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Plant genetic resources: What can they contribute toward increased crop productivity?

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ABSTRACT To feed a world population growing by up to 160 people per minute, with >90% of them in developing countries, will require an astonishing increase in food production. Forecasts call for wheat to become the most important cereal in the world, with maize close behind; together, these crops will account for ≈80% of developing countries' cereal import requirements. Access to a range of genetic diversity is critical to the success of breeding programs. The global effort to assemble, document, and utilize these resources is enormous, and the genetic diversity in the collections is critical to the world's fight against hunger. The introgression of genes that reduced plant height and increased disease and viral resistance in wheat provided the foundation for the “Green Revolution” and demonstrated the tremendous impact that genetic resources can have on production. Wheat hybrids and synthetics may provide the yield increases needed in the future. A wild relative of maize, *Tripsacum*, represents an untapped genetic resource for abiotic and biotic stress resistance and for apomixis, a trait that could provide developing world farmers access to hybrid technology. Ownership of genetic resources and genes must be resolved to ensure global access to these critical resources. The application of molecular and genetic engineering technologies enhances the use of genetic resources. The effective and complementary use of all of our technological tools and resources will be required for meeting the challenge posed by the world's expanding demand for food.

Today, on the eve of a new millennium, we are approaching a critical era in the evolution of our planet and species—we are in a race between growing population and food production. This era was cast in Paul Ehrlich's *The Population Bomb* (1), perhaps prematurely, as a time when population would outpace the earth's resources, including its capacity to produce food. The threat of the Malthusian crisis forecast by Ehrlich appears to have diminished as we have witnessed a slowdown in the rate of population growth. But the challenge of feeding a world population growing by up to 160 people every minute (>90% of them in developing countries) remains daunting. It is forecast that, by 2050, world population will increase from the current level of ≈6 billion to >8 billion people. Feeding this population will require an astonishing increase in food production. In fact, it has been estimated that the world will need to produce as much food during the next 50 years as was produced since the beginning of agriculture 10,000 years ago (2)! Today, it appears more likely that a population/food crisis may be born, not from an exponentially increasing world population (though in some of the world's poorest regions, population growth remains exceedingly high), but from an ill-founded sense of complacency about food production.

Our staggering requirement for food must be viewed in the context of statistics that indicate that the area available for food production has, essentially, remained constant since 1960 (3). Despite some new land being brought into cultivation, soil erosion and urbanization have offset these gains. In addition, less resources (both human and financial) are being devoted to overcoming major production constraints. Financial support for agricultural research has decreased for the last several years and is expected to continue its slow decline as most developed nations continue to focus on domestic issues rather than addressing the multitude of problems facing the world's developing nations.

How will we feed the world in the coming years? For the foreseeable future, conventional agriculture will be our primary response, with cereal grains playing a pivotal role. The International Food Policy Research Institute has predicted that, by the year 2020, almost 96% of the world's rice consumption, two-thirds of the world's wheat consumption, and almost 60% of the world's maize consumption will be in developing countries. Forecasts call for wheat to surpass rice in its apical role in feeding the poor of those nations. It will likely become the most important cereal in the world, with maize close behind; together, these crops will account for ≈80% of the cereal import requirements of developing countries. Many economists stress, however, that increased production in developing countries will be essential for achieving food security. Maize and wheat are each expected to have an annual global demand of ≈775 million tons each[†] and will be of critical consequence in the race between crop production and population growth. This paper focuses on the potential of genetic resources, particularly those of maize and wheat, to help meet the continually expanding demand for these major grains. It will indicate how such resources have contributed in the past, and how they may advance our efforts in the future.

The Role of the Consultative Group on International Agricultural Research (CGIAR) in Preserving Genetic Resources

Simply stated, plant breeding depends on the correct combination of specific alleles at the 50–60,000 genetic loci present in a plant's genome. The knowledge of where these alleles are best found and the combination and evaluation of these into a

Abbreviations: CGIAR, Consultative Group on International Agricultural Research; CIMMYT, Centro Internacional de Mejoramiento de Maiz y Trigo; FAO, Food and Agriculture Organization; IPR, intellectual property rights.

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single species can be considered the “art” of breeding. Obviously, access to a wide range of genetic diversity is critical to the success of any breeding program.

The work of the 16 centers that collectively form CGIAR represents the largest concerted effort toward collecting, preserving, and utilizing global agricultural resources. Together, the centers hold nearly 600,000 samples of the estimated 6 million accessions stored globally (Table 1). The remaining germplasm are stored in other international, regional, and national gene banks, many of which collaborate closely with the CGIAR centers. If one considers that the Food and Agriculture Organization (FAO) has estimated that the total number of unique accessions globally are on the order of 1–2 million, the CGIAR centers account for an estimated 30–60% of the world’s unique holdings under long-term conservation. Given that the CGIAR has focused its efforts on the crops of highest significance in world agriculture, this proportion could be even greater.

The materials in the CGIAR gene banks include traditional varieties and landraces, nondomesticated species, advanced cultivars, breeding lines, and genetic stocks. The effort required to assemble, document, and maintain these collections is enormous but well justified as the genetic diversity present in the gene banks represents a critical component in the world’s fight against hunger.

The International Center for Maize and Wheat Improvement, better known by its Spanish name of Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT), has a global mandate for improving the productivity and sustainability of maize and wheat in developing countries. The collection, documentation, and evaluation of the genetic resources of maize and wheat are a critical part of meeting this mandate. CIMMYT’s newly established Genetic Resource Center contains ≈120,000 accessions of wheat and 18,000 accessions of Latin American maize (of the 25,000–35,000 accessions in partner gene banks in Latin America). This represents the largest collection of these two important cereals. It is, perhaps, the only effort that is actively pursuing the documentation and evaluation of its collection on a routine basis.

Before discussing several issues related to the use of these genetic resources, it is important to mention a few examples of their contributions to crop improvement. Although these examples have been drawn mostly from maize and wheat, there

are a large number of similar examples for many other major food crops handled by the CGIAR Centers.

Contributions of Wheat Genetic Resources

Wheat is truly global, being one of the few crops grown over most of the world. It belongs to the genus *Triticum*, which originated almost 10,000 years ago in the historic Fertile Crescent, an area in the Middle East. *Triticum* arose from the cross (supposedly in nature) of two diploid wild grasses to produce tetraploid wheat, which today includes the many cultivated durum (pasta or macaroni) wheats (*Triticum turgidum* L. var. Group *durum* Desf. $2n = 4x = 28$). Tetraploid wheat later crossed to diploid goat grass (*Triticum tauschii*) and gave rise to hexaploid, or bread wheat (*Triticum aestivum* L. em Thell. $2n = 6x = 42$).

There are hundreds of thousands of wild species, landraces, and local cultivars within the *Triticum* species that constitute the wheats of the world. The main center of diversity of the species is southwest Asia, near the Fertile Crescent, extending from the Mediterranean coast in the west to the Tigris-Euphrates plain in the east. In this region, diploid and polyploid *Triticum* species coexist in mixed populations and exhibit tremendous morphological and ecological diversity.

Thousands of species of *Triticum* have been collected and are currently stored in the various genetic resources centers, including the one at CIMMYT headquarters in Mexico. Much has been written about the lack of utility of genetic resources contained in collections, but few studies have attempted to estimate their contribution to wheat improvement. Chapman (5) examined the role of genetic resources (defined as wild materials and landraces) in wheat breeding, but found it difficult to estimate. He concluded that these materials may have been used in ≈10% of all crosses based on the pedigrees of recently released cultivars. CIMMYT’s effort to develop a full pedigree database of the global wheat genetic resources (the International Wheat Information System) allows a more complete estimate of landrace and wild material contributions to modern varieties by providing pedigree information that goes back to the original landrace parents. More recently, Smale (6) performed an in-depth analysis of the use of wheat genetic resources and the international flow of wheat genetic resources. The study found that the number of different landraces in pedigrees of modern wheat varieties has steadily increased during the past 30 years and that the geographical origin of the landraces has broadened. Going beyond rather general and poorly defined contributions to modern varieties, several specific genes that have made major impacts on wheats can be directly traced to contributions from genetic resources.

Dwarfing Genes. “Norin 10,” a cultivar from Japan, provided two very important genes, *Rht1* and *Rht2*, that resulted in the reduced height (or dwarf) wheats. Norin 10, in turn, inherited these genes originally from “Shiro Daruma,” a Japanese landrace (7). When Norman Borlaug first arrived in Mexico under the joint Rockefeller/Mexico project, wheat productivity was extremely low. The tall varieties being planted were prone to lodging and would not respond to added fertilizer inputs. Borlaug speculated that, by reducing the height of the wheat plant, it would suffer less lodging even under the higher input levels. The incorporation of the *Rht1* and *Rht2* genes into the new varieties that Borlaug ultimately was able to develop and deploy illustrated the difficulty of using genes from unadapted materials. But more importantly, it led to what is now been termed the “Green Revolution” (8, 9). While it was originally thought that these genes contributed to higher production simply through reduced lodging via reduced height, it is now clear that they have other direct effects on yield via better nutrient uptake and tillering capacity (8, 10).

Table 1. Summary of CGIAR’s germplasm holdings (4)

Center	Total holdings	Major species
CIAT	70,940	Cassava, Phaseolus, rice
CIMMYT	136,637	Maize, wheat
CIP	13,911	Potato, sweet potato
ICRAF	2,448	Agroforestry species
ICARDA	109,029	Lentil, chickpea
ICRISAT	110,478	Chickpea, sorghum, groundnut
IITA	39,756	Yam, rice, maize, cassava
ILRI	13,470	Forage legumes and grasses
IPGRI	1,051	Banana, plantain
IRRI	80,646	Rice
WARDA	17,440	Rice
Total	595,806	

IITA, International Institute for Tropical Agriculture; CIAT, Centro Internacional de Agricultura Tropical; CIP, Centro Internacional de Papa; ICRAF, International Centre for Research in Agroforestry; ICARDA, International Center for Agriculture in the Dry Areas; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; ILRI, International Livestock Research Institute; IPGRI, International Plant Genetic Resources Institute; IRRI, International Rice Research Institute; WARDA, West African Rice Development Association.

Rust Resistance. Some of the most devastating and universal crop diseases are caused by fungal pathogens. Among them, the rust pathogens are the most widespread and generally cause the largest crop losses per season. Many genes have been found that provide resistance to specific races of each rust pathogen. Within wheat, leaf, yellow, and stem rusts are major pathogens. Fungicides can provide a level of control; however, the chemical option is often limited for many farmers, particularly in developing countries, by high costs and lack of knowledge about application. In addition, the negative environmental effects of chemical applications can be considerable.

The incorporation of host plant resistance genes into modern wheat varieties has allowed yields of resistant wheat that have not been treated with fungicides to nearly equal those of the same varieties under fungicide applications (6). Many of these varieties have incorporated single major genes that convey resistance to specific races of the rust pathogen. Of >40 known genes for leaf rust resistance, 12 originated in species other than *T. aestivum* and *T. turgidum* while 20 of the 41 known genes for stem rust resistance originated in species other than *T. aestivum* and *T. turgidum* (ref. 11; also see Table 2). Even among the genes originating from *T. aestivum*, many come from landraces.

Unfortunately, many of these major genes have already been "broken"; i.e., the specific race has mutated to become virulent against the specific resistance gene. Efforts to identify and incorporate genes that confer "durable" resistance are therefore preferable. Several such genes have been identified and incorporated into modern wheat varieties. One of the most important is *Lr34*, which was originally found in the cultivar "Frontana" (13). *Lr34* has been incorporated into >50% of the wheat varieties grown in the world today; together with several modifier genes, it has resulted in stable resistance to leaf rust

Table 2. Important genes in wheat that were found in related species (12)

Trait	Locus	Source
Disease resistance		
Leaf rust	<i>Lr9</i>	<i>Aegilops umbellulata</i>
	<i>Lr18</i>	<i>Triticum timopheevi</i>
	<i>Lr19</i>	<i>Thinopyrum</i>
	<i>Lr23</i>	<i>T. turgidum</i>
	<i>Lr24</i>	<i>Ag. elongatum</i>
	<i>Lr25</i>	<i>Secale cereale</i>
	<i>Lr29</i>	<i>Ag. elongatum</i>
	<i>Lr32</i>	<i>T. tauschii</i>
	Stem rust	<i>Sr2</i>
<i>Sr22</i>		<i>Triticum monococcum</i>
<i>Sr36</i>		<i>Triticum timopheevii</i>
Stripe rust	<i>Yr15</i>	<i>Triticum dicoccoides</i>
Powdery mildew	<i>Pm12</i>	<i>Aegilops speltoides</i>
	<i>Pm21</i>	<i>Haynaldia villosa</i>
	<i>Pm25</i>	<i>T. monococcum</i>
Wheat streak mosaic virus	<i>Wsm1</i>	<i>Ag. elongatum</i>
Karnal bunt	Quantitative trait loci	<i>T. turgidum</i>
Pest resistance		
Hessian fly	H21	<i>S. cereale</i>
	H23, H24	<i>T. tauschii</i>
	H27	<i>Aegilops ventricosa</i>
Cereal cyst nematode	<i>Cre3 (Ccn-D1)</i>	<i>T. tauschii</i>
Quality traits		
Grain protein	Quantitative trait loci	<i>T. turgidum</i>
High protein		<i>T. dicoccoides</i>
Low molecular weight glutenins		<i>T. turgidum</i>

in the 1980s and 1990s. Most of these durable sources of resistance have not come from alien sources but from cultivars and landraces that evolved in the past to contain broad levels of resistance to pathogens.

The cultivar "Hope," bred in the United States earlier in the century (14), was later used by Borlaug as a source of stem rust resistance in the Rockefeller/Mexico wheat program. The Hope resistance was based on the *Sr2* gene that, when combined with other unidentified genes, produced a more durable resistance. The *Sr2* originally came from a tetraploid wheat variety known as emmer and has since been incorporated into many wheat varieties worldwide, providing excellent levels of resistance. Recently, a linked molecular marker was developed (15) that may allow more rapid identification and manipulation of this important gene. It is fair to say that the incorporation of the *Sr2* and *Lr34* genes from genetic resources into cultivated wheat varieties represent milestones in the grain's genetic advancement. Most likely, the gains of the Green Revolution could not have been made without them.

Veery Wheats. Genetic resources have contributed more than single genes to crop improvement efforts; entire chromosomal segments also have been introduced with noteworthy results. Perhaps the most important of these is the 1B/1R translocation that was identified as a simple transfer between rye and wheat in the former Soviet Union cultivar "Kaukaz." The 1B/1R translocation, which carries a number of genes from rye, confers resistance to various diseases (fungal and viral pathogens) and adaptation to marginal environments (16). This translocation has been deemed so important that it has been incorporated into >60 wheat varieties, including the prominent Veery lines, that occupy >50% of all developing country wheat area, almost 40 million hectares (17).

Yield Potential. Yields of the major cereal crops (rice, wheat, and maize) have increased steadily over the past years, although the rate of these yield increases appears to have slowed.‡ To meet cereal production demand in the next decade, we must continue to increase yields; even more daunting, we must increase them at an ever-increasing rate. How will such growth be supported, particularly when the rates of increase over the past few years appear to have declined?

For rice and wheat, the use of hybrids may be one possibility, although it remains to be demonstrated what level of heterosis (hybrid vigor) can be achieved in either crop. Heterosis levels currently detected in wheat are ≈10–25%, lower than the 25–35% levels historically found in maize, one of the first hybrid cereal crops. The reasons for wheat's lower heterosis levels have not been determined, but one possibility is the lower level of diversity generally found in self-pollinated crops such as rice and wheat. Many groups continue to search for alternatives to the existing germplasm. In wheat, it is possible to reproduce the hybridization event that created hexaploid wheats from a cross of tetraploid with diploid wheat. These so-called "synthetics" represent a source of novel genetic variation (18). Research at CIMMYT has led to the development of >600 new synthetic wheats, crosses between various durum wheats and *T. tauschii* accessions. Many of these crosses have produced rapid improvements in important characteristics, including disease resistance, abiotic stress tolerance, and yield.

Although much work remains to be done, the use of molecular genetic techniques now allows us to identify the gene segments most likely responsible for improved performance and, thus, to focus on more directed crosses in the future. A recent example, now under investigation at CIMMYT, is the role of the *Lr19*-containing segment. This gene (or segment) originally came from *Agropyron elongatum* and was

‡Rosegrant, M. W., Sambilla, M. A., Gerpacio, R. V. & Ringler, C., Illinois World Food and Sustainable Agriculture Program Conference, May 27, 1997, Urbana-Champaign, IL.

first incorporated into the wheat variety "Agatha" (11). Yield trial data indicates that varieties containing the *Lr19* gene yield at least 10% more than counterparts without *Lr19* (Ravi Singh, personal communication). The gene was originally transferred for its possible role in conferring leaf rust resistance, but its potential to increase yields may become a more important factor for breeders, thus demonstrating the often unanticipated potential of these alien transfers.

Use of Genetic Resources in Maize Improvement

Unlike wheat, the use of genetic resources in maize improvement has not been well documented at the global level and may not be as great. Although $\approx 50,000$ accessions of maize exist in germplasm banks around the world (19, 20), most of these have never been adequately evaluated for useful traits. Reasons cited for low utilization include lack of evaluation data, documentation, and information; poor coordination of national policies; and poor linkages between gene banks and breeders (21). The untapped potential of these genetic resources is indicated to some extent by the progress that U.S. breeders achieved through a combination of plant improvement and pedigree breeding. Using double and three-way crosses, varieties were produced that helped double U.S. yields between 1930 and 1966; by 1995, single crosses and the use of better hybrid materials by breeders helped triple 1930 yields.

Meanwhile, there have been frequent warnings about the genetic vulnerability of maize and the potential of exotic germplasm to reduce the threat (22–24). It has been estimated that, in the U.S., $<1\%$ of the germplasm base is exotic germplasm (20). On a global basis, only $\approx 5\%$ of the available maize germplasm is used commercially (25).

Concerns over the lack of genetic diversity in maize used for production go beyond the realms of academic argument and theory. The devastating 1970 epidemic of southern corn leaf blight (caused by the fungal pathogen *Bipolaris maydis* Nisikado Shoemaker, race T) was due to the widespread deployment of genetically uniform varieties, all containing T-cytoplasm. In addition to increased susceptibility to diseases and pests, low diversity levels do not bode well for yield plateaus lurking on the horizon. Increases on the order of 1.5–2.0% per year of genetic gain for yield are still being achieved, but some question whether they can be sustained. The incorporation of exotic germplasm into adapted lines may give rise to additional hybrid vigor, lessening the chance for a yield plateau (26). In addition, several studies have demonstrated that exotic germplasm contains significant variation for many quality traits (27–30). Because many of the genetic resources of maize have undergone extensive selection over centuries for indigenous uses such as feed, food, and beverages, it seems likely that abundant new grain qualities and characteristics remain to be discovered.

While innumerable sources of exotic maize remain untapped for crop improvement, wild relatives—an excellent and robust source of novel characteristics—have received notable attention. Of particular interest are the species of teosinte, considered by some to be the most likely progenitor of domesticated maize (31). The classification of the teosintes is still controversial (31), although the species has clearly differentiated into various races, species, plant habits (annual and perennial), and into two ploidy levels ($2n$ and $4n$). In many parts of Mexico and Guatemala, maize and teosinte can be found growing together in farmers' fields. Hybrids between the two can be found, although the farmers usually cull them at the time of flowering. Very few investigations have been conducted to identify useful characteristics in teosinte that may be introgressed into modern maize varieties. Studies by Doebley (32, 33) have determined the genetic basis for the major morphological differences between maize and teosinte. These studies provide the

basis for further investigations into the specific genes and alleles that teosinte could contribute to maize improvement.

The species of *Tripsacum*, yet more distant relatives to maize, also offer promising potential. The genus consists of a number of species with varying levels of ploidy and a base chromosome number of 18. The species, mostly perennials, contain a number of interesting genes; however, only a few studies have referred to the possible use of *Tripsacum* segments for maize. Benefits have been demonstrated for increased yield (34) and for disease resistance [an *Ht* gene derived from *Tripsacum floridanum* (35)]. The characteristic of apomixis—asexual reproduction of a plant through the seed—is found in many of the polyploid species of *Tripsacum* (36) and may be of great import to the maize-growing world. In developing countries, many farmers cannot take advantage of hybrid technology that would increase their yields because high-quality hybrid seed is either unavailable or unaffordable. If hybrid seed could be produced via apomictic hybrids, public and private sector seed companies could produce larger quantities of high quality seed, at lower cost, to meet the new demand. Farmers would have the opportunity to recycle high-quality seed from generation to generation, providing another option for meeting an often unpredictable planting cycle. The introduction of hybrid technology to these countries would undoubtedly boost yields, both through heterosis and by providing effective options for introducing resistances and tolerances.

In developed countries, the private sector has dominated the seed industry; hybrids have played an important and often controversial role. Apomictic seed would not be a great benefit to the industries as a commercial product, but it could be important in the production of hybrid seed. Much work remains before we witness the first apomictic diploid maize plant; however, the work of several research groups, at various locations around the world, in maize and other cereals makes us optimistic that this will be achieved soon. The potential impact on maize agriculture would be tremendous, and efforts must continue to ensure that this technology will be available to all farmers, particularly those in developing countries.

Apomixis is not the only trait of importance in *Tripsacum*. Many *Tripsacum* species are resistant to important diseases and pests and can survive in some of the world's harshest environments. In Africa, for example, the parasitic weed *Striga* spp. is a significant pest of maize and other cereal crops. Little resistance has been found within maize, even following extensive testing of a wide collection of exotic sources. CIMMYT and a sister CGIAR center, the International Institute for Tropical Agriculture, are working to identify genes associated with resistance and to develop molecular techniques to more effectively transfer the traits to maize varieties. Some resistance has been found in certain teosinte species and accessions. Recent efforts in screening a range of *Tripsacum* species have identified several promising accessions with near immunity to *Striga* infestation. Some of these accessions are within the diploid species and, thus, are more amenable to genetic investigation and introgression into maize. A collaboration between CIMMYT and the Kenyan Agricultural Research Institute is actively exploring this resistance. Molecular linkage maps of the genes are being developed with the ultimate aim of transferring the resistance to local maize varieties.

Undoubtedly, teosinte and *Tripsacum* represent significant untapped genetic resources for the improvement of maize. Through the application of molecular techniques, the genomes of these species will be opened for further investigation and, ultimately, for the isolation of critical genes, which can be transferred to other crop plant species.

Intellectual Property Rights Issues Related to the Utilization of Genetic Resources

During the past several years, there has been an increasing trend toward the application of intellectual property rights

(IPR) to agricultural products, even plant varieties. This is in great contrast to the 1960s and 1970s, when such protection was considered a detriment to global progress in plant improvement. With initiatives such as the 1991 strengthening of the Union for the Protection of New Varieties of Plants Convention and the 1993 Multilateral Trade Negotiating Rounds in the General Agreement on Tariffs and Trade, IPR was widened to include inventions and breeding technology.

Looking to better protect genetic resources, FAO established the International Undertaking on Plant Genetic Resources in 1983. At its outset, the Undertaking subscribed to the rule of free and unrestricted interchange of germplasm and recognized all plant genetic resources as the "heritage for mankind." The Undertaking was modified in 1989 and 1991 to include resolutions regarding compensation and ownership of genetic resources.

In 1992, the Convention on Biological Diversity officially recognized the sovereign rights of individual nations over biological diversity and the resources within their territories. The Treaty has been ratified by most developing countries and many developed countries but has yet to be ratified by the U.S. A result of the Convention has been a modification of the agreement between FAO and the CGIAR centers. In 1994, each CGIAR Center signed an agreement with FAO putting their genetic resources "in trust" under the auspices of the FAO. These agreements describe the roles and responsibilities of the centers as trustees and include articles that state: (i) The Center shall hold the designated germplasm in trust for the benefit of the international community, in particular, developing countries; (ii) neither the Center, or any recipient, will seek IPR protection over the designated germplasm or related information; and (iii) the Center will undertake to make samples of the designated germplasm and related information available directly to users for the purpose of scientific research, plant breeding, or genetic resource conservation without restriction.

Hawtin and Reeves (37) provide an excellent review of the historic aspects and current status of IPR in the CGIAR centers. The authors point out that several important issues must still be resolved, such as the meaning of the phrase "germplasm and related information" and the definition of when a variety is sufficiently different from the original in-trust germplasm from which it was derived (the issue of derived varieties). These are under study, and it is expected that, following the next round of negotiations, some, if not all, of these issues will be clarified. What effects these agreements will have on the use of genetic resources is unclear. The interpretation of related information, in particular, will have implications for IPR options. If the interpretation restricts IPR over materials such as genes obtained from genetic resources held in trust, these important resources will continue to be incorporated in conventional ways, but the application of biotechnology may be more limited.

Molecular Approaches to Utilization of Genetic Resources

There is a multitude of examples illustrating the use of genetic resources to improve modern plant varieties, but one can readily posit that biotechnology could substantially enhance this use. Molecular genetics now allows the routine genetic analysis of nearly any characteristic of interest. As these traits are better understood, the underlying genes can be isolated and used to identify corresponding genes in a wide range of genetic resources.

Molecular genetics has already had a tremendous impact on plant breeding. Progress in the development of new PCR-based marker systems (amplified fragment length polymorphisms and microsatellites) has opened the vast majority of plant genomes to investigation. Linkage maps for many species have been developed and often have been combined with

suitable phenotypic data to identify genomic regions containing the genes coding for specific traits of interest. Many of these regions have been further characterized (e.g., by map-based cloning) and even manipulated (via genetic engineering and marker-assisted selection) in breeding programs (38). Undoubtedly, these efforts will continue and will even be enhanced by newer molecular techniques such as DNA arrays (39) and automation.

DNA markers also have been used extensively to characterize germplasm, a process popularly known as fingerprinting, to evaluate the genetic relationships among accessions (genetic diversity) and provide important information in the areas of ecology, population genetics, and evolution. Within wheat, several studies have reported the application of molecular markers within Asiatic wheat landraces (40). Molecular marker technology has advanced our understanding of genetic resources more than any other type of genetic data.

A major hurdle, however, must be overcome soon: how to store, access, and analyze the vast amounts of data that will be produced by using molecular markers. Databases, such as the International Crop Information System, are under development to store pedigree and performance information for most of the crop species within the CGIAR. Efforts are also underway to expand the capability of the system to include molecular genetic and diversity information. This data will allow scientists to more exactly determine "relatedness" between accessions and even trace specific genomic segments through pedigrees. The potential uses of this information capability for gene identification and verification are enormous and point to the importance of this area. Fortunately, computing hardware and software systems are keeping pace with advances in molecular technology so that appropriately large-scale and real-time applications should be feasible. Bioinformation has been called the next revolution in the world; it is certainly of major import to our utilization of genetic resources.

Genetic Resources: What Are the Potential Impacts?

Agriculture before the 18th century completely depended on landraces for new varieties. During the industrial revolution, the entire nature and practice of agriculture was transformed forever. The discovery of genetics by Mendel in the mid-19th century and the subsequent work of other plant geneticists provided the knowledge base that made dramatic increases in agricultural productivity possible. Undeniably, these discoveries have led to vast improvements in agriculture, but they also have led to a decline in the genetic diversity of the crops in many farmers' fields. Landraces and traditional varieties have been replaced by less diverse modern cultivars and hybrids.

What lies ahead? A tremendous challenge now awaits us—an increased demand for food production spurred on by an increasing world population, a decreasing natural resources base, and declining investments in agricultural research. How will this challenge be met?

Genetic resources will be fundamental to our efforts to improve agricultural productivity. These resources, fortunately stored in gene banks around the world, evolved an assortment of alleles needed for resistance and tolerance to the diseases, pests, and harsh environments found in their natural habitats. Consumer characteristics enter the picture when one considers that farmers over the years have selected their preferred varieties based on yield, color, texture, and taste. Many of these combinations cannot be easily duplicated artificially, even with the help of modern molecular techniques. What should be alarming is the fact that many of these valuable genetic resources are essentially "sitting on the shelf" in what have been dismissively termed "gene morgues." The conservation of a resource only becomes important if the resource has or

acquires recognized value. This clearly requires that the resources be evaluated in a search for critical genetic material.

Why are many researchers reluctant to include genetic resources in their programs? A major reason is the difficulty in evaluating materials with widely differing phenotypes such as flowering dates, heights, and growth morphologies. These differences make accurate assessments and comparisons difficult, if not impossible. Even if useful characteristics can be identified, the difficulty of transferring the characteristics to a cultivated species is often considerable, requiring embryo rescue and cytological expertise. Time is also a major factor; complete transfer can take several years, although the time is often nearly equal to that required by crossing programs using conventional approaches. In addition, because the transfer is usually based on phenotypic selection at each stage, more than just the desired gene is transferred, a phenomenon called "linkage drag." The additional gene or genes often result in inferior phenotypes, making the transfer of little value.

Given these difficulties, the incorporation of genetic resources into cereal improvement has more often been extremely limited and somewhat serendipitous, rather than directed. For genetic resources to be a major factor in plant improvement, new methods must be directed to their analysis and transfer into improved varieties. Fortunately, some promising new approaches are becoming available. Physiological measures of various plant parameters are becoming more exact, rapid, and applicable to large populations. Such advances should allow the more accurate determination of new sources of useful characteristics.

Hopefully, biotechnology will soon overcome the constraints related to the actual transfer of desired genes into their respective hosts. Molecular genetics can provide higher resolution of the genome of any species, allowing precise gene identification before attempted transfers. The subsequent use of the associated markers then provides an indirect, but highly heritable, selectable marker for the trait. It has been proposed that marker-assisted selection could halve the time required to introgress a specific gene segment, with less linkage drag than conventional backcross approaches (41).

An example of this approach is the recent work of Tanksley and McCouch (42) who demonstrated the importance of wild species of tomato that contributed alleles that improved agronomically valuable traits in a cultivated tomato. This contribution comes despite the fact that, phenotypically, the wild species was extremely poor for the trait of interest. It is time that we review the vast array of resources available in the world with fresh eyes. Molecular dissection is much more powerful for determining the usefulness of a species than casual analysis at the morphological or physiological level. Useful alleles exist in both the related and unrelated species of all crop plants. Scientists must strive to identify these alleles and incorporate them into modern varieties.

Speculation on potential impacts in any area of science is difficult; projecting the use of genetic resources in meeting world food requirements is not any different. Major impacts to date have been principally in the areas of biotic and abiotic stress resistances and tolerances. Agronomic crops will continue to be attacked by diverse pests and pathogens. Crops are being grown on more marginal lands and in harsher and ever-changing environments. Screening programs aimed at identifying new sources of resistance and tolerance should include a wide range of genetic resources, including related and unrelated species.

A variety's yield can be considered the final response of a plant's genome to the environment in which it is grown. In this manner, the addition of enhanced stress resistances leads to improved yields. For many developing countries, even slight improvements in stress tolerances would significantly increase yields. Given the shortcomings in policy, infrastructure, and even civil stability in some developing countries, having the

farmer (often the net consumer) produce additional food in his or her own fields may be the surest and quickest way to increase food security in these countries

Can genetic resources contribute to maintaining the rate of yield increase for the major crop species (or even increase it) without requiring significantly higher inputs (human and financial)? Molecular genetic studies indicate that self-pollinating species generally have lower levels of molecular diversity (as measured by the level of molecular polymorphism). Controversy still exists as to the exact relationship between molecular diversity and yield potential, although studies with maize indicate that at least among related materials, molecular diversity is positively and significantly correlated with yield (43, 44). Based on these studies, measures of molecular diversity could be used to identify new germplasm sources that, when crossed with existing varieties, would result in enhanced yields. Work at CIMMYT using synthetic wheat clearly indicates that this strategy is extremely promising.

The array of resources at our disposal, together with new biotechnology techniques, provides us with a healthy measure of optimism for meeting the world's future food requirements. One technique or resource alone will not suffice; rather, the effective and complementary use of all of our technological tools and materials will be required to meet this enormous challenge. We should not, however, let our growing capabilities lull us into complacency. We cannot afford to wait on this issue—we must move quickly and effectively. The world must commit itself now to feeding its future generations to ensure that, indeed, there is enough time for us to produce plants that can provide food for all humankind.

1. Ehrlich, P. R. (1975) *The Population Bomb* (Ameron, Mattituck NY).
2. James, C. (1997) *ISAAA Briefs No. 4*. (International Service for the Acquisition of Agro-biotech Applications, Ithaca, NY), pp. 31.
3. Evans, L. T. (1998) *Feeding the 10 Billion: Plants and Population Growth* (Cambridge Univ. Press, London).
4. Langridge, P. & Chalmers, K. (1998) in *Proceedings of the 9th International Wheat Genetics Symposium, Saskatoon, Saskatchewan, Canada*, ed. Slinkard, A. E. (Univ. of Saskatchewan Press, Saskatoon, Canada), Vol. 1, pp. 107–117.
5. Chapman, C. G. D. (1986) *Plant Genet. Resources Newslett.* **65**, 2–5.
6. Smale, M., Aquino, P., Crossa, J., del Toro, E., Dubin, J., Fischer, T., Fox, P., Khairallah, M., Mujeeb-Kazi, A., Nightingale, K. J., *et al.* (1996) *Understanding Global Trends in the Use of Wheat Diversity and International Flows of Wheat Genetic Resources: Economics Working Paper 96–02* (CIMMYT, Mexico City).
7. Kihara, H. (1983) in *Proceedings of the 6th International Wheat Genetic Symposium*, ed. Sakamoto, S. (Plant Germplasm Institute, University of Kyoto, Kyoto, Japan).
8. Krull, C. F. & Borlaug, N. E. (1970) in *Genetic Resources in Plants: Their Exploration and Conservation*, eds. Frankel, O. H. & Bennett, E. (Blackwell Scientific, Oxford).
9. Borlaug, N. E. (1988) *J. R. Swedish Acad. Agric. Forestry* **21**, Suppl., 15–55.
10. Gale, M. D. & Yousefian, S. (1986) in *Progress in Plant Breeding*, ed. Russell, G. E. (Butterworth, London).
11. McIntosh, R. A., Hart, G. E., Devos, K. M., Gale, M. D. & Rogers, W. J. (1998) in *Proceedings of the 9th International Wheat Genetics Symposium Saskatoon, Saskatchewan, Canada*, ed. Slinkard, A. E. (Univ. of Saskatchewan Press, Saskatoon, Canada), Vol. 5, p. 236.
12. System-wide Genetic Resources Program (1996) *Report of the Internally Commissioned External Review of the CGIAR Genebank Operations* (System-wide Genetic Resources Group, Rome).
13. Dyck, P. L. & Samborski, D. J. (1982) *Can. J. Plant Pathol.* **7**, 351–354.
14. McFadden, E. S. (1930) *J. Am. Soc. Agron.* **22**, 1020–1031.
15. Johnston, S. J., Sharp, P. J., McIntosh, R. A., Guillén-Andrade, H., Singh, R. P. & Khairallah, M. (1998) *Proceedings of the 9th International Wheat Genetics Symposium, Saskatoon, Saskatchewan*

- wan, Canada, ed. Slinkard, A. E. (Univ. of Saskatchewan Press, Saskatoon, Canada), Vol. 1, pp. 3, 117–119.
16. Villareal, R. L., Rajaram, S., Mujeeb-Kazi, A. & Del Toro, E. (1991) *Plant Breeding* **106**, 77–81.
 17. Skovmand, B., Villareal, R., van Ginkel, M., Rajaram, S. & Ortiz-Ferrera, G. (1997) *Semi-Dwarf Bread Wheats: Names, Pedigrees and Origins* (CIMMYT, Mexico City).
 18. Mujeeb-Kazi, A. & Hettel, G. P. (1995) *Utilizing Wild Grass Biodiversity in Wheat Improvement: 15 Years of Wide Cross Research at CIMMYT: CIMMYT Research Report No. 2* (CIMMYT, Mexico City).
 19. Ayad, G., Toll, J. & Esquinas-Alcázat, J. T. (1980) *Directory of Germplasm Collections: III. Cereals. 2. Maize* (Int. Board for Plant Genetic Resources, Rome).
 20. Goodman, M. M. (1983) *Report of the 1983 Plant Breeding Research Forum* (Pioneer Hi-Bred Int., Ames, Iowa), pp. 195–249.
 21. Pollak, L. M. (1993) *Trop. Agric. (Trinidad)* **70**, 8–12.
 22. Goodman, M. M. (1990) *J. Hered.* **81**, 11–16.
 23. Walsh, J. (1981) *Science* **214**, 161–164.
 24. Wilkes, G. (1989) in *Biotic Diversity and Germplasm Preservation: Global Imperatives*, eds. Knutson, L. & Stoner, A. K. (Kluwer, Dordrecht, The Netherlands), pp. 13–41.
 25. Brown, W. L. (1975) *Annu. Corn Sorghum Res. Conf. Proc.* **30**, 81–89.
 26. Geadelmann, J. L. (1984) *Annu. Corn Sorghum Res. Conf. Proc.* **39**, 98–100.
 27. Hameed, A., Pollak, L. M. & Hinz, P. N. (1994) *Crop. Sci.* **34**, 265–269.
 28. Campbell, M. R., White, P. J. & Pollak, L. M. (1995) *Cereal Chem.* **72**, 389–392.
 29. Dunlap, F., White, P. J. & Pollak, L. M. (1995) *J. Am. Oil Chem. Soc.* **72**, 989–993.
 30. Ng, K.-Y., Pollak, L. M., Duvick, S. A. & White, P. J. (1997) *Cereal Chem.* **74**, 836–841.
 31. Galinat, W. C. (1988) in *Corn and Corn Improvement*, eds. Sprague, G. F. & Dudley, J. W. (Am. Soc. Agron., Madison, WI), pp. 1–31.
 32. Doebley, J. (1990) *Econ. Bot.* **44**, 6–27.
 33. Doebley, J. (1990) *Maydica* **35**, 143–150.
 34. Cohen, J. I. & Galinat, W. C. (1984) *Crop Sci.* **24**, 1011–1015.
 35. Hooker, A. L. & Perkins, J. M. (1980) *Proceedings of the 35th Annual Corn and Sorghum International Research Conference*, (Am. Seed Trade Assoc., Washington, DC), pp. 68–87.
 36. Savidan, Y. & Berthaud, J. (1994) in *Biotechnology in Agriculture and Forestry*, ed. Bajaj, Y. P. S. (Springer, Berlin), Vol. 25, pp. 69–83.
 37. Hawtin, G. & Reeves, T. (1998) *Intellectual Property Rights III: Global Genetic Resources: Access and Property Rights* (Am. Soc. Agron., Madison, WI), pp. 41–58.
 38. Ribaut, J.-M. & Hoisington, D. (1998) *Trends Plant Sci.* **3**, 236–239.
 39. Shalon, D., Smith, S. J. & Brown, P. O. (1996) *Genome Methods* **6**, 639–645.
 40. Ward, R. W., Yang, Z. L., Kim, H. S. & Yen, C. (1998) *Theor. Appl. Genet.* **96**, 312–318.
 41. Tanksley, S. D., Young, N. D., Paterson, A. H. & Bonierbale, M. W. (1989) *Biotechnology* **7**, 257–264.
 42. Tanksley, S. D. & McCouch, S. R. (1997) *Science* **277**, 1063–1066.
 43. Melchinger, A. E., Lee, M., Lamkey, K. R., Hallauer, A. R. & Woodman, W. L. (1990) *Theor. Appl. Genet.* **80**, 488–496.
 44. Bernardo, R. (1994) *Crop Sci.* **34**, 20–25.