultivars with a narrow genetic base.

Significant crop genetic diversity continues to be kept on farm as traditional landraces, especially for major staple foods that have a higher diversity richness and evenness than non-staple crops (Jarvis et al. 2008). It is very important, therefore, to continue managing crop diversity by maintaining on farm landrace genetic resources in their agroecosystems (Jarvis et al. 2011). This approach will largely

depend on how farmers and their community benefit from such an endeavor, for example, as an insurance for addressing the changing climate or meeting their priority livelihoods needs.

Crop wild relatives are either ancestors or species from a closely related taxon. A recent inventory of wild relatives of 173 priority crops contains 1667 taxa, divided between 37 families, 108 genera, 1392 species, and 299 sub-specific taxa (http://www.cwrdiversity.org/checklist/) (Vincent et al. 2012). A gap analysis of ex situ germplasm collections may allow guiding the collecting of missing crop wild relatives in genebanks (Ramírez-Villegas et al. 2010). This wild plant germplasm may be used in plant breeding because they have desired trait(s) unavailable in the cultigen pool (Dwivedi et al. 2008). For example, various tomato cultivars were bred since the 1940s using genes from wild *Solanum* species endemic to the South American Andes and showing host plant resistance to various pests, enhancing adaptation to stressful locations, or improving fruit quality. Tomato breeding continues benefiting from finding alleles for target traits in genebanks, particularly because the cultigen pool lacks enough diversity (Bai and Lindhout 2007). Research with DNA markers supports the genetic "bottleneck" for this crop as a result of domestication and further worldwide migration, perhaps based on selecting on a single or few plants. This genetic drift reduced diversity in the tomato cultigen pool. The overall use of crop wild relatives in plant breeding, remains, however, limited despite the large number of available accessions in genebanks, knowledge about their use, enhanced methods for intercrossing species across genepools, and DNA marker-aided advanced backcrossing (Hajjar and Hodgkin 2007).

Gene Pools

This term refers to the ability for gene exchange or flow within the cultigen and with its wild relatives. The primary gene pool consists of all populations of the same species or the cultigen pool, that is, landraces, improved cultivars, and breeding lines. Free gene flow and no barrier for intraspecific crosses characterized this gene pool, which sometimes includes wild species. The primary gene pool of some polyploid crops may also include the diploid ancestors. Hence, the primary gene pool refers to the biological species of a group since they are supposed to be completely interfertile. The secondary gene pool comprises populations that are able to exchange genes with the primary pool through interspecific hybridization that overcome isolation barriers such as hybrid sterility. The species in the tertiary gene pool could cross with the primary gene pool through special techniques such as "bridge species" and (immature) embryo rescue though most of the ensuing hybrids may be often anomalous, lethal, or completely sterile.

Cytogenetics provide insights on gene pools. For example, research on chromosome pairing can determine homology between genomes. However, such results should be always taken with caution because there are many simply inherited meiotic mutant genes. Likewise, DNA markers help identifying useful alleles in these

gene pools and assist in their further introgression or incorporation in the cultigen pool (Simmonds 1993). Introgression refers to the transfer of one or few useful alleles from exotic germplasm to breeding populations lacking such allele(s) and often requires prior characterization before introducing them into locally adapted or elite breeding materials. Incorporation of exotic germplasm is used by large-scale breeding programs with the aim of broadening the genetic base of locally adapted populations, which may contribute to enhancing crop performance and its stability.

Describing Variation and Identifying Redundancy

Genebanks should fully exploit their available plant diversity; otherwise they may become museums of plant accessions or living herbaria. Hence, the extent of phenotypic variation and genetic diversity of genebank accessions should be fully determined to enhance the use of this endowment in the population improvement and cultivar development. This knowledge also allows a proper germplasm organization in the genebank.

The successful management of plant genetic resources should be based on germplasm appraisals according to morphological descriptors, the determination of the agronomic value of the germplasm, and the establishment of relationships between and within species. The information obtained is used for collection management or verifying that an accession belongs to the original description, query answering to supply users with the most suitable accession or with information that will allow them to select their own accessions, and for genetic resources research, for example, defining diversity patterns and relating them to its origin and crop history. The assessment of plant genetic resources includes its characterization using morphological characters or DNA markers, and its evaluation that assists on determining the agronomic and quality value of genebank accessions for further use by plant breeding. It also provides means for classifying germplasm and establishing relationships between and within species. The resources and time spent on germplasm characterization and evaluation depend on the program goals, funding, available data on genetic diversity (and pedigree information), and knowledge and importance of traits being investigated.

At the time of collecting plant genetic resources, enough care should be taken to record passport data such as the site of the original collection. After assembling the collection in the genebank, the curator should use proper descriptors (or characteristics that measure variation in the germplasm), which will allow analyzing the number and types of useful polymorphisms among the descriptors. Further research will help to evaluate germplasm diversity using specific but variable descriptors, and to analyze the data with proper statistical tools with the aim of selecting genebank accessions according to the end user goals.

Germplasm characterization is the recording of distinctly identifiable and heritable traits, which are easily seen by the human eye and consistently expressed across environments. Genetic diversity assessment of the extent of variation among

genebank accessions is the main aim of germplasm characterization, that is, the ability to distinguish accessions from each other as a first step to identify those accessions for further screening of useful traits. It also helps to describe accessions using diagnostic traits, which could lead to identifying duplicates, classifying accessions into groups, assessing interrelationships between accessions or among traits and between geographic groups of accessions. This activity may start when collecting plant genetic resources or at introducing new accessions in the genebank, and it should end with a publication such as a catalog, journal, or newsletter article, or a web inventory. This information should be shared with end users at the time of seed shipment. This knowledge facilitates the management of plant genetic resources by end users.

The ex situ characterization of genebank accessions is often carried out in precision fields by spaced planting under adequate agronomic conditions and plant protection. For each genebank accession several traits are recorded using plant descriptors. The systematic description of each accession leads to its classification in small and well-organized groups of accessions that will facilitate their enhanced utilization by end users. Genebank accessions are characterized in batches over the years and their further screening against stresses or for food quality are undertaken in an interdisciplinary fashion. Some traits used for germplasm characterization are often taxonomic characters, for example, stem color or pubescence, inflorescence or seed shape.

Duplicated accessions should be identified within a collection and between genebanks, to avoid waste of capacity. Duplicates may be common when accessions are derived from a common original population with all alleles in common, partial if accessions derived from same original population but having only a part of the alleles or genotypes in common, or compound because all the alleles are included in one of the accessions. Putative duplicates can be first identified on the basis of passport data and thereafter these putative duplicates should be characterized with a minimum descriptor list in the field. Further, laboratory research with DNA markers must confirm their expected duplication. These duplicate accessions should be included in a bulk to prevent loss of alleles in case of partial duplication.

Germplasm Evaluation

Preliminary evaluation involves the description of genebank accessions by recording a limited number of agronomic traits that are desirable by users of a particular crop, for example, vernalization requirements, tillering, or flowering, maturity and harvest time. This first step will assist in the selection of interesting plant materials for further assessments by genebank users. Further evaluation refers to the recording of agronomic traits that determine the usefulness of a genebank accession for specific purposes as defined by the end user, for example, stress tolerance, host plant resistance, or quality. This follow-up activity is often outside the domain of most genebank curators.

Germplasm evaluation may be expensive and time consuming but is of great value for a precise phenotyping of genebank accessions of interest. The sowing and cultural practices used for evaluation are the ones common to other crop experiments. Control or check line(s)—often the most used locally adapted cultivar(s)—are included as a reference standard(s) for comparisons with the accessions being evaluated. The check line(s) provide(s) a means to assess within and between trial variation, and confidence in scoring, especially for assessing host plant resistance, in which known resistant and susceptible cultivars or accessions should be used.

The experimental unit size depends on the crop, number of testing accessions, experimental design, nature of experimental materials, and seed availability. Growing a uniform field of a standard accession and recording data at various plot sizes in the same field can determine the optimum plot size (Ortiz 1995). Coefficient of variation can be calculated for each plot size and graph them (Y-axis) versus the plot size (X-axis) to identify the inflection point, which will define the optimum plot size. Blocking reduces the experimental error whereas the experimental design takes care of the background or "noise" variation. The estimates of the variance components are used to calculate phenotypic variances and the allocation of resources, that is, number of testing environments and replications therein (Ortiz et al. 2008a). Field plot techniques improve, therefore, the design and efficiency of plant genetic resources trials.

The evaluation for complex characters or multigenic traits should be regarded as an interdisciplinary endeavor that provides essential information for germplasm utilization. Bacteriologists, entomologists, pathologists, virologists, weed biologists should assess host plant resistance in the lab, greenhouse and field, and physiologists and agronomists do multisite field screening for abiotic stress adaptation. Interdisciplinary interactions with genebank curators and geneticists will allow developing techniques for evaluation of specific pests or stresses, as well as laboratory, greenhouse and field screening methods through natural and artificial infection or stress and for interpreting results. For example, the finding of sources of host plant resistance among genebank accessions does not necessarily mean that each resistant accession possess genetically distinct alleles. They need to be crossed with standard testers—either resistant or susceptible—to establish the allelic relationships. This resistance gene cataloging reduces the number of useful sources of host plant resistance that could be used in crop genetic enhancement and kept as a distinct stock in the genebank.

Descriptors

The genetic basis for the recorded attributes or descriptors is the underlying concept for characterization and evaluation of genetic resources, that is, traits described are inherited or passed from generation to generation within an accession or expected to appear in the offspring of a cross. The characterization and evaluation of genebank accessions distinguish traits that are environmentally stable (the former) from those

whose expression often depends on the environment where the plant genetic resources are grown. Ideally, germplasm characterization and evaluation should rely on describing the genebank accessions in terms of genes and alleles rather than on phenotypic descriptors, but rarely this aim is achieved.

A descriptor is an identifiable and measurable trait or characteristic. Most of the descriptors for characterization and evaluation are species-specific. Their number depends on the crop and the importance of the crop's description. The descriptor list is the collation of descriptors for a species or crop. They are regarded as a standardized characterization system, which provide an international format and a universally understood "language" for plant genetic resources data. Their use allows a rapid, reliable, and efficient means for information exchange, storage, retrieval, and communication, thereby facilitating the utilization of plant genetic resources.

The characterization and evaluation of germplasm starts with the adoption of an appropriate descriptor list. These descriptor lists are targeted at farmers, genebank curators, plant breeders, crop scientists, and users with interest on plant genetic resources collections. There are guidelines to assist genebank curators, breeders, plant scientists, and other users of genetic resources working with specific crops and gene pools to develop their own descriptor lists in order to characterize their material and make information available to others in a systematic and unambiguous form. They are available at http://www.bioversityinternational.org/index.php?id=19&user_bioversitypublications_pi1[showUid]=3070.

Experience determines the descriptor quality or utility and whether it should remain in the list, be changed by another descriptor that measures the trait better, or be eliminated. Researchers who are characterizing and evaluating plant genetic resources define the name, state, and scale for any descriptor. There are agronomic traits such as edible yield with low repeatability but of high interest for end users due to their practical value. Information regarding the testing environment—which could be years, locations, or growing seasons—where quantitative data were recorded should be always provided.

The descriptors could be qualitative and quantitative traits. The qualitative descriptors are morphological, physiological, and molecular (biochemical and DNA) traits, whereas the quantitative descriptors are subject to environmental factors, for example, edible yield and components, host plant resistance, and stress tolerance. Key qualitative descriptors are useful for assigning most accessions to their respective species, whereas intraspecific multivariate diversity could be better assessed by quantitative descriptors (Ortiz et al. 2010).

Descriptors states are a numeric value, a code within a scale, or a qualifier for any trait. The environment seldom affects genetic markers and most qualitative descriptors, though some qualitative descriptors may have a complex genetic control. Some qualitative traits may show incomplete penetrance and variable expressivity. Penetrance refers to the frequency of the trait among individuals with same genotype, for example, individuals of the same accession are homozygous for a character but not all of them show the expected phenotype. Such variation does not result from segregation but as a result of incomplete penetrance, which is expressed as a percentage of individuals showing the expected phenotype. Expressivity indicates

the variation in trait expression, for example, color intensity across a range: from pink through red to purple. The environment influences both penetrance and expressivity. Hence, qualitative traits to be used as qualitative descriptors should not be affected by either because in theory they need only to be scored once.

Genetic diversity assessment using DNA markers and qualitative descriptors has been useful in taxonomic research, to find center of species diversity, to trace the domestication route, to investigate the relation between environment and diversity, and to determine the complete crop gene pool diversity or in a specific part of this gene pool. In addition, distinct classes based on grouping using DNA markers and qualitative descriptors have allowed the investigation of multi-locus structure within each group. Mapping traits and their analysis also facilitated by DNA markers unveil loci and dissect characters related to plant domestication and crop evolution. Fine mapping and gene cloning also provided further insights on genes related to domestication.

Quantitative descriptors depend on the genotype, the environment, and their interaction. They are often not suitable for diversity assessments (Abu Alrob et al. 2004). Most quantitative variation has multigenic control and its similarity arise from convergence. Hence, quantitative descriptors are often used for studying similar adaptation patterns. They are nevertheless useful traits to define potential divergent heterotic groups for further hybrid production. High repeatability values are useful for choosing quantitative characterization descriptors because such descriptors are not affected by the testing environment and the genotype-by-environment interaction (Ortiz and Sevilla 1995). The repeatability is calculated as the ratio between accession variance and the sum of the corresponding variance components among environments and accession-by-environment interactions. Descriptors for germplasm grouping should show a high heritability because the phenotype may vary across environments (Ortiz et al. 2008b). Heritability is calculated as the ratio between accession and phenotypic variances. If the genotype-by-environment interaction does not affect significantly the trait, the heritability will be high. Quantitative descriptors with high heritability should be used for grouping germplasm (Ortiz et al. 2008c). Heritability may be also useful for selecting quantitative classification descriptors. Heritability has no value, however, in germplasm characterization because its calculation does not include the environmental variance. Quantitative descriptors should be also accurate or unbiased, and precise or with minimum or nil error measurements, that is, their coefficient of variation must be low.

Descriptors for germplasm catalogues are those easy to score and which have a constant phenotypic expression in all environments, that is, high repeatability due to low or nil environmental variance. Hence, the environment does not bias these descriptors. Descriptors with low or nil genotype-by-environment interaction and high heritability are more important for agronomic evaluation or selection, although the environment may affect them. Quantitative descriptors showing continuous variation are often used in a natural system of classification, even when the environment or the genotype-by-environment interaction significantly affects their phenotypic expression. The environmental effect and the genotype-by-environment interaction can be lessen by assessing the germplasm in several environments and using the

mean values, by evaluating the germplasm in several environments and defining similar phenotypic responses in each specific environment and by comparing only those traits that are not affected by the environment.

Documentation and Bioinformatics

Documenting data records is essential for a genebank management to allow efficient and effective use of germplasm. Characterization and evaluation data are of little use if they are not adequately documented and incorporated into an information system that can facilitate access to data. Information plays a significant role in plant genetic resources conservation. Accurate information about conserved materials is essential for greater use of plant genetic resources in research and plant breeding.

Computerized documentation systems enable rapid dissemination of information to users as well as assist curators to manage the collections more efficiently. There may be distinct documentation systems but all of them should agree on the descriptors. The descriptor lists as well as the descriptor states must be well defined and available in a code dictionary. Descriptors lists should be revised and updated as required. Final record sheets should have this information for each accession for data input in the computer system. Information should be published in a catalogue that should be easy to retrieve and read. Web or printed versions should only have useful information on accessions available for any external user.

Bioinformatics provides means such as software tools for storing, retrieving, organizing, analyzing, and visualizing biological data. The emphasis given in recent years to the use of DNA markers for characterizing genebank accessions calls for using bioinformatics for making such datasets easily available to others (Davenport et al. 2004). This may facilitate finding patterns underlying genetic diversity and further use of this knowledge to enhance the use of germplasm collections in genetic research and plant breeding.

Geo-documentation to Identify Germplasm

The search for promising accessions can be facilitated through free exchange of ideas and information among scientists. Furthermore, outstanding sources of host plant resistance or abiotic stress adaptation may be found where the pathogens, pests or stresses are endemic. An intensive screening of accessions originating from such stressful areas may lead to identifying high levels or host plant resistance or stress adaptation.

Tests of taxonomic and biogeographic prediction rely on the assumption that either taxonomically related organisms or those found in geographic vicinity are likely to share traits (Peeters et al. 1990). The underlying concept assumes that plant populations are not randomly arranged assemblages of genotypes but they possess a

structure in space, time, and history, which results from the combined effects of mutation, migration, selection, and genetic drift. For example, the environment or their geographic distribution can influence host plant resistance to pathogens or pests (Flanders et al. 1992; Flanders et al. 1997; Bonman et al. 2007) and climate adaptation (Barboni et al. 2004). Hence, genetic variation for such a trait may be found in plant genetic resources originating from homologous locations sharing same physical environment and weather profile (Endresen 2010; Endresen et al. 2011).

Geographical information systems (GISs) and satellite imagery tools help in searching for germplasm with specific traits, monitoring changes in crops and cultivars, or deciding where to locate an in situ reserve. The focused identification of germplasm strategy (FIGS) can select genebank accessions using passport data for further screening for host plant resistance or stress adaptation (Bari et al. 2012). The FIGS uses geo-coordinates of collecting sites, environmental and agroecological data, and GIS technology to select "best-bet" genebank accessions that could have evolved under selection pressures for the trait(s) of interest. In this approach, the a priori information based on quantifying the trait–environment relationship defines the subset of accessions in which new trait variation will be sought. This trait-based approach seems to be very useful for selecting genebank accessions for further screening as shown by recent research in grain crops (Bhullar et al. 2009; El-Bouhssini et al. 2009; El-Bouhssini et al. 2010).

Genebank Sampling and Core Subsets

Genebank holding sizes are becoming large and diffuse. This growth could lead to an ineffective management and nonrational utilization of plant genetic resources by plant breeders and others. Genebank curators should therefore develop a minimal set of accessions keeping most of the diversity available in the total collection. This subset of accessions serves as an entry point to the whole collection and improves the access of the germplasm collection to plant breeders, research geneticists, and other users.

The assessment of genetic diversity will help in the establishment of a core collection, which is a subset of large germplasm collection that contains chosen accessions representing the genetic variability of the whole germplasm collection. Hence, a core collection helps the management and utilization of a germplasm collection. The structuring of a core subset provides means for optimizing the composition of ex situ germplasm collections (van Treuren et al. 2009). It may assist on identifying under- and overrepresented accessions distribution within or across genebanks.

Grouping accessions and sampling within these groups will assist assembling core collections. A multistep approach to develop core collection should consider giving priority to regions by often weighing toward traditional growing areas, grouping germplasm according to agroecological origin using GIS, using morpho-physiological data on specific discriminating characters, and maximizing allele richness in the core subset with the aid of DNA markers for sampling. An allocation

method provides further criteria for determining the number of accessions to be selected from each cluster (Franco et al. 2005). This methodology should lead to samples with enough diversity and high variance for continuous quantitative traits.

The core subset should include with minimum redundancy the genetic diversity of a crop species and its wild relatives. Often, a core collection consists of 10% of the collection (with a maximum of 3000 accessions for each species within the genebank), which contains 70% of the alleles of whole collection (Brown 1989). Theoretically, an upper limit of 3000 accessions allows maintaining alleles with a frequency of 10^{-4} in the species. This sampling procedure is based on the theory of neutral marker alleles and considers the incorporation of rare widespread alleles in the core collection. Common widespread alleles will be surely in the core collection and successful grouping will ensure common localized alleles in this subset of the whole collection. Rare localized alleles are not considered because of the impracticability of conserving everything. Sampling for the development of a core collection must consider a hierarchical structure of the gene pool, that is, stratification into groups sharing common characteristics, for example, taxonomy, geographic or ecological origin, and neutral or non-neutral descriptors. Core collections are available for almost all important food crops, as well as for a few of their wild relatives and feed or fiber crops: barley (van Hintum and Haalman 1994), bean (Tohme et al. 1995), cabbage (Boukema et al. 1997), cassava (Chavarriaga-Aguirre et al. 1999), chickpea (Upadhyaya et al. 2001), cotton (Xu et al. 2006; Wang et al. 2008), cowpea (Mahalakshmi et al. 2007a), finger millet (Upadhyaya et al. 2006), foxtail millet (Upadhyaya et al. 2009), perennial *Glycine*—a wild soybean (Brown et al. 1987), groundnut or peanut (Upadhyaya et al. 2003), hot and sweet peppers (Thies and Fery 2002), lentil (Erskine and Muehlbauer 1991), lettuce (Jansen and van Hintum 2007), maize (Taba et al. 1998; Franco et al. 2007), annual and perennial *Medicago*—wild alfalfa or lucerne (Diwan et al. 1995; Basigalup et al. 1995), mungbean (Bisht et al. 1998a), pea (Coyne et al. 2005), pearl millet (Bhattacharjee et al. 2007), pigeonpea (Reddy et al. 2005), potato (Huamán et al. 2000), quinoa (Ortiz et al. 1998), rice (Yan et al. 2007), perennial ryegrass (Charmet and Balfourier 1995), sesame (Bisht et al. 1998b; Xiurong et al. 2000), sorghum (Grenier et al. 2001), sweetpotato (Huamán et al. 1999), tomato (https://www.eu-sol.wur.nl/dynamic/passport/aboutTheCC.php), bread and durum wheat (Balfourier et al. 2007; Spagnoletti Zeuli and Qualset 1993), and yams (Mahalakshmi et al. 2007b).

Core subsets consisting of 10% of total accessions for large germplasm collections (>10,000) could be regarded as an unwieldy proposal for trait screening by plant breeding programs. Minicore subsets with a significantly reduced size that still capture most of the genetic diversity will promote the utilization plant genetic resources in crop improvement, because they will be a point of entry for an appropriate exploitation of germplasm collections (Upadhyaya and Ortiz 2001). They are defined by evaluating the core collection for various morphological, agronomic, and quality traits, which provides the basis for selecting a minicore subset of about 10% accessions from this core collection.

Static core collections selected a priori by the genebank curator are often of limited use for those users interested in a specific trait. This conflict arises because

of the preference for allele richness rather than ensuring allele representativeness in the core subset. Interactive core selections meeting specific user needs may further enhance germplasm utilization (Mahalakshmi et al. 2003). A stratified selection methodology will allow any user to choose the domain of interest. The size of this stratified core selection ranges between 1 and 10% of the total germplasm collection size. The selection algorithms are based on either the proportional or logarithmic sampling strategy. A minimum of one entry per group is chosen to ensure the representation of small groups. As a result, the genebank users obtain a focused selection of the germplasm with more useful diversity of the trait of interest than core collections. Likewise, algorithms such as Core Hunter assist defining core subsets based on user preference but having enough genetic diversity and appropriate average genetic distance among accessions (Thachuk et al. 2009). Core Hunter can also find small core subsets that still keep all unique alleles found in the reference germplasm collection.

Genomics of Plant Genetic Resources

DNA markers are descriptors that normally offer reproducible results due to their predictable genetic basis. Their ability to assess polymorphisms, identify duplicates, and estimate genetic relationships in germplasm collections made them an important tool in the conservation and management of genetic resources in genebanks. Unique materials could be lost or discarded due to the inability to properly assess genetic diversity in the collection. DNA markers should be able to determine genetic diversity within a population and identify distinct accessions with maximum genetic diversity. Furthermore, some assessments facilitated by DNA markers are revealing the impacts of plant breeding on improved crop genepools, which may either narrow or widen their genetic base, and shift their genetic background. Research with DNA markers shows that the genome-wide reduction of crop genetic diversity accompanying genetic improvement over time may be minor vis-à-vis the significant allelic reduction at individual chromosomal segments. Further research needs to determine what proportion of lost alleles is associated with undesirable traits. In this regard, biometrical methods, which deal correctly with the analysis of molecular marker data, are required to obtain reliable measures of genetic diversity in genebanks. There are several easy access and user-friendly software programs that analyze—based on population genetics theory—DNA marker data (Labate 2000). Their use depends on the DNA marker types and the kind of analysis sought.

A broad range of reproducible DNA marker systems are available and could be used depending on the needs and capability of the user, for example, restriction and amplified fragment length polymorphisms, microsatellite or simple sequence repeats, expressed sequenced tags, and single nucleotide polymorphisms. Research and the application of results to characterization and conservation of germplasm will also benefit from regional collaboration and pooling of resources. In this regard, researchers using DNA markers should adopt a common approach with community

standards in order to generate and exchange directly comparable data and, in the medium term, create a universal curated molecular marker database to facilitate information flow and knowledge sharing.

Phylogenetic analysis using DNA markers provides insights to plant domestication. DNA markers reveal relationships among crop genomes and trait evolution. They are very useful to establish genome synteny or the preserved order of loci on chromosomes of related species likely arising because of a common ancestor. This knowledge could facilitate the transfer of traits between related species, particularly if they cannot be easily hybridized. The sharing of some traits in spite of independent domestication could suggest that few loci would have been involved in the changes from wild species to crops (Paterson et al. 1995). Genome colinearity confirmed that same genes or their pathways were selected across species during plant domestication. However, trait sharing in same chromosome location may not always indicate that genes are identical (Paterson 2002). Synteny may allow predicting gene order in related crops though further DNA sequencing revealed that many small genome regions do not show synteny across species.

Large genome screening based on bulk of DNA samples can assist to identify markers located near quantitative trait loci (QTL) related to the domestication syndrome (Papa et al. 2007). This inexpensive population genomics approach can be regarded as a prescreening of DNA markers for association genetics research and to find QTL for adaptive variants. Morphological and physiological differences can be further analyzed using comparative mapping QTL related to domestication traits among species (Isemura et al. 2007). Such research can identify new QTL or determine their previously unexpected effects. This information may be useful for improving the related traits across species. For example, large seed in soybean ensued from accumulating minor changes at many QTL, which did not belong to same linkage cluster that facilitates their introgression from wild species into the cultigen pool (Liu et al. 2007). Transgressive segregation for seed size could account for such variation in the offspring derived from intervarietal mating.

DNA sequence diversity analysis of a large number of genes from cultivars or inbred lines and wild relatives may provide evidence of human selection, for example, identifying population "bottlenecks" that reduced diversity related to plant domestication and crop breeding (Yamasaki et al. 2007). These population "bottlenecks" could occur across the plant genome and influence the distribution of diversity among loci. They led to high-frequency polymorphisms and increased linkage disequilibrium, which can be further increased by human selection. A large-scale screening for artificial selection will further identify loci controlling traits even when the gene function and their phenotypes are unknown. DNA sequence(s) of a complex trait can be also used to construct phylogenetic trees and expose the origins of a crop. This approach led to establish the diphyletic origin of barley—an early crop of ancient farmers—based on a nucleotide re-sequencing of a marker on the *brittle rachis* locus for the cultigen, wild relatives and weedy species (Azhaguvel and Komatsuda 2007).

Genome sequencing can assist in studying the origin of genes related to domestication, determine the timing of sequence divergence among species, and show how

genes evolve in crops, particularly for polyploid species. For example, comparative genomics based on genetic maps or DNA sequences was useful to determine that ancient polyploidization about 70 million years ago and thereafter the loss of many duplicate genes through diploidization shaped the genomes of species in the Poaceae family (Paterson et al. 2004). Further research needs to elucidate whether duplicate genes provided a selective advantage during crop domestication and evolution. Polyploidy could have some selective advantage such as fixing heterosis, allowing evolution of gene function or providing plasticity under stress, because amphiploids or disomic polyploids enlarged their allelic diversity while polysomic polyploids increased the allelic copy number. Understanding the evolutionary relationships between domesticated plants and their wild relatives will facilitate the use of these genetic resources in crop breeding.

Mutants are useful plant genetic resources to explore gene function and to find the genes making a crop, particularly for traits that distinguish the cultigen from its wild relatives. Eco-tilling may allow gene discovery by directly identifying polymorphisms arising from natural mutations in wild species and landraces (Comai et al. 2004).

Putting Genes into Usable Forms

Germplasm enhancement is often used to designate the phase between identifying a useful character, "capturing" its genetic diversity, and putting those genes into a "usable" form (Ortiz 2002). End products of germplasm enhancement may be deficient in certain traits but they are still attractive to breeding programs because they are improved when compared to the original source of variation: wild species or other unadapted germplasm. The long-term crop improvement agenda must therefore include developing advanced breeding materials with the desirable alleles or traits from these exotic germplasm in a suitable genetic background.

Most useful plant genetic resources materials are modern elite cultivars and their closer wild relatives, especially materials that are adapted in the local environment or closely similar environments. Plant breeders' and farmers' selection practiced over large number of generations increased the frequency of favorable alleles and favorable lower combinations of alleles. Such multi-allelic combinations or "linkats" developed in specific habitats should be preserved and enhanced. This genepool may not be enough, however, for sustainable long-term crop genetic enhancement, especially when higher-order interactions are important. The discovery and incorporation of genes from crop wild relatives and other exotic germplasm provides perhaps one of the few means of sustaining crop improvement in the long term. There are some rare alleles that may be worth saving; especially those that have arisen recently under cultivation such as genes for produce quality, useful products, or host plant resistance. Although, durability of resistance cannot be predicted, the use of increased genetic diversity through preventive breeding may help buffering against crop losses arising as the pathogen or pest population changes.

Plant breeding gives a relative ranking when defining priority traits, but most programs still aim "high yield, high quality and quantity, extension of adaptation ability to climate and soil conditions and tolerance or resistance to pests" (Ulukan 2011). Such simultaneous trait selection in plant breeding seldom uses a selection index derived from economic weights, as done in animal breeding (Sölkner et al. 2008). Very often plant breeding programs arbitrarily decide on thresholds for each trait and select against plants that do not meet the target level. A program for gene search and use in plant breeding should, therefore, consist of at least the following four steps: (i) characterizing and evaluating genetic and phenotypic diversity available in the genebank for a better understanding of its available variation for further use, (ii) screening the genebank accessions—perhaps through a core subset—for desirable trait or allele diversity, (iii) finding the trait or allele(s) of interest and thereafter searching into remaining accessions of the whole collection for screening accessions of similar geographic area, and (iv) incorporating such desired trait or allelic diversity into the breeding populations of a crop improvement program.

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