Plant Genetic Resources Conservation and Utilization: The Accomplishments and Future of a Societal Insurance Policy

Paul Gepts*

ABSTRACT

Concerns about the genetic erosion of crop genetic resources (CGR) were first articulated by scientists in the mid-20th century and have since become an important part of national policies and international treaties. The C-8 (Plant Genetic Resources) section of the Crop Science Society of America (CSSA) was created in 1990 in response to these concerns. Over the last 50 yr, both ex situ and in situ conservation have been set up to maintain threatened CGR. During this period, a set of tools (core collections, molecular markers, and geographic information systems) has been adopted to facilitate conservation and utilization by breeders. Current and future trends include characterization of the genotypic basis of phenotypic variation and the evolutionary, ecological, and human factors that have shaped CGR. The intellectual property regime to which CGR are subjected since 1980 has limited the exchange of germplasm. It remains to be seen if these regimes will evolve so as to achieve basic goals of conservation of genetic diversity and traditional knowledge associated with diversity, while at the same time reward breeders and farmers. Funding of biodiversity conservation remains a critical point. Finally, broadening the conservation circle to establish closer collaborations with grassroots conservation movements and community seed banks is necessary to better conserve the broad range of CGR and as an essential starting point for participatory breeding efforts.

T HE C-8 SECTION is the youngest section in the CSSA. The first C-8 articles in Crop Science appeared in Volume 31 of the 1991 publications. The current membership of the section includes some 82 members (first choice). An additional 280 members list C-8 as a second choice. The section plays an active role in the Annual Meeting and the Society by organizing symposia and workshops, either individually or jointly with other sections, and by its involvement in the Meyer and Sperling awards. On an annual basis it also recognizes the best C-8 papers published in Crop Science. The following individuals (in alphabetical order) were involved in the creation of the C-8 section: Don Duvick, Steve Eberhart, Jerry Nelson, Cal Qualset, and Henry Shands.

The inception of the C-8 section was one of the outcomes of a growing concern about the fate of genetic diversity available for plant breeding. As the raw material of future elite cultivars and an indicator of sustainability of agricultural production, the status of genetic diversity is of utmost concern for agricultural production, specifically, and for societies, in general. World food demand is expected to double or triple by 2050. This increase will result from a rise in world population from 6 billion to 8 to 10 billion people as well as an increase in per capita consumption (Green et al., 2005; United Nations, 2004). Currently, some 854 million people (or 14% of world population) are currently chronically or acutely malnourished, particularly in Africa (more than 30%). More than two billion people suffer from micronutrient deficiencies ("hidden hunger"). Among the many causes of hunger is low agricultural productivity, especially in tropical Africa and remote parts of Latin America and Asia. Malnutrition also plays a role in resistance to diseases. For example, 60% of malaria deaths are due to malnutrition (Sánchez and Swaminathan, 2005). Good nutrition is cited as a factor to combat AIDS (South Africa Department of Health, 2001). Reducing hunger is an explicit target of both the World Food Summit and the Millennium Development Goals. It is also an essential condition for achieving other development goals (FAO, 2005).

From 1961–1999, global food production has managed to outstrip population growth. This has been achieved by an increase of cultivated land (12% in global crop land area, 10% in the area of permanent pastures), of output per unit area (106% in food crop yield per unit area), and, above all, by an increase in inputs (increase of 97% in irrigated lands, 638% in nitrogen fertilizer, 203% in phosphorus fertilizer, and 854% in pesticides) (Green et al., 2005). In the context of increased agriculture production, agriculture has become the single most important threat to biodiversity as suggested by the analysis of Green et al. (2005) on the causes of bird threats or extinctions. Two solutions have been proposed to address the threat posed by agriculture: wildlife-friendly farming (which increases the presence of wildlife on farmland, possibly at the cost of agricultural yields) and land sparing (which sets aside extra land for wildlife conservation by increasing agricultural yields) (Green et al., 2005; Balmford et al., 2005).

The expression *crop genetic resources* usually refers to the sum total of genes, gene combinations, or genotypes available for the genetic improvement of crop plants. Following the proposal of Harlan and de Wet (1971), plant genetic resources were classified in three gene pools that reflected the increasing difficulty in performing sexual crosses and obtaining viable and fertile progenies. Gene Pool I includes the crop species itself and its wild progenitor. Crosses within Gene Pool I can generally be made easily and the resulting progeny is viable and fertile. This gene pool corresponds to the biological species concept. Gene pools II and III include other species that are related, yet different from the crop species of interest. Crosses between Gene Pool I and II are

Paul Gepts, Dep. of Plant Sci./MS1, Section of Crop and Ecosystem Sci., Univ. of California, 1 Shields Ave., Davis, CA 95616-8780. Received 20 Mar. 2006. *Corresponding author (plgepts@ucdavis.edu).

Abbreviations: CGR, crop genetic resources; CSSA, Crop Science Society of America.

possible but are usually more difficult to achieve. The progeny shows reduced viability and fertility. Finally, crosses between Gene Pools I and III are the most difficult. Special techniques such as tissue culture have to be used to obtain a progeny from these crosses. The progeny often show a severe reduction in viability and fertility.

The operational definition of Harlan and de Wet (1971) has been very useful because it reflects the realities of the breeding process, particularly the introduction of new genetic diversity into the populations of a breeding program by sexual hybridizations. Nevertheless, one could argue that this definition may need to be expanded to a Gene Pool IV based on advances in scientific technology and increased awareness of the benefits of biodiversity in general (Gepts, 2000). Comparative genomics now plays an important role in the discovery of genetic diversity by facilitating the identification of genes that are responsible for important agronomic traits through the determination of macrocolinearity (by comparative mapping) and microcolinearity (sequence comparison). Thus, comparative genomics can lead to the identification of candidate genes within the species of interest or other species. In turn, this information can lead to a better understanding of the genetic basis of the trait of interest and a more direct selection for this trait.

The availability of plant transformation techniques, by either *Agrobacterium* (Gelvin, 2000) or biolistics (Birch, 1997), has extended the reach of plant breeding beyond the limitations imposed by sexual cross-compatibility. With plant transformation, all organisms become a potential source of genetic diversity, including prokaryotes, fungi, and animals. However, although the potential benefits are frequently touted, the specific number of traits that have actually been commercialized remains very limited for a variety of reasons, including the current lack of knowledge about actual genes (and their interactions) underlying major agronomic traits, the inability to accelerate the breeding process, and the limited number of genes that can be dealt with per transformation event (Bingham, 1983; Gepts, 2002; Goodman, 2004). Thus, although the main contribution of genetic engineering to plant breeding could be a broadening of the gene pool, it has had so far a limited role in this regard.

For the foreseeable future, the main sources of genetic diversity for plant breeding, therefore, remain the three gene pools as defined by Harlan and de Wet (1971). Agricultural production increases are attributed generally in equal proportions to genetic improvement (development of elite cultivars) and improved cultural practices (e.g., fertilization, pesticide application, planting time and density, and irrigation) (Fehr, 1984). Genetic diversity is the raw material that spurs genetic improvement, both to increase yield potential per se (i.e., production per unit area) and to decrease reliance on production inputs. Crop genetic diversity provides an assurance of future genetic progress and an insurance against unforeseen threats to agricultural production such as disease epidemics or climate changes. Thus, the fate of genetic diversity in these gene pools is of utmost importance if plant breeding will continue to address pressing needs of society such as increased yield, genetic resistance to diseases and pests, improved nutritional and processing quality of crop products, and reduction in environmental effects.

In the remainder of this article, I will successively describe the major accomplishments in the area of CGR conservation. I will then also describe several current and future trends in this area. To limit the scope of this article, related aspects of agrobiodiversity, such as microbial (soil) biodiversity, beneficial insect diversity, and other aspects of floral or faunal biodiversity that are important to maintain sustainability, stability, and productivity of agricultural production systems, will not be dealt with here. The reader is referred to Collins and Hawtin (1999) for further details.

ACCOMPLISHMENTS IN THE FIELD OF PLANT GENETIC RESOURCES STUDIES

Among the accomplishments of the field of plant genetic resources, one can list the following. First, there has been an increasing awareness and documentation of the benefits of biodiversity and the risks associated with genetic erosion. Second, in response to the first point, different methods have been developed to conserve CGR and make them available to breeders. Third, as a corollary to the second point, methods of analysis have been developed to characterize genetic diversity and make its management more efficient. These three achievements are discussed in the following sections.

Increased Awareness and Documentation

For most of the 10000 yr of the agricultural era of human evolution (Smith, 1995; Harris, 1996; Damania et al., 1998; Piperno and Pearsall, 1998), a diversification of the plants and crops used by humans has taken place. It would be very difficult to imagine our lives and surroundings before this diversification. While hunter-gatherers and early farmers relied on local plants, migration of farming societies from centers of domestication to other regions of the world expanded both the range of plants at their disposal and the adaptation of their crops. The existence of agriculture was a condition for the development of early civilizations as agriculture, on average, produced a surplus of food, which allowed labor and craft specializations that led to the appearance of increasingly complex and hierarchical societies. It is therefore not surprising that many of these early civilizations arose near centers of crop and animal domestications, even though the civilizations were not involved in domestication of their crops.

An example of such civilizations is Ancient Egypt (3000–300 Before the Current Era, BCE), which relied on crops such as durum wheat (*Triticum turgidum* L.) and olive (*Olea europaea* L.) domesticated in southwest Asia. The earliest botanical expedition dates from Ancient Egypt. It is believed that around 1500 BCE Queen Hatshepsut dispatched five ships to gather valuable plants, animals and precious goods from the Land of Punt, including the resin from *Boswellia* sp. (frankincense) and *Commiphora* sp. (myrrh). Inscriptions on the

wall of the temple of Karnak celebrate the fact that at least thirty-one of the transplants survived and were established in the temple grounds (www.plantexplorers. com/explorers/history/index.html; verified 6 June 2006).

Acquisition of new plant resources continued actively over the next millennia. The voyages of Christopher Columbus were motivated by the desire to find an alternative route to the spice-producing regions of Asia. The arrival of Columbus in the Americas led to an exchange of Old and New World crops (called the Columbian Exchange by Crosby, 1972), which led to amazing changes in agriculture and human diet on a worldwide scale. Whereas Columbus did not achieve his goal of finding a more direct passage to eastern Asia and, in the process, amass countless riches, the crops and other economic plants from the Americas provided a trove of wealth. Furthermore, colonial powers sought to increase their economic opportunities by securing additional plant resources, such as nutmeg (*Myristica fragrans* Houtt.), rubber [*Hevea brasiliensis* (Willd. Ex A. Juss.) Mull. Arg.], and coffee (*Coffea Arabica* L. or *Coffea canephora* Pierre ex A. Froehner) (Milton, 1999; Dalby, 2000; Hobhouse, 1999, 2003; Musgrave and Musgrave, 2000). During the first century of the Columbian Exchange, less than 100 new plants were introduced into England. In the 17th century, some 1000 plants and in the 18th century some 9000 were introduced (Lemmon, 1968). Plant collectors roamed the world to collect new plants and deposit them in botanical gardens and herbaria (Short, 2003). Some of these plants would contribute to the development of the pharmaceutical, dye, and horticultural industries in Europe. The U.S. also became very active in the acquisition of plant resources, which eventually became part of the National Plant Germplasm System (www.ars-grin.gov/npgs/; verified 6 June 2006). Exploration and introduction were instrumental in establishing a diverse agriculture in this country (e.g., Sumner, 2004). The third president of the U.S., Thomas Jefferson, famously stated that "The greatest service which can be given any country is to add a useful plant to its culture."

This increase in overall phenotypic diversity came to an end in the 20th century, through an overall reduction in intra-specific diversity but also through a concentration of human activities on a more limited number of crop plants. Historically, humans utilized more than 7000 plant species to meet their basic food needs. Currently, due to the limitations of modern large-scale, mechanized farming, only 150 plant species are under cultivation, and 90% of the per caput food plant supplies of all nation states are provided by only about 100 crops (FAO, 1997). This paper focuses primarily on the intra-specific genetic diversity to limit the overall scope of the review. As early as 1936, Harlan and Martini raised the issue of genetic erosion in a USDA report devoted to barley breeding (Harlan and Martini, 1936): "In the great laboratory of Asia, Europe, and Africa, unguided barley breeding has been going on for thousands of years. Types without number have arisen over an enormous area… The progenies of these fields with all their surviving variations constitute the world's priceless reservoir of germ plasm… Unfortunately, from the breed-

er's standpoint, it is now being imperiled…. Trade and commerce of a sort have always existed. They have existed, however, on a scale so small that agriculture has been little affected. Modern communication is a real threat. A hundred years ago, when the grain crop of north Africa failed, the natives starved. Today, in years of shortage, the French supply their dependent populations with seed from California. Arab farmers in Mariout sometimes sell short to European buyers and import seed grains from Palestine. In a similar way changes are slowly taking place in more remote places. When new barleys replace those grown by the farmers of Ethiopia or Tibet, the world will have lost something irreplaceable. When that day comes our collections, constituting as they do but a small fraction of the world's barleys, will assume an importance now hard to visualize…"

Several decades later, scientists such as Harlan (1972), Frankel and Bennett (1970), Hawkes (1971), and Wilkes (1977), expressed concern about the disappearance of genetic diversity, particularly the destruction of the genetic trove found in landraces of crops and their substitution by a genetically narrow subset of improved cultivars. In 1970, a disease epidemic struck the maize crop in the U.S. This epidemic occurred because of the genetic uniformity of the crop, which resulted from the widespread reliance on cytoplasmic male sterility (CMS-T) for hybrid seed production. Inadvertently, this CMS-T also conferred susceptibility to a rare strain of southern corn leaf blight caused by *Helminthosporium maydis* (Nisikado & Miyake) (now called *Cochliobolus heterostrophus* [Drechs.] Drechs). This epidemic was by no means the first one with negative consequences [e.g., *Phytophtora* leaf blight epidemic in Western Europe, notably Ireland in the 1840s; coffee rust epidemic in Ceylon (now Sri Lanka) in the 1860s; for other crop diseases of concern, see Table 1 of Qualset and Shands, 2005], but it highlighted to a broad cross-section of the public the need to maintain genetic diversity in domesticated populations to counteract the increased risk of epidemics (and increasingly volatile changes in weather and climate) (Qualset and Shands, 2005). It also led to an influential National Research Council (1972) report on the status of genetic diversity in U.S. crops.

To understand this reversal in trends affecting phenotypic diversity, it is necessary to remember the basic factors that have influenced the evolution of genetic diversity in crops during the three major phases of crop evolution: (i) domestication; (ii) cultivation post-domestication in centers of origin and dispersal to and cultivation in other regions; and (iii) plant breeding starting in the 20th century. Since the beginnings of agriculture, agriculture had been characterized by an overall increase in phenotypic diversity of crop cultivars. This increase reflected the broadening of the environmental conditions and human cultures under which crops had been grown since plants were first domesticated. At any point in time, the level and distribution of genetic diversity in a crop species depends on three types of variables: (i) the biological characteristics of the species, including its reproductive system, ploidy level, and further genetic characteristics; (ii) the biotic and

abiotic environments; and (iii) the human environment (Gepts, 2004a). It is the existence of the third set of factors, namely the human environment, which sets apart crop evolution from natural evolution.

As crops were dispersed from their center of domestication to other regions or continents, they were subjected to selection for adaptedness (Darwin, 1868; Simmonds and Smartt, 1999). The process leading to adaptedness involved both natural and human selection, the former acting in response to environmental (both biotic and abiotic) conditions and the latter in response to decisions made by farmer (and, through the farmer, the consumer). For example, dispersal from centers of domestication to other regions of the world usually has involved changes in daylength leading to selection for adaptedness to a different photoperiod requirement in several crops such as rice and common bean. They also included selection for disease resistance, temperature adaptation, and growth habit changes. In addition, in these new areas, other cultures developed different preferences or uses for the crop, which, in turn, led to different farmer- or consumer-selected phenotypes, such as plant composition and fruit and seed color, shape, and size (as shown, for example, by catalogs of the 19th and early 20th centuries: Burr 1863; Vilmorin-Andrieux 1885; Hedrick 1931; USDA 1933). The relative importance of natural and human selection has been variable but human selection is likely to have increased to culminate with the introduction of plant breeding in the 20th century.

Plant breeding, with its emphasis on elite × elite crosses in the incessant pursuit of higher performance (Kelly et al., 1998) and close adherence to norms imposed by the market, is a strong force in the reduction in genetic diversity. Furthermore, improved cultivars also lead to a reduction in genetic diversity through displacement of native heirloom or landrace cultivars. This phenomenon has been illustrated particularly with the advent of Green Revolution cultivars; however, it is a more general phenomenon that has impacted many regions in the world, especially in the second half of the 20th century (see more below). Thus, paradoxically, plant breeding has been undermining the very genetic basis on which it rests, leading to an overall phenomenon of de-diversification or genetic erosion. Plant breeders have become aware of this situation and have attempted to rectify this situation by broadening the genetic basis of their cultivar gene pool (Duvick, 1984; Smale et al., 2001; Kelly, 2004). However, it remains that the genetic diversity represented in the elite gene pools is only a small fraction of that present in the entire gene pool of crop plants. Hence, there is an enduring concern about the disappearance of genetic diversity over the long term.

From these initial scientific observations, concerns about genetic diversity of crops and biodiversity in general have reached the general public. Attempts to address these concerns are now being inserted in public policy and international treaties as illustrated by the latest United Nations summit on Sustainable Development in Johannesburg in 2002 (www.un.org/esa/sustdev/index.html; verified 6 June 2006). At this summit, five major areas were identified, two of which have a significant impact on CGR, namely agriculture and biodiversity, in addition to water, energy, and health. Further efforts are necessary to make sure that concerns about genetic erosion get translated into new treaties and legislation.

Phenomenon of Genetic Erosion

Genetic erosion, or the reduction in genetic diversity in crop plants, takes on various shapes depending on one's standpoint, including the reduction in the number of different crop species being grown and the decrease in genetic diversity within crop species. In addition, other organisms both within and outside agroecosystems are increasingly taken into account when an assessment is made of the biodiversity as it relates to agriculture (Collins and Qualset, 1999; Hillel and Rosenzweig, 2005). Over the course of their history, humans have utilized more than 7000 plant species to meet their basic food needs, either by cultivation or gathering. Today, due to the limitations of modern large-scale, mechanized farming, only 150 plant species are under extensive cultivation. The majority of humans live on only 15 plant species, which account for over 90% of human energy needs.

Agriculture, forestry, and human settlements now claim 95% of terrestrial environments, whereas non-developed areas represent only 3.2% (Lacher et al., 1999). Human activities now appropriate one third to one half of global ecosystem production. Crop lands and pastures have become one of the largest biomes on the planet. They encompass some 40% of the land surface, similar to forest. Although world grain harvests have greatly increased in the last 40 yr, this increase has been at the cost of substantial environmental damage (including degradation of water quality due to fertilizer use, salinization of lands due to irrigation, erosion of croplands, and loss of native habitats). Thus, agriculture has traded short-term increases in food production for long-term losses in ecosystem services, including losses in CGR (Foley et al., 2005).

Within crop species, landraces have been displaced by bred cultivars. The rate depends on the crop, the region, and the environment. The causes of genetic erosion are numerous. Although the Green Revolution is widely blamed, this displacement has been part of a broader trend taking place since the beginning of the 20th century. This has affected most, if not all, crops and not just the Green Revolution crops such as rice and wheat. Cabanilla et al. (1999; cited by Day Rubenstein et al., 2005) point out that only 15% of the rice area was planted to landraces (in irrigated lowlands). For wheat, landraces occupy 23% for the durum wheat area, 12% of the winter bread wheat area, and 3% of spring bread wheat area. In contrast, 60% of the maize area is planted to landraces in the developing world. Of the nearly 8000 varieties of apple that grew in the United States at the turn of the century, more than 95% no longer exist. In Mexico, only 20% of the corn types recorded in 1930 can now be found. Only 10% of the 10000 wheat varieties grown in China in 1949 remain in use.

Other causes include changes in agricultural production systems, overgrazing and excessive harvesting, deforestation and land clearance, introduction of new pests and diseases, and policy and international treaties (FAO, 1996). Ultimately, however, most of these causes can be traced back to two primordial reasons, namely (i) the increasing population pressure faced currently by developing countries as part of a demographic transition; and (ii) increased globalization of communications, travel, and trade. This increased globalization leads to a loss of cultural diversity, which ultimately also leads to a reduction in biodiversity (Sutherland, 2003; Maffi, 2001, 2005).

Increasingly, traditional knowledge associated with biodiversity, including crop genetic diversity, is also considered to be a resource (Brush and Stabinsky, 1996; Brush, 2004). Traditional knowledge encompasses the empirical knowledge about genetic resource use practices transmitted by oral tradition in indigenous groups. Just like crop biodiversity, this resource is being threatened by cultural extinction, such as the widespread disappearance of indigenous languages, and other forms of acculturation, regardless of their cause (Benz et al., 2000). There is an apparent contradiction between the desire of governments of developing countries to introduce advanced technologies to improve the quality of life of local and indigenous groups, and the maintenance of traditional knowledge (Foster, 1962; cited by Benz et al., 2000).

DEVELOPMENT OF CONSERVATION METHODS

Ex situ and In situ Conservation

Two main, complementary methods have been developed to conserve CGR. Ex situ (off-site) conservation seeks to maintain genetic resources off site, i.e., in special facilities called gene banks (Plucknett et al., 1987). In 1970, there were less than ten gene banks. Currently, there are approximately 1500 gene banks maintaining 5.5 million samples according to FAO estimates. Eleven international gene banks operate under the aegis of the Consultative Group on International Agricultural Research (CGIAR). These banks maintain primarily genetic resources of basic food crops and forages, but generally no vegetable or forest germplasm. The accessions in CGIAR gene banks are held in-trust for the FAO as a representative of the world community. In addition, there are national and regional banks. Among the former are the U.S. National Plant Germplasm System (National Research Council, 1991; Shands, 1995), the Chinese Institute of Crop Germplasm, the N.I. Vavilov Institute of the Russian Federation, and the National Bureau of Plant Genetic Resources of India. Among the latter, are the Asian Vegetable Research and Development Center in Taiwan and the Center for Tropical Agricultural Research (for further information, see Box 1 in Qualset and Shands, 2005).

In 90% of the cases, genetic resources are conserved as seeds in cold storage. This is the case for species that have *orthodox seeds*, or seeds that can be conserved at low relative humidity (down to 3–7%) and, hence, low temperature, e.g., −20°C (Roberts, 1973; Berjak and Pammenter, 2003). Crops with orthodox seeds include all the major cereals (such as maize, wheat and rice), many legume species, such as bean, chickpea, lentil, and soybean, many vegetables, such as the onion family, the potato family, the cabbages, and the cucurbits. Recalcitrant seeds are those that cannot withstand the desiccation of the seeds without loss of viability. Species with such seeds are generally tropical trees, including avocado (*Persea Americana* Mill.), cacao (*Theobroma cacao* L.), coconut (*Cocos nucifera* L.), and nutmeg (*Myristica fragrans* Houtt.). Together with vegetatively propagated species such as cassava (*Manihot esculenta* Crantz), and banana/plantain (*Musa* spp.), or long-lived crops, these species are conserved as living plants in field gene banks. Germplasm can also be maintained in vitro (in test tubes on plant nutrient medium) such as the cassava, potato, and *Musa* collections at CIAT, CIP, and INIBAP, respectively. More specialized and technically intensive methods are being used or investigated such as cryopreservation (liquid nitrogen: −196°C), artificial seeds, pollen, and DNA (Harding, 2004; Maruyama et al., 1998; FAO, 1997).

The second general category of conservation methods is in situ (on-site) conservation (Collins and Hawtin, 1999). This type of conservation can take place in farmers' fields for domesticated materials or in natural environments for wild relatives of crop plants or wild species. For some species, such as tropical trees, this is the only form of conservation currently possible. Originally, this approach was promoted by environmentalists and conservationists, who directed their efforts primarily toward the conservation of ecosystems and species diversity. In the case of CGR, the emphasis is directed to the maintenance of intraspecific diversity of crop plants. Vavilov (1926) had already pointed out that crop genetic diversity is unequally distributed in the world. It is concentrated in centers of diversity, which are often the centers of crop domestication (Harlan, 1971). While the boundaries of such centers are still being debated, such centers are prime targets for in situ conservation. Several options exist for in situ conservation, including natural or wilderness areas (limited or no human activities), national parks (carefully regulated human activities), and special management areas within agricultural areas to maintain or increase diversity of key species. An example of the latter is the UNESCO Man and the Biosphere program, which oversees more than 250 biosphere reserves, such as the Sierra de Manantlán Biosphere Reserve in Mexico (Collins and Hawtin, 1999). Other examples of in situ conservation projects are provided by FAO (1997). They include projects in Turkey for crop-related wild relatives of cereals, horticultural and ornamental flower crops, medicinal plants and forest trees with support from the Global Environment Facility and in central Asia countries (Turkmenistan, Azerbaijan, and Kyrgyzstan) for the protection of forest genetic resources of wild fruit trees and shrubs.

In a comparison of ex situ and in situ conservation, the purported advantages of ex situ conservation are the capability of storing a large number of accessions (entries) in a collection, the ready access of the germplasm

for characterization, evaluation and distribution, and the secure conservation conditions. In situ conservation, in contrast, is promoted because landraces are an essential component of indigenous cultures, it supposedly allows evolution to proceed, its cost is low, and it is the primary form of conservation for wild crop relatives. The statement that large numbers of accessions can safely be maintained in ex situ collections has to be tempered with the observation that germplasm collections are generally underfunded, the viability of accessions is threatened by lack of timely regeneration, and their utilization is inadequate because of limited characterization and evaluation. The evolutionary potential of in situ conservation is limited by the rapidity and magnitude of anthropogenic impacts on our planet, as outlined earlier. However, farmers can manage their genetic resources not only to maintain high levels of diversity in their fields but also to select for essential traits in their particular environment, often by combining diversity from landraces and cultivars (Brush, 1992, 1995; Birnbaum et al., 2003; Perales et al., 2003b; Zizumbo-Villarreal et al., 2005). Hence, the current approach is to combine both methods of conservation, depending on such factors as reproductive biology, nature of the storage organs and propagules, and availability of human, financial, and institutional capabilities (Bretting and Duvick, 1997). The inclusion of in situ conservation fits in the emphasis currently placed on the long-term sustainability of production systems and protection of the natural resource basis (Collins and Hawtin, 1999). An important element in in situ conservation is information about traditional knowledge accompanying local genetic resources and socio–economic data, which are necessary conditions to successful local conservation programs (Salick et al., 1997; Brookfield et al., 2002).

Core Collections

As defined by Brown (1995), a core collection is a selected and limited set (5–20% of the total collection) of accessions derived from an existing germplasm collection, chosen to represent the genetic spectrum in the whole collection (reserve collection) and including as much as possible of its diversity. Core collections were initially proposed by O. Frankel and A.H.D. Brown in 1984 to address the issue of large germplasm collections (Brown, 1995). The very size of some of these collections represents a daunting challenge for characterization and evaluation. A core collection could constitute an entry way into the larger collection by providing an opportunity to identify phenotypic variants in preliminary analyses of a more modest-sized sample. For example, identifying accessions with phosphorus use efficiency in a particular region, such as Bolivia, West Mexico and South Mexico-West Guatemala in common bean suggests that a more thorough evaluation of this germplasm in other Latin American regions with a similar environment could reveal further sources of tolerance (Beebe et al., 1997; for further examples, see Table 4 in van Hintum et al., 2000).

For further information on the sampling methods to develop core collections, case studies of the develop-

ment of core collections in different crops, and different uses of these collections, the reader is referred to Hodgkin et al. (1995), Johnson and Hodgkin (1999) and van Hintum et al. (2000). In addition to potentially facilitating the identification of useful traits in a collection, core collections can assist in setting priorities among the different traits and accessions and increase the ease of management of whole collections. Concerns about core collections include rendering the reserve collection more vulnerable to loss, lack of representation of rare, endemic alleles, and poor relation to the specific needs of users. To address the latter concern, specialized core collections have been established around a particular trait, region, or type of material (e.g., wild vs. domesticated) (Brown and Spillane, 1999).

Use of Molecular Markers

It is beyond the scope of this article to discuss in depth the different types of biochemical and molecular markers, their advantages and disadvantages, and the statistical methods of analysis. These have been reviewed before (e.g., Hamrick and Godt, 1997; Avise, 2004; Collard et al., 2005; Spooner et al., 2005; Mohammadi and Prasanna, 2003; Schlötterer, 2004; Weising et al., 2005). Molecular marker studies have made significant contributions to our understanding of genetic diversity and relatedness (Gepts, 1993; Doebley 1989, 1992; Sytsma and Hahn, 1997; Spooner et al., 2005). The main benefit of using molecular markers is that they are good indicators of genetic distances among accessions because of their selective neutrality. Thus, molecular markers have been used to identify putative centers of domestication such as in maize (Doebley et al., 1984; Matsuoka et al., 2002), common bean (Gepts, 1988), and einkorn wheat (Heun et al., 1997) by identifying those wild populations that are most closely related to the domesticated gene pool. This approach assumes that the similarity between wild and domesticated accessions is due to progenitor–descendant relationships and not to gene flow, an assumption that has not been verified. Molecular markers have also been used to identify ecogeographic races within the domesticated or wild gene pools of crop species (e.g., Singh et al., 1991; Fiedler et al., 1998; Liviero et al., 2002; Yu et al., 2003).

Furthermore, molecular markers are being used to assist in gene bank management. Molecular markers help direct germplasm explorations toward missing or underrepresented populations such as populations of *Phaseolus vulgaris* (L.) in Ecuador and northern Peru, which are the presumed ancestors of this species based on DNA sequence data of the phaseolin multigene family (Kami et al., 1995). These populations were identified following several rounds of exchange of geographic and field data, on the one hand, and allozyme and phaseolin protein electrophoretic data (Koenig and Gepts, 1989; Koenig et al., 1990; Debouck et al., 1993). Using isozymes, Lamboy et al. (1996) observed that populations from eastern Kazakhstan of *Malus sieversii* (Ledeb.) M. Roem., the progenitor of the domesticated

apple, formed a large panmictic population. To capture the genetic diversity of these populations, a thorough sampling of a few large populations would therefore suffice. Further examples of the use of molecular markers in gene bank management are provided by Spooner et al. (2005). They include assessing the level of redundancy within and between collections, the assembly of core collections, assessment of the genetic integrity of accessions during the course of gene bank operations such as regeneration, and the presence and magnitude of gene flow.

Genomics is providing a substantial source of additional DNA-sequence-based markers, not only in model species and major crop plants, but also in other species without a formal genomics research program. Indeed, regions with sequence similarities, or even identities, can be identified among species with sequence information. In turn, these sequences provide a substrate for PCR amplification in other species for which no sequence information is available. In practice, this procedure is targeted to exons (more conserved sequences) surrounding an intron (less conserved). Such a procedure has been applied successfully in animals (Lyons et al., 1997) and plants (e.g., Zhu et al., 2005; Alo et al., 2006). Such abundance of molecular markers can also be used to conduct association mapping studies to locate genes underlying agronomic traits as an alternative to quantitative trait locus mapping (Gupta et al., 2005). With the availability of large-scale DNA infrastructure and sequencing projects, assessments of allelic DNA diversity have also been initiated, notably in maize (See section on Current and Future Trends). In contrast with previous endeavors (see above), which used selectively neutral sequences, these studies seek to identify sequences that are subject to selection (e.g., display reduced or no variation compared to selectively neutral sequences) (e.g., Yamasaki et al., 2005).

Geographic Information Systems and Geographic Positioning Systems

The 1990s have seen the introduction of geographic information systems (GIS), specifically applied to the genetic resources conservation. A geographic information system is a database management system that can simultaneously handle digital spatial data and attached, non-spatial, attribute data. Spatial or location data are acquired via geographic positioning system devices, which are now quite inexpensive and have become part of the obligatory equipment for field explorations. In addition, an increasing body of geo-referenced data has become available, i.e., data associated with coordinate and altitude information. These georeferenced data include both biological (e.g., landcover, cattle density) and non-biological (e.g., climate, topography, soil, and human activity) data. The non-spatial attributes are any biological, including genetic, data associated with the individual accessions collected. Thus, GIS is a tool to visualize and analyze spatial patterns in genetic data in relation to ecological data; it is also a hypothesis-generating tool to investigate processes that shape genomes. Furthermore, information generated by GIS analysis can help in conserving and using genetic diversity as effectively and efficiently as possible (Greene and Guarino, 1999; Jarvis et al., 2005a).

Examples of GIS applications include (i) study of isolation by distance and its effect on genetic structure of gene pools by comparing genetic and geographic distances; (ii) linking diversity and environmental heterogeneity; (iii) determination of species distribution and areas of greatest diversity (e.g., wild *Arachis* spp.: Ferguson et al., 2005; other examples: Steiner, 1999); (iv) identification of germplasm with specific adaptation; (v) predicting the distribution of species of interest and identifying new areas for germplasm exploration [e.g., *Capsicum flexuosum* (Sendtn.) in Paraguay (Jarvis et al., 2005b); wild *Vigna* spp. in Africa (Maxted et al., 2004)]; (vi) planning germplasm exploration trips, in addition to identifying areas likely to contain germplasm of interest: identification of highly diverse areas, ecologically dissimilar areas, under-conserved areas, areas containing threatened species, timing of the exploration, and additions to passport data (Guarino et al., 1999); (vii) designing zoning plans for in situ conservation integrated with socio-economic and indigenous knowledge data (Guarino et al., 1999); and (viii) establishment of core collections (e.g., based, in part, on environmental variables such as length of the growing region, photoperiod, soil type, and moisture regime: Tohme et al., 1995).

Some GIS tools, such as DIVA-GIS (www.diva-gis.org/; verified 6 June 2006) and WORLDMAP (www.nhm.ac.uk/research-curation/projects/worldmap/worldmap/demo2.htm; verified 6 June 2006) are freely available. Floramap (www.floramap-ciat.org/; verified 6 June 2006) is available for a modest contribution. In the future these tools will no doubt be used more intensively than up to now.

CURRENT AND FUTURE TRENDS
The Molecular, Evolutionary, and Ecological Basis of Crop Biodiversity

Genetic resources conservation is often perceived as a descriptive science. Characterization and evaluation of genetic resources, whether they are maintained in situ or ex situ, is an essential part of the conservation process and promotes the utilization of these genetic resources. Curators know what traits are included or not in their collection; they also need this information to preserve the identity of their accessions. Users can use accessions from a gene bank directly if they know the specific traits carried by these accessions.

I contend that genetic resources conservation needs to move beyond its descriptive nature and actively seek to understand the distribution of genetic diversity within and among accessions, as well as the genotypic basis of phenotypes of economic importance. This then becomes the holy grail of the science of genetic resources movement. Identifying the genotypic basis of economically important traits and the evolutionary, ecological, and human interaction causes that have driven the appearance of these traits, will facilitate both the conservation and the utilization of genetic resources. Ideally, accessions should be

characterized by the genes they contain rather than the phenotypes they exhibit. This information will be important in determining which accessions will be maintained and utilized. At first sight, this may be a tall order, particularly for genetically complex, quantitatively-inherited traits. Different gene actions, epistatic interactions, epigenetic effects, and genotype × environment interactions all conspire to make a genetic analysis more difficult. However, to a certain extent, this approach has already been initiated with major genes. It is now possible to flag accessions with major genes they carry, such as disease or pest resistance genes, male sterility factors, or growth habit genes. This information allows curators to make sure that the different genes are represented in the collection. It also allows breeders to pyramid disease resistance genes to obtain a more broadly based resistance.

To further illustrate this point, one can ask why certain accessions are resistant to a pathogen and others not. This is a common observation in evaluation nurseries of germplasm collections. The answers will obviously be different depending on one's viewpoint but they will all point to an enhanced genetic knowledge of the accessions available.

Molecular and Genomic Basis of Phenotypic Variation

A molecular or cellular biologist would argue that the resistance is due to the presence or absence of genes involved in the recognition of the pathogen and the ensuing cascade of signal transduction (Beckers and Spoel, 2006; Jalali et al., 2006). Given that there are many resistance genes distributed in the genome, either individually or in clusters (Young, 2000; Wisser et al., 2006), different genes may control resistance by different mechanisms or have different specificities. Information about the action of individual genes becomes important to maintain a diverse germplasm collection, but also to pyramid genes with different resistance mechanisms to increase the possibility of a stable resistance. Genomics is becoming increasingly important to locate and isolate genes underlying not only disease resistance genes but also other genes. Yamasaki et al. (2005) identified putative candidate genes that resulted from selection either during domestication or breeding subsequent to domestication by screening for genes with low or no diversity in landraces or inbred lines. While the actual function of these genes remains to be identified, the approach of Yamasaki et al. (2005) does not require prior knowledge of the morphological or biochemical function of the gene and, therefore, allows casting a wider net in the identification of genes involved in specific function. Because the Yamasaki et al. (2005) approach relies on the lack of diversity as a criterion to identify candidate genes, it may also miss certain genes, which, while polymorphic in the domesticated gene pool, fulfill nevertheless an important function.

Evolutionary Basis of Phenotypic Variation

To return to my question about the diversity for disease resistance in a germplasm sample, an evolutionary biologist will consider the phenomenon of host-pathogen co-

evolution and its potential outcomes, such as local adaptation, which depends on the geographic scale of gene flow, in addition to mutation rate, generation time, and population size (Gandon and Michalakis, 2002; Dybdahl and Storfer, 2003; Nuismer and Kirkpatrick, 2003; Thrall and Burdon, 2003) and an *arms race*, in which the metabolic cost of virulence and resistance play a role in determining the prevalence of virulence and resistance (Bergelson et al., 2001; Kniskern and Rausher, 2001). Which of these phenomena are at play on a large geographic scale in common bean remains to be determined. However, in this species the geographic divergence between an Andean and a Mesoamerican gene pool is matched by geographically comparable gene pools in *Rhizobium* and several pathogens including those causing angular leafspot, anthracnose, rust, and common bacterial blight pathogens (Guzmán et al., 1995; Kelly and Vallejo, 2004; Mkandawire et al., 2004; Aguilar et al., 2004).

Ecological Basis of Phenotypic Variation

In response to the same question, an ecologist would consider the varied outcomes—in natural and agricultural ecosystems—of the three-way interaction between host, pathogen, and environment. These outcomes include the magnitude of a disease epidemic (Parker and Gilbert, 2004), the nature of adaptation to pathogens, and the speed at which (new) hosts and pathogens appear and evolve (Harvell, 2004). The integration of genetics and community and landscape ecology into community genetics (Neuhauser et al., 2003) and landscape genetics (Manel et al., 2003), respectively, also provides opportunities for a better understanding of the patterns of genetic diversity in host plant and pathogen.

Other examples of the importance of an ecological approach to our understanding of crop biodiversity involve the role of gene flow among populations, particularly between wild and domesticated types. In addition to its role in generating troublesome weeds that are difficult to control, gene flow can also lead to either crop diversification (Harlan 1965, 1995; Jarvis and Hodgkin, 1999) or genetic assimilation (Papa et al., 2005), or a combination of both at different times and in different locations. The specific results are likely to differ from crop to crop and are difficult to generalize. Jarvis and Hodgkin (1999) list several conditions affecting hybridization, including spatial and temporal overlap in flowering times, reproductive systems, fitness of the hybrids, and human selection and management. In pearl millet [*Pennisetum glaucum* (L.) R. Br.], for example, Miura and Terauchi (2005) have shown that the maintenance of distinct wild and domesticated populations is due to, on the one hand, the existence of a *super-gene* or linkage block, including genes for domestication traits such as non-shattering habit and reduced branching, and on the other hand, sterility of the WW (wild) homozygote for this linkage block.

The Role of Farmers in Maintaining and Generating Crop Phenotypic Variation

Farmers play an important, if neglected, role in the maintenance of crop genetic diversity. Far from being

averse to change, farmers do experiment with new plant materials and adopt them if they turn out to be superior to traditional varieties or landraces. The latter are generally superior in the case of marginal environmental, production, and economic conditions, to satisfy specific consumption goals (such as specific dishes or rituals), and when they produce desired by-products (Perales et al., 2003a). However, Perales et al. (2003a) describe a high-altitude region in Mexico where traditional varieties of maize are still grown in spite of the lack of marginality. In this region, local maize varieties are advantageous because they are higher-yielding, resist infestation by weevils better, and are more tolerant to drought and lodging than modern cultivars. Other examples of continued maintenance of traditional varieties by farmers include potato (Brush et al., 1995), rice (Bellon et al., 1997), and barley (Ceccarelli, 1994).

Farmers are also adept at maintaining genetic diversity within and between varieties. Perales et al. (2003b) attribute the wide adaptation of the two main varieties in their study—Chalqueño and Cónico—to the large amount of genetic diversity they still contain. Perales et al. (2005) showed how differences in ear morphology between the Olotón (Tzotzil ethnic group) and Comiteco (Tzeltal ethnic group) landraces correlate with local adaptation. They suggest that these differential cultural preferences for ear shape allow the two ethnic groups to identify local, well-adapted varieties, without conducting extensive experiments. Zizumbo-Villarreal et al. (2005) observed that common bean landraces in central Mexico harbored as much genetic diversity as the local wild populations (in spite of a well-documented domestication bottleneck). They attributed this high diversity to spontaneous crosses among landraces, active exchange of seeds, and cultivation of a large number of landraces by farmers.

Through farming practices (time of planting, weeding, thinning, and seed selection), farmers are able to keep landraces adapted to their growing conditions and sociocultural preferences. For example, pearl millet farmers in the Sahel select for the most vigorous plants in the planting pocket and later during the crop cycle before selecting for domesticated-type seeds at harvest. In so doing, they indirectly select for domesticated (as opposed to wild or hybrid) types and limit the contamination by wild germplasm (Couturon et al., 2003). In a similar fashion, farmers in French Guyana select for the most vigorous cassava seedlings (resulting from sexual reproduction) during weeding. In doing so, they are indirectly selecting for increased heterozygosity (Pujol et al., 2005).

Thus, in traditional agricultural ecosystems, farmers make decisions on various aspects of crop management, including planting, cultivation, harvesting, and processing. Each operation represents a possible selection step for a specific morphology, adaptation to a microenvironment, and suitability to a cropping system (Jarvis and Hodgkin, 1999). Other examples of farmer management and putative selection are discussed by Altieri and Merrick (1987), Brush et al. (1995), and Salick et al. (1997). Further information is needed, however, to determine how effective this selection is and to compare its magnitude to that of natural selection, which undoubtedly operates also in these same farmers' fields.

Intellectual Property Rights and International Treaties on Biodiversity

Over the last 25 to 30 yr, there has been a profound change in the legal landscape with regard to ownership of biodiversity, in general, and CGR, in particular. In 1980, the U.S. Supreme Court overturned a Patent Office decision not to award a patent for a genetically modified bacterium capable of degrading petroleum products (U.S. Supreme Court, 1980). In doing so, it effectively allowed in the U.S. utility patents for living organisms and their components, including genes, but also cultivars (following additional decisions clarifying the scope of the 1980 decision: *Ex parte* Hibberd 1985; J.E.M. Ag Supply vs. Pioneer Hi-Bred International 2001). Before 1980, biodiversity had been considered the common heritage of humanity, in effect preventing ownership by any individual or entity. This new, post-1980 intellectual property (IP) regime became controversial almost immediately and for several reasons.

It was suggested that it would lead to an asymmetry in terms of trade between the North and the South, with the latter providing the raw material (i.e., germplasm) for free and the former developing improved cultivars to be sold to the South. Although this asymmetry was an oversimplification, it did touch a raw nerve because it reflected the actual imbalance in the distribution of breeding capability, on the one hand, and germplasm, on the other hand, between the North and the South (Gepts, 2004b). This change in the legal framework for biodiversity led to a new, international treaty, the Convention on Biological Diversity (Convention on Biological Diversity, 1992), which assigns sovereignty over biodiversity to national governments, promotes the conservation and sustainable use of biological diversity, and encourages the equitable sharing of resulting benefits (so-called Access and Benefits Sharing), on a bilateral basis.

Utility patents provide a stronger intellectual property protection than the preexisting Plant Breeder's Rights or Plant Variety Protection (governed by the international Union pour la Protection des Obtentions Variétales or UPOV Convention) because they do not include farmers' (reuse of seeds for personal use is allowed) nor breeders' (use of cultivar as a parent in crosses) exemptions. Yet, this same lack of exemptions has raised the issue of an imbalance toward IP rights owners to the detriment of the public interest (e.g., Adelphi charter: www.adelphicharter.org/; verified 2 June 2006). How do IP rights on biodiversity, the CBD, and other international treaties such as the Trade-Related Intellectual Property rights (or TRIPS: www.wto.org/english/tratop_e/trips_e/trips_e.htm; verified 2 June 2006) affect germplasm exchange and genetic diversity? Anecdotal information strongly suggests that germplasm flows have been hampered (either slowed down or prevented entirely) because the new IP regime focuses primarily on owner's rights (a situation labeled

"hyperownership" by Safrin, 2004). Yet, germplasm exchange has been one of the signature characteristics of plant breeding programs. Thus, it remains to be determined to what extent the strong emphasis on IP rights for biodiversity will really promote the conservation and use of biodiversity and overall crop genetic diversity. Interestingly, the principle of common heritage, which had been set aside by the 1980 U.S. Supreme Court decision, is being reconsidered and has been included already in the latest international treaty affecting CGR, namely the International Treaty on Plant Genetic Resources for Food and Agriculture [www.fao.org/AG/cgrfa/itpgr.htm (verified 6 June 2006); Brush, 2005]. This treaty governs the free exchange of germplasm for several (but not all) crops in a multilateral agreement and imposes a payment for any benefit arising from commercialization of a crop that incorporates genetic material from the multilateral system. Crops not covered by this treaty include soybean [*Glycine max* (L.) Merr.], sugarcane (*Saccharum officinarum* L.), groundnut (*Arachis hypogea* L.), tropical forages, tomato (*Lycopersicon esculentum* Mill.), grape (*Vitis vinifera* L.), cocoa (*Theobroma cacao* L.), coffee (*Coffea* spp.), and industrial crops such as oil palm (*Elaeis guineensis* Jacq.) and rubber [*Hevea brasiliensis* (Willd. ex A. Juss.) Mull. Arg.]. For the latter crops, certain countries felt that they could gain more from selling resources bilaterally than by including them in a multilateral exchange system (Fowler et al., 2003). Johnson et al. (2003) compared the benefits derived through a 10% royalty or increased economic productivity as a result of free exchange of germplasm and the ensuing breeding opportunities. They showed that most countries benefited more from a free exchange of germplasm than a royalty regime. Thus, the tactic of withholding genetic resources in the hope of collecting royalties may not provide the expected benefits.

Dutfield (2004) observed that the TRIPS agreement, which imposes the existence (or the introduction if it does not exist already) of a U.S.—or E.U.—style IP rights regime to World Trade Organization member countries, had led to a U.S. $ 20 billion transfer of wealth from technology-importing countries to technology exporters. He argues that developing countries should be allowed to develop their own IP standards suitable for their level of economic or technological development and that of their citizens. One of the peculiarities that is particularly relevant to developing countries is that farmers play an important role in maintaining crop genetic diversity. This has led to proposals to protect so-called farmers' rights over their genetic resources and the knowledge associated with these genetic resources. How to reward these farmers for the conservation services they provide is still unresolved (Brush, 2005; Van Overwalle, 2005).

Valuation of Biodiversity and Funding of Conservation Activities

Determining the value of germplasm per se is difficult to achieve because it is difficult to separate the contributions of breeders from the contribution of the germplasm accessions with which they work (Day Rubenstein et al., 2005). Investments in genetic enhancement have generally generated large returns. Frisvold et al. (2003) estimated that in the period of 1975 to 1992, the genetic component of yield increases of five commodities (maize, soybean, wheat, cotton, and sorghum) had led to an increase in global welfare of U.S. $ 590 million, of which 60% benefited the U.S., 25% other developed countries, and 15% developing countries. Pardey et al. (1996) determined that the benefit-cost ratio of U.S. investment in CGIAR breeding programs was 48:1 for rice and 190:1 for wheat. Evenson and Gollin (1997) estimated that the present value of an added rice landrace (in a variety introduced by IRRI) was $50 million.

Whereas these numbers show that genetic diversity can ultimately (after utilization in breeding) have high societal benefits, these benefits cannot always be captured by individuals to realize private benefits (Gollin and Smale, 1998). Genetic diversity is a public good as the global community benefits from genetic diversity, but there are currently no mechanisms to provide farmers with a share of these global benefits. Thus, farmers will not have incentives to grow landraces unless these landraces provide a sufficiently high private benefit, which would explain the low rate of landrace conservation (Gollin and Smale, 1998). Whereas some accessions may have high value because they are the source of an economically important trait, such as a disease resistance, on average most accessions have little value because they do not carry traits of current interest or, if they do, these traits can be substituted. Like biodiversity for pharmaceutical applications (Simpson et al., 1996), the marginal value of an accession is low because any accession is generally redundant: the same trait can be found in other accessions as well and there can be alternatives to the trait in question (other genetic disease resistances vs. pesticide application vs. cultural controls).

The issue of maintenance cost is of paramount importance because it has been estimated that, of the 400 gene banks with medium- to long-term storage capabilities in 1995, only 35 met international standards for long-term storage. There is an urgent need to upgrade facilities and provide adequate operating funds (Qualset and Shands, 2005). Conservation costs of CGR are generally labeled as expensive. Koo et al. (2003) estimated that the storage costs/accession/year for the 11 gene banks of the CGIAR system were U.S. $ 1.50 for most crops, $ 2.16 for maize (cross-pollination), and $ 11.98 for cassava (in vitro conservation). Estimates from different bodies of the worldwide cost to fund ex situ gene banks arrive at amounts of a similar order of magnitude (Day Rubenstein et al., 2005): U.S. $ 300 million (Keystone Center, 1991), U.S. $ 240 million (National Research Council, 1993), 150 to 455 U.S. $ million (FAO, 1997). The Global Crop Diversity Trust seeks a U.S. $ 260 million endowment to disburse some $ 12 million annually to address urgent needs of gene banks.

Whether these amounts qualify as expensive depends on one's perspective. It is good to keep in mind, however, that genetic diversity conservation is a form of

insurance as stated by Perrings (1995). Payments for a hypothetical future event, either to support further progress from breeding or to avert a catastrophic epidemic, will never be popular but provide the responsible action to pursue.

Broadening the Conservation Circle

The addition of in situ conservation as a conservation tool to complement ex situ conservation raises the broader issue of the actual scope of conservation of CGR. While the number of accessions held in ex situ gene banks may seem large, the number and type of accessions are actually inherently limited when one considers the geographic and ecological distribution of wild and domesticated CGR, especially when taking into account the population structure of these accessions. Various forms of decentralized or distributed in situ conservation opportunities should be actually pursued.

Farmers, especially in centers of domestication, have for a long time been *de facto* curators of genetic diversity (Bretting and Duvick, 1997). There is a close intertwining of biological and cultural factors responsible for the diversity of the domesticated gene pool, especially in centers of origin. Thus, domesticated plants are also human artifacts, valued for multiple qualities such as utility, taste, color, shape, symbolism, and rituals. In addition to fulfilling a utilitarian function as a crop and a source of genetic diversity for breeding, domesticated plants are also an essential part of the daily social and cultural lives (Zimmerer, 1996; Brush, 1992; Rhoades and Nazarea, 1999). In subsistence systems, there is an active maintenance of a wide range of species and varieties as a way to meet basic physical, social, and spiritual needs. Subsistence farmers and their families are both producers and consumers, leading to experimentation and a wide range of selection or decision-making criteria (Altieri and Merrick, 1987; Rhoades and Nazarea, 1999).

However, communities and households within communities that tend to maintain more biodiversity tend also to be disenfranchised from the dominant order surrounding them. Marginality measured at various scales is a key common designator for landrace in situ curation and other plant use (Rhoades and Nazarea, 1999). For example, in the Sierra de Manantlán of Mexico, three of the most marginal and isolated communities recognize and use a larger number of species than less marginalized communities (Benz et al., 2000). One of the challenges of in situ conservation is, therefore, to maintain diversity and the accompanying traditional knowledge in response to external pressures, such as modernization.

One of the tools in promoting the continued use of local resources (and, hence, the continuation of traditional knowledge) is to promote local seed banks and seed fairs. An analysis of the local village seed systems in Niger by Ndjeunga (2002) showed that the informal sector represented by local farmers can grow pearl millet seeds of acceptable quality (large grain size, low inert matter content, and low incidence of diseases and pests). In comparison with formal seed systems, the informal system is more efficient at supplying seeds to the farmers. Collectively, a broader range of variety is maintained. In such circumstances, it is important to understand the way in which farmers handle their seed stocks (Perales et al., 2003b; Alvarez et al., 2005).

Other grassroots movements include the Greenbelt movement initiated by 2004 Nobel Prize winner Wangari Maathai (Maathai, 2004). Although it is not directed to CGR, it does fulfill an important role in biodiversity by planting a variety of trees and by planting two trees for every tree felled. In developed countries, several organizations have sprung up, each of which with its own geographic and conservation emphasis. The Slow Food movement (www.slowfood.com/; verified 6 June 2006), which originated in northern Italy and now has a worldwide membership, seeks to promote the diversity of food and wine culture from the field to the table. Hence, an important objective is to safeguard plant and animal species that are the ingredients of these foods through its Slow Food Foundation for Biodiversity. The Seed Savers Exchange of Decorah, Iowa (www.seedsavers.org/; verified 2 June 2006), maintains an outstanding collection of over 11000 heirloom varieties of vegetables, fruits, and grains. Native Seeds/SEARCH (www.nativeseeds.org/; verified 6 June 2006) preserves seeds of over 2000 crop varieties specifically grown in the arid Southwest U.S. and northwest Mexico, especially by Native American communities. Seeds of Change (www.seedsofchange.com/; verified 2 June 2006) offers organically-grown seeds of some 600 vegetable, flower, and herb varieties. Each of these organizations fulfills an important conservation and scientific role.

In turn, these local seed saving activities, especially in developing countries, are a useful starting point for genetic improvement through participatory breeding (Cleveland and Soleri, 2002). These local, community-based efforts rely on collaboration between farmers (who provide the landraces for improvement and the selection criteria) and breeders (who provide selection methods and additional sources of genetic diversity as needed). The desired outcome is improved cultivars with local adaptation through exploitation of genotype × environment interactions. Ceccarelli et al. (2000, 2003) obtained evidence that breeders were more efficient at selecting higher-yielding materials at research stations under high rainfall, whereas farmers were more efficient in selecting under stress conditions. Nevertheless, the selection environment (farm vs. research station) had a much larger effect than the identity of the selector (farmer vs. breeder). These observations suggest that a decentralization of breeding operations to include farmers fields would increase the efficiency of breeding for farmer-adapted cultivars. It is beyond the scope to fully discuss participatory breeding here, but this area is one of the most promising ones to further advance both conservation of CGR and plant breeding.

CONCLUSIONS

The challenges for the future in the area of plant genetic resources conservation are technical and scientific, socioeconomical, legal and political, including public

awareness (Esquinas-Alcazar, 2005). The field of germ-plasm conservation will have to address how to best integrate technological advances in the areas of molecular genetics, genomics, cryopreservation and other conservation techniques, and geographic information system, to further facilitate conservation and utilization of these resources. A long-term political agenda and commitment will have to be developed to assure long-term public-sector investment in in situ and ex situ conservations. A closer cooperation between farmers and breeders will have to be developed, especially in developing countries, to bring the fruits of plant breeding to a broader cross-section of farmers. From a legal standpoint, the current intellectual property regime will have to be greatly streamlined (if not downright reformed) to eliminate unnecessary barriers to germplasm exchange and utilization. Last but not least, public awareness of this great biological resource will have to be increased.

ACKNOWLEDGMENTS

REFERENCES

Aguilar, O.M., O. Riva, and E. Peltzer. 2004. Analysis of *Rhizobium etli* and of its symbiosis with wild *Phaseolus vulgaris* supports coevolution in centers of host diversification. Proc. Natl. Acad. Sci. USA 101:13548–13553.

Alo, F., E. Akhunov, B.J. Furman, P. Gepts, and J. Dvorak. 2006. Characterization of a lentil germplasm collection by direct sequencing of sequence-tagged sites produced with primers based on *Medicago truncatula* ESTs and *Arabidopsis thaliana* genomic sequence www.intl-pag.org/14/abstracts/PAG14_P423.html (verified 2 June 2006). Plant and Animal Genome XIV, San Diego, CA. January 14–18, 2006.

Altieri, M.A., and L.C. Merrick. 1987. *In* situ conservation of crop genetic-resources through maintenance of traditional farming systems. Econ. Bot. 41:86–96.

Alvarez, N., E. Garine, C. Khasah, E. Dounias, M. Hossaert-McKey, and D. McKey. 2005. Farmers' practices, metapopulation dynamics, and conservation of agricultural biodiversity on-farm: A case study of sorghum among the Duupa in sub-sahelian Cameroon. Biol. Conserv. 121:533–543.

Avise, J.C. 2004. Molecular markers, natural history and evolution. 2nd ed. Sinauer, Sunderland, MA, USA.

Balmford, A., R.E. Green, and J.P.W. Scharlemann. 2005. Sparing land for nature: Exploring the potential impact of changes in agricultural yield on the area needed for crop production. Glob. Change Biol. 11:1594–1605.

Beckers, G.J.M., and S.H. Spoel. 2006. Fine-tuning plant defence signalling: Salicylate versus jasmonate. Plant Biol. 8:1–10.

Beebe, S., J. Lynch, N. Galwey, J. Tohme, and I. Ochoa. 1997. A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. Euphytica 95:325–336.

Bellon, M.R., J.-L. Pham, and M.T. Jackson. 1997. Genetic conservation: A role for rice farmers. p. 263–289. *In* N. Maxted et al (ed.) Plant genetic conservation: The *in situ* approach. Chapman & Hall, London.

Benz, B.F., J. Cevallos, F. Santana, J. Rosales, and S. Graf. 2000. Losing knowledge about plant use in the Sierra de Manantlan biosphere reserve, Mexico. Econ. Bot. 54:183–191.

Bergelson, J., G. Dwyer, and J.J. Emerson. 2001. Models and data on plant-enemy coevolution. Annu. Rev. Genet. 35:469–499.

Berjak, P., and N.W. Pammenter. 2003. Chapter 4: Orthodox and recalcitrant seeds: [Online]. Available at www.rngr.net/Publications/

ttsm/ch4/view (verified 2 June 2006). Reforestation, nurseries, and genetics resources: www.rngr.net/ (verified 2 June 2006).

Bingham, T. 1983. Molecular engineering vs plant breeding. Plant Mol. Biol. 2:222–224.

Birch, R. 1997. Plant transformation: Problems and strategies for practical application. Annu. Rev. Plant Physiol. Plant Mol. Biol. 48:297–326.

Birnbaum, K., R. DeSalle, C.M. Peters, and P.N. Benfey. 2003. Integrating gene flow, crop biology, and farm management in on-farm conservation of avocado (Persea americana, Lauraceae). Am. J. Bot. 90:1619–1627.

Bretting, P., and D. Duvick. 1997. Dynamic conservation of plant genetic resources. Adv. Agron. 61:1–51.

Brookfield, H., C. Padoch, H. Parsons, and M. Stocking (ed.). 2002. Cultivating biodiversity: Understanding, analysing and using agricultural diversity. ITDG, London.

Brown, A.H.D. 1995. The core collection at the crossroads. p. 3–19. *In* T. Hodgkin, et al. (ed.) Core collections of plant genetic resources. John Wiley & Sons, New York.

Brown, A.H.D., and C. Spillane. 1999. Implementing core collections-principles, procedures, progress, problems and promise. p. 1–9. *In* R.C. Johnson and T. Hodgkin (ed.) Core collections for today and tomorrow. International Plant Genetic Resources Institute, Rome.

Brush, S.B. 1992. Ethnoecology, biodiversity, and modernization in Andean potato agriculture. J. Ethnobiology 12:161–185.

Brush, S.B. 1995. *In situ* conservation of landraces in centers of crop diversity. Crop Sci. 35:346–354.

Brush, S.B. 2004. Farmers' bounty. Yale Univ. Press, New Haven, CT.

Brush, S.B. 2005. Farmers' rights and protection of traditional agricultural knowledge [Online]. Available at www.capri.cgiar.org/pdf/capriwp36.pdf (verified 2 June 2006). CGIAR Systemwide Program on Collective Action and Property Rights.

Brush, S., R. Kesseli, R. Ortega, P. Cisneros, K. Zimmerer, and C. Quiros. 1995. Potato diversity in the Andean center of crop domestication. Conserv. Biol. 9:1189–1198.

Brush, S.B., and D. Stabinsky (ed.). 1996. Valuing local knowledge: Indigenous people and intellectual property rights. Island Press, Washington, DC.

Burr, F. 1863. The field and garden vegetables of America American Botanist. Chillicothe, IL.

Ceccarelli, S. 1994. Specific adaptation and breeding for marginal conditions. Euphytica 77:205–219.

Ceccarelli, S., S. Grando, R. Tutwiler, J. Baha, A.M. Martini, H. Salahieh, A. Goodchild, and M. Michael. 2000. A methodological study on participatory barley breeding. I. Selection phase. Euphytica 111:91–104.

Ceccarelli, S., S. Grando, M. Singh, M. Michael, A. Shikho, M. Al Issa, A. Al Saleh, G. Kaleonjy, S.M. Al Ghanem, A.L. Al Hasan, H. Dalla, S. Basha, and T. Basha. 2003. A methodological study on participatory barley breeding. II. Response to selection. Euphytica 133:185–200.

Cleveland, D., and D. Soleri (ed.). 2002. Farmers, scientists, and plant breeding: Integrating knowledge and practice. CABI, Wallingford, Oxon, UK.

Collard, B.C.Y., M.Z.Z. Jahufer, J.B. Brouwer, and E.C.K. Pang. 2005. An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. Euphytica 142:169–196.

Collins, W.W., and G.C. Hawtin. 1999. Conserving and using crop plant biodiversity in agroecosystems. p. 267–282. *In* W.W. Collins and C.O. Qualset (ed.) Biodiversity in agroecosystems. CRC, Boca Raton, FL.

Collins, W.W., and C.O. Qualset. 1999. Biodiversity in agroecosystems. CRC, Boca Raton, FL.

Convention on Biological Diversity. 1992. Convention text [Online]. Available at www.biodiv.org/convention/articles.asp (verified 2 June 2006). Secretariat of the Convention on Biological Diversity, United Nations Environment Program.

Couturon, E., C. Mariac, G. Bezançon, J. Lauga, and J.F. Renno. 2003. Impact of natural and human selection on the frequency of the F1 hybrid between cultivated and wild pearl millet (Pennisetum glaucum (L.) R. Br.). Euphytica 133:329–337.

Crosby, A. 1972. Columbian exchange: Biological and cultural consequences of 1492. Greenwood, Westport, CT.

Dalby, A. 2000. Dangerous tastes: The story of spices. Univ. of California Press, Berkeley, CA.

Damania, A., J. Valkoun, G. Willcox, and C. Qualset (ed.). 1998. The origins of agriculture and crop domestication. ICARDA, Aleppo, Syria.

Darwin, C. 1868. The variation of plants and animals under domestication. J. Murray, London.

Day Rubenstein, K., P. Heisey, R. Shoemaker, J. Sullivan, and G. Frisvold. 2005. Crop genetic resources: An economic appraisal [Online]. Available at www.ers.usda.gov/publications/eib2/ (verified June 2 2006). USDA-ERS, Washington, DC.

Debouck, D.G., O. Toro, O.M. Paredes, W.C. Johnson, and P. Gepts. 1993. Genetic diversity and ecological distribution of Phaseolus vulgaris in northwestern South America. Econ. Bot. 47:408–423.

Doebley, J. 1989. Isozymic evidence and the evolution of crop plants. p. 165–191. In D.E. Soltis and P.S. Soltis (ed.) Isozymes in plant biology. Dioscorides, Portland, OR.

Doebley, J. 1992. Molecular systematics and crop evolution. p. 202–222. In P. S. Soltis, et al. (ed.) Molecular systematics of plants. Chapman Hall, New York.

Doebley, J.F., M.M. Goodman, and C.W. Stuber. 1984. Isoenzymatic variation in Zea (Gramineae). Syst. Bot. 9:203–218.

Dutfield, G. 2004. Does one size fits all? The international patent regime [Online]. Available at http://hir.harvard.edu/articles/1257/2/ (verified 2 June 2006). Harvard International Review 26:50–54.

Duvick, D.N. 1984. Genetic diversity in major farm crops on the farm and in reserve. Econ. Bot. 38:161–178.

Dybdahl, M.F., and A. Storfer. 2003. Parasite local adaptation: Red Queen versus Suicide King. Trends Ecol. Evol. 18:523–530.

Esquinas-Alcazar, J. 2005. Protecting crop genetic diversity for food security: Political, ethical and technical challenges. Nat. Rev. Genet. 6:946–953.

Evenson, R.E., and D. Gollin. 1997. Genetic resources, international organizations and improvement in rice varieties. Econ. Dev. Cult. Change 45:471–500.

FAO. 1996. Global Plan of Action for the Conservation and Sustainable Utilization of Plant Genetic Resources for Food and Agriculture and the Leipzig Declaration adopted by the International Technical Conference on Plant Genetic Resources, Leipzig, Germany 17–23 June 1996 [Online]. Available at www.fao.org/ag/AGP/AGPS/Pgrfa/Pdf/GPAENG.PDF (verified 2 June 2006). Food and Agriculture Organization, Rome.

FAO. 1997. The state of the world's plant genetic resources for food and agriculture [Online]. Available at www.fao.org/ag/AGP/AGPS/Pgrfa/pdf/swrfull.pdf (verified 2 June 2006). Food and Agriculture Organization of the United Nations, Rome.

FAO. 2005. The state of food insecurity in the world 2005 [Online]. Available at www.fao.org/documents/show_cdr.asp?url_file=/docrep/008/a0200e/a0200e00.htm (verified 2 June 2006). Available from Food and Agriculture Organization, Economic and Social Department.

Fehr, W.R. 1984. Genetic contributions to yield gains of five major crop plants. CSSA, Madison, WI.

Ferguson, M.E., A. Jarvis, H.T. Stalker, D.E. Williams, L. Guarino, J.F.M. Valls, R.N. Pittman, C.E. Simpson, and P.J. Bramel. 2005. Biogeography of wild Arachis (Leguminosae): distribution and environmental characterisation. Biodivers. Conserv. 14:1777–1798.

Fiedler, J., G. Bufler, and F. Bangerth. 1998. Genetic relationships of avocado (Persea americana Mill) using RAPD markers. Euphytica 101:249–255.

Foley, J.A., R. DeFries, G.P. Asner, C. Barford, G. Bonan, S.R. Carpenter, F.S. Chapin, M.T. Coe, G.C. Daily, H.K. Gibbs, J.H. Helkowski, T. Holloway, E.A. Howard, C.J. Kucharik, C. Monfreda, J.A. Patz, I.C. Prentice, N. Ramankutty, and P.K. Snyder. 2005. Global consequences of land use. Science 309:570–574.

Fowler, C., G. Moore, and G.C. Hawtin. 2003. The international treaty on plant genetic resources for food and agriculture: A primer for the Future Harvest Centers of the CGIAR [Online]. Available at www.ipgri.cgiar.org/publications/pubsurvey.asp?id_publication=877 (verified 2 June 2006). International Plant Genetic Resources Institute, Rome.

Frankel, O., and E. Bennett. 1970. Genetic resources in plants—their exploration and conservation Blackwell, Oxford.

Frisvold, G.B., J. Sullivan, and A. Raneses. 2003. Genetic improvements in major US crops: The size and distribution of benefits. Agric. Econ. 28:109–119.

Gandon, S., and Y. Michalakis. 2002. Local adaptation, evolutionary potential and host-parasite coevolution: Interactions between migration, mutation, population size and generation time. J. Evol. Biol. 15:451–462.

Gelvin, S. 2000. Agrobacterium and plant genes involved in T-DNA transfer and integration. Annu. Rev. Plant Physiol. Plant Mol. Biol. 51:223–256.

Gepts, P. 1988. Phaseolin as an evolutionary marker. p. 215–241. In P. Gepts, ed. Genetic resources of Phaseolus beans. Kluwer, Dordrecht, the Netherlands.

Gepts, P. 1993. The use of molecular and biochemical markers in crop evolution studies. Evol. Biol. 27:51–94.

Gepts, P. 2000. A phylogenetic and genomic analysis of crop germplasm: A necessary condition for its rational conservation and utilization. p. 163–181. In J. Gustafson, ed. Proc. Stadler Symposium. Plenum, New York.

Gepts, P. 2002. A comparison between crop domestication, classical plant breeding, and genetic engineering. Crop Sci. 42:1780–1790.

Gepts, P. 2004a. Domestication as a long-term selection experiment (Part 2). Plant Breed. Rev. 24:1–44.

Gepts, P. 2004b. Who owns biodiversity and how should the owners be compensated? Plant Physiol. 134:1295–1307.

Gollin, D., and M. Smale. 1998. Valuing genetic diversity: Crop plants and agroecosystems. p. 237–265. In W.W. Collins and C.O. Qualset (ed.) Biodiversity in Agroecosystems. CRC Press, Boca Raton, FL.

Goodman, M.M. 2004. Plant breeding requirements for applied molecular biology. Crop Sci. 44:1913–1914.

Green, R.E., S.J. Cornell, J.P.W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science 307:550–555.

Greene, S.L., and L. Guarino. 1999. Linking genetic resources and geography: Emerging strategies for conserving and using crop biodiversity. ASA and CSSA, Madison, WI.

Guarino, L., N. Maxted, and M. Sawkins. 1999. Analysis of georeferenced data and the conservation and use of plant genetic resources. p. 1–9. In S.L. Greene and L. Guarino (ed.) Linking genetic resources and geography: Emerging strategies for conserving and using crop biodiversity. ASA and CSSA, Madison, WI.

Gupta, P.K., S. Rustgi, and P.L. Kulwal. 2005. Linkage disequilibrium and association studies in higher plants: Present status and future prospects. Plant Mol. Biol. 57:461–485.

Guzmán, P., R.L. Gilbertson, R. Nodari, W.C. Johnson, S.R. Temple, D. Mandala, A.B.C. Mkandawire, and P. Gepts. 1995. Characterization of variability in the fungus Phaeoisariopsis griseola suggests coevolution with the common bean (Phaseolus vulgaris). Phytopathology 85:600–607.

Hamrick, J.L., and M.J.W. Godt. 1997. Allozyme diversity in cultivated crops. Crop Sci. 37:26–30.

Harding, K. 2004. Genetic integrity of cryopreserved plant cells: A review. Cryo Letters 25:3–22.

Harlan, J. 1965. The possible role of weed races in the evolution of cultivated plants. Euphytica 14:173–176.

Harlan, J.R. 1971. Agricultural origins: Centers and non-centers. Science 174:468–474.

Harlan, J.R. 1972. Genetics of disaster. J. Environ. Qual. 1:212–215.

Harlan, J.R. 1995. The living fields. Cambridge Univ. Press, Cambridge, UK.

Harlan, H.V., and M.L. Martini. 1936. Problems and results in barley breeding. Yearbook of agriculture. USDA, Washington, DC. For an online version of this report: http://barley.ipk-gatersleben.de/archives/Harlan&Martini1936.htm (verified 6 June 2006).

Harlan, J.R., and J.M.J. de Wet. 1971. Towards a rational classification of cultivated plants. Taxon 20:509–517.

Harris, D. (ed.). 1996. The origins and spread of agriculture and pastoralism in Eurasia. University College, London.

Harvell, D. 2004. Ecology and evolution of host-pathogen interactions in nature. Am. Nat. 164:S1–S5.

Hawkes, J.G. 1971. Conservation of plant genetic resources. Outlook Agric. 6:248–253.

Hedrick, U. 1931. The vegetables of New York. I. Legumes, curcurbits, corn, alliums, asparagus. Part II. Beans. J.B. Lyon, Albany, NY.

Heun, M., R. Schafer-Pregl, D. Klawan, R. Castagna, M. Accerbi, B. Borghi, and F. Salamini. 1997. Site of einkorn wheat domestication identified by DNA fingerprinting. Science 278:1312–1314.

Hillel, D., and C. Rosenzweig. 2005. The role of biodiversity in agronomy. Adv. Agron. 88:1–34.

Hobhouse, H. 1999. Seeds of change: Six plants that transformed mankind. 2nd ed. Papermac, London.

Hobhouse, H. 2003. Seeds of wealth. Macmillan, London.

Hodgkin, T., A.H.D. Brown, T.J.L. van Hintum, and E.A.V. Morales. 1995. Core collections of plant genetic resources. International Plant Genetic Resources Institute, Rome.

Jalali, B.L., S. Bhargava, and A. Kamble. 2006. Signal transduction and transcriptional regulation of plant defence responses. J. Phytopathol. 154:65–74.

Jarvis, D.I., and T. Hodgkin. 1999. Wild relatives and crop cultivars: Detecting natural introgression and farmer selection of new genetic combinations in agroecosystems. Mol. Ecol. 8:S159–S173.

Jarvis, A., S. Yeaman, L. Guarino, and J. Tohme. 2005a. The role of geographic analysis in locating, understanding, and using plant genetic diversity. p. 279–298. *In* E. Zimmer (ed.) Molecular Evolution: Producing the Biochemical Data, Part B. Elsevier, New York.

Jarvis, A., K. Williams, D. Williams, L. Guarino, P. Caballero, and G. Mottram. 2005b. Use of GIS for optimizing a collecting mission for a rare wild pepper (*Capsicum flexuosum* Sendtn.) in Paraguay. Genet. Resour. Crop Evol. 52:671–682.

Johnson, R.C., and T. Hodgkin. 1999. Core collections for today and tomorrow. International Plant Genetic Resources Institute, Rome.

Johnson, N.L., D. Pachico, and O. Voysest. 2003. The distribution of benefits from public international germplasm banks: The case of beans in Latin America. Agric. Econ. 29:277–286.

Kami, J., B. Becerra Velásquez, D.G. Debouck, and P. Gepts. 1995. Identification of presumed ancestral DNA sequences of phaseolin in *Phaseolus vulgaris*. Proc. Natl. Acad. Sci. USA 92:1101–1104.

Kelly, J.D. 2004. Advances in common bean improvement: Some case histories with broader applications. Acta Hortic. 637:99–122.

Kelly, J.D., and V.A. Vallejo. 2004. A comprehensive review of the major genes conditioning resistance to anthracnose in common bean. HortScience 39:1196–1207.

Kelly, J.D., J.M. Kolkman, and K. Schneider. 1998. Breeding for yield in dry bean (*Phaseolus vulgaris* L.). Euphytica 102:343–356.

Keystone Center. 1991. Final consensus report: Global initiative for the security and sustainable use of plant genetic resources. Keystone International Dialogue Series on Plant Genetic Resources, Oslo Plenary Session. Genetic Resources Communications Systems, Washington, DC.

Kniskern, J., and M.D. Rausher. 2001. Two modes of host-enemy coevolution. Popul. Ecol. 43:3–14.

Koenig, R., and P. Gepts. 1989. Allozyme diversity in wild *Phaseolus vulgaris*: Further evidence for two major centers of diversity. Theor. Appl. Genet. 78:809–817.

Koenig, R., S.P. Singh, and P. Gepts. 1990. Novel phaseolin types in wild and cultivated common bean (*Phaseolus vulgaris*, Fabaceae). Econ. Bot. 44:50–60.

Koo, B., P. Pardey, and B. Wright. 2003. The price of conserving agricultural biodiversity. Nat. Biotechnol. 21:126–128.

Lacher, T.E.J., R.D. Slack, L.M. Coburn, and M.I. Goldstein. 1999. The role of agroecosystems in wildlife biodiversity. p. 147–165. *In* W.W. Collins and C.O. Qualset (ed.) Biodiversity in agroecosystems. CRC Press, Boca Raton, FL.

Lamboy, W.F., J. Yu, P.L. Forsline, and N.F. Weeden. 1996. Partitioning of allozyme diversity in wild populations of *Malus sieversii* L. and implications for germplasm collection. J. Am. Soc. Hortic. Sci. 121:982–987.

Lemmon, K. 1968. The golden age of plant hunters. Phoenix House, London.

Liviero, L., E. Maestri, M. Gulli, E. Nevo, and N. Marmiroli. 2002. Ecogeographic adaptation and genetic variation in wild barley: Application of molecular markers targeted to environmentally regulated genes. Genet. Resour. Crop Evol. 49:133–144.

Lyons, L., T. Laughlin, N. Copeland, N. Jenkins, J. Womack, and S. O'Brien. 1997. Comparative anchor tagged sequences (CATS) for integrative mapping of mammalian sequences. Nat. Genet. 15:47–56.

Maathai, W. 2004. The greenbelt movement. Lantern Books, New York.

Maffi, L. (ed.). 2001. On biocultural diversity: Linking language, knowledge, and the environment. Smithsonian Institution Press, Washington, DC.

Maffi, L. 2005. Linguistic, cultural, and biological diversity. Annu. Rev. Anthropol. 34:599–617.

Manel, S., M.K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: Combining landscape ecology and population genetics. Trends Ecol. Evol. 18:189–197.

Maruyama, E., K. Ishii, and I. Kinoshita. 1998. Alginate encapsulation technique and cryogenic procedures for long-term storage of the tropical forest tree *Guazuma crinita* Mart. in vitro cultures. Jpn Agric. Res. Q. 32:301–309.

Matsuoka, Y., Y. Vigouroux, M.M. Goodman, G.J. Sanchez, E. Buckler, and J. Doebley. 2002. A single domestication for maize shown by multilocus microsatellite genotyping. Proc. Natl. Acad. Sci. USA 99:6080–6084.

Maxted, N., P. Mabuza-Dlamini, H. Moss, S. Padulosi, A. Jarvis, and L. Guarino. 2004. African *Vigna*: An ecogeographic study. International Plant Genetic Resources Institute, Rome.

Milton, G. 1999. Nathaniel's Nutmeg. Penguin, New York.

Miura, R., and R. Terauchi. 2005. Genetic control of weediness traits and the maintenance of sympatric crop-weed polymorphism in pearl millet (*Pennisetum glaucum*). Mol. Ecol. 14:1251–1261.

Mkandawire, A.B.C., R.B. Mabagala, P. Guzman, P. Gepts, and R.L. Gilbertson. 2004. Genetic diversity and pathogenic variation of common blight bacteria (*Xanthomonas campestris* pv. *phaseoli* and *X. campestris* pv. *phaseoli* var. *fuscans*) suggests pathogen co-evolution with the common bean. Phytopathology 94:593–603.

Mohammadi, S.A., and B.M. Prasanna. 2003. Analysis of genetic diversity in crop plants–Salient statistical tools and considerations. Crop Sci. 43:1235–1248.

Musgrave, T., and W. Musgrave. 2000. An empire of plants. Cassell, London.

National Research Council. 1972. Genetic vulnerability of crops. National Academy of Sciences, Washington, DC.

National Research Council. 1991. Managing global genetic resources: The U.S. National Plant Germplasm System. Committee on Managing Global Genetic Resources: Agricultural Imperatives, Board on Agriculture, National Academy Press, Washington, DC.

National Research Council. 1993. Managing global genetic resources: Agricultural crop issues and policies. Committee on Managing Global Genetic Resources: Agricultural Imperatives, Board on Agriculture, National Academy Press, Washington, DC.

Ndjeunga, J. 2002. Local village seed systems and pearl millet seed quality in Niger. Exp. Agric. 38:149–162.

Neuhauser, C., D.A. Andow, G.E. Heimpel, G. May, R.G. Shaw, and S. Wagenius. 2003. Community genetics: Expanding the synthesis of ecology and genetics. Ecology 84:545–558.

Nuismer, S.L., and M. Kirkpatrick. 2003. Gene flow and the coevolution of parasite range. Evolution Int. J. Org. Evolution 57:746–754.

Papa, R., J. Acosta, A. Delgado-Salinas, and P. Gepts. 2005. A genome-wide analysis of differentiation between wild and domesticated *Phaseolus vulgaris* from Mesoamerica. Theor. Appl. Genet. 111:1147–1158.

Pardey, P.G., J.M. Alston, J.E. Christian, and S. Fan. 1996. Hidden harvest: U.S. benefits from international research aid. International Food Policy Research Institute, Washington, DC.

Parker, I.M., and G.S. Gilbert. 2004. The evolutionary ecology of novel plant-pathogen interactions. Annu. Rev. Ecolog. Syst. 35:675–700.

Perales, H., S.B. Brush, and C.O. Qualset. 2003a. Landraces of maize in Central Mexico: An altitudinal transect. Econ. Bot. 57:7–20.

Perales, H., S.B. Brush, and C.O. Qualset. 2003b. Dynamic management of maize landraces in Central Mexico. Econ. Bot. 57:21–34.

Perales, H.R., B.F. Benz, and S.B. Brush. 2005. Maize diversity and ethnolinguistic diversity in Chiapas, Mexico. Proc. Natl. Acad. Sci. USA 102:949–954.

Perrings, C. 1995. Biodiversity conservation as insurance. p. 69–78. *In* T. M. Swanson (ed.) The economics and ecology biodiversity decline. Cambridge Univ. Press, Cambridge.

Piperno, D., and D. Pearsall. 1998. The origin of agriculture in the neotropics. Academic Press, San Diego.

Plucknett, D.L., N.J.H. Smith, J.T. Williams, and N. Murthi Anishetty. 1987. Gene banks and the world's food. Princeton Univ. Press, Princeton, NJ.

Pujol, B., P. David, and D. McKey. 2005. Microevolution in agricultural environments: How a traditional Amerindian farming practice favours heterozygosity in cassava (*Manihot esculenta* Crantz, Euphorbiaceae). Ecol. Lett. 8:138–147.

Qualset, C.O., and H.L. Shands. 2005. Safeguarding the future of U.S. agriculture: The need to conserve threatened collections of crop diversity worldwide [Online]. Available at www.grcp.ucdavis.edu/publications/SafeAgdex.htm (verified 5 June 2006). University of California, Division of Agriculture and Natural Resources, Genetic Resources Conservation Program, Davis, CA.

Rhoades, R.E., and V.D. Nazarea. 1999. Local management of biodiversity in traditional agroecosystems. p. 215–236. In W.W. Collins and C.O. Qualset (ed.) Biodiversity in agroecosystems. CRC Press, Boca Raton, FL.

Roberts, E.H. 1973. Predicting the storage life of seeds. Seed Sci. Technol. 1:499–514.

Safrin, S. 2004. Hyperownership in a time of biotechnological promise: The international conflict to control the building blocks of life. Am. J. International Law 98:641–685.

Salick, J., N. Cellinese, and S. Knapp. 1997. Indigenous diversity of cassava: Generation, maintenance, use and loss among the Amuesha. Peruvian Upper Amazon. Econ. Bot. 51:6–19.

Sánchez, P.A., and M.S. Swaminathan. 2005. Cutting world hunger in half. Science 307:357–359.

Schlötterer, C. 2004. The evolution of molecular markers—just a matter of fashion? Nat. Rev. Genet. 5:63–69.

Shands, H.L. 1995. The US National Plant Germplasm System. Can. J. Plant Sci. 75:9–15.

Short, P. 2003. In pursuit of plants. Timber Press, Portland, OR.

Simmonds, N.W., and J. Smartt. 1999. Principles of crop improvement. 2nd ed. Blackwell, Oxford.

Simpson, R., R. Sedjo, and J. Reid. 1996. Valuing biodiversity for use in pharmaceutical research. J. Polit. Econ. 104:163–185.

Singh, S.P., P. Gepts, and D.G. Debouck. 1991. Races of common bean (Phaseolus vulgaris L., Fabaceae). Econ. Bot. 45:379–396.

Smale, M., M.P. Reynolds, M. Warburton, B. Skovmand, R. Trethowan, R.P. Singh, I. Ortiz-Monasterio, J. Crossa, M. Khairallah, and M.I. Almanza-Pinzon. 2001. Dimensions of diversity in CIMMYT bread wheat from 1965 to 2000. CIMMYT, Mexico, D.F.

Smith, B. 1995. The emergence of agriculture. Scientific American Library, New York.

South Africa Department of Health. 2001. South African national guidelines on nutrition for people living with TB, HIV/AIDS and other debilitating diseases [Online]. Available at www.sahealthinfo.org/nutrition/sanational.htm (verified 5 June 2006). Ministry of Health, Pretoria, South Africa.

Spooner, D., R. van Treuren, and M.C. de Vicente. 2005. Molecular markers for genebank management. IPGRI Technical Bulletin No. 10 [Online]. Available at www.ipgri.cgiar.org/publications/pdf/1082.pdf (verified 5 June 2006). International Plant Genetic Resources Institute, Rome.

Steiner, J.J. 1999. Exploring the relationship of plant genotype and phenotype to ecogeography. p. 39–50. In S.L. Greene and L. Guarino (ed.) Linking genetic resources and geography: Emerging strategies for conserving and using crop biodiversity. CSSA Spec. Publ. 27. ASA and CSSA, Madison, WI.

Sumner, J. 2004. American household botany. Timber Press, Portland, OR.

Sutherland, W.J. 2003. Parallel extinction risk and global distribution of languages and species. Nature 423:276–279.

Sytsma, K.J., and W. Hahn. 1997. Molecular systematics: 1994–1995. Prog. Bot. 58:470–499.

Thrall, P.H., and J.J. Burdon. 2003. Evolution of virulence in a plant host-pathogen metapopulation. Science 299:1735–1737.

Tohme, J., P. Jones, S. Beebe, and M. Iwanaga. 1995. The combined use of agroecological and characterization data to establish the CIAT Phaseolus vulgaris core collection. p. 95–107. In T. Hodgkin et al. (ed.) Core collections of plant genetic resources. International Plant Genetic Resources Institute, Rome.

U.S. Supreme Court. 1980. Diamond v. Chakrabarty, 447 U.S. 303 [Online]. Available at http://supct.law.cornell.edu/supct/cases/447us303.htm (verified 2 June 2006).

United Nations. 2004. The world population prospects: The 2004 revision [Online]. Available at www.un.org/esa/population/publications/WPP2004/wpp2004.htm (verified 2 June 2006). United Nations Department of Economic and Social Affairs, New York.

USDA. 1933. Vegetable Variety Type Books, 1933–1941. Superintendent of Documents, Washington, DC.

van Hintum, T.J.L., A.H.D. Brown, C. Spillane, and T. Hodgkin. 2000. Core collections of plant genetic resources. IPGRI Technical Bulletin No. 3. International Plant Genetic Resources Institute, Rome.

Van Overwalle, G. 2005. Protecting and sharing biodiversity and traditional knowledge: Holder and user tools. Ecological Economics 53:585–607.

Vavilov, N.I. 1926. Centers of origin of cultivated plants. p. 22–135. In V.F. Dorofeyev (ed.) Origin and geography of cultivated plants, English translation of Vavilov's works, 1992 ed. Cambridge Univ. Press, Cambridge.

Vilmorin-Andrieux, M.M. 1885. The vegetable garden: Illustrations, descriptions, and culture of the garden vegetables of cold and temperate climates. J. Murray, London.

Weising, K., H. Nybom, K. Wolff, and G. Kahl. 2005. DNA fingerprinting in plants: Principles, methods, and applications. CRC Press, Boca Raton, FL.

Wilkes, G. 1977. The world's crop plant germplasm: An endangered resource. Bull. At. Sci. 33:8–16.

Wisser, R.J., P.J. Balint-Kurti, and R.J. Nelson. 2006. The genetic architecture of disease resistance in maize: A synthesis of published studies. Phytopathology 96:120–129.

Yamasaki, M., M.I. Tenaillon, I. Vroh Bi, S.G. Schroeder, H. Sanchez-Villeda, J.F. Doebley, B.S. Gaut, and M.D. McMullen. 2005. A large-scale screen for artificial selection in maize identifies candidate agronomic loci for domestication and crop improvement. Plant Cell 17:2859–2872.

Young, N.D. 2000. The genetic architecture of resistance. Curr. Opin. Plant Biol. 3:285–290.

Yu, S.B., W.J. Xu, C.H.M. Vijayakumar, J. Ali, B.Y. Fu, J.L. Xu, Y.Z. Jiang, R. Marghirang, J. Domingo, C. Aquino, S.S. Virmani, and Z.K. Li. 2003. Molecular diversity and multilocus organization of the parental lines used in the International Rice Molecular Breeding Program. Theor. Appl. Genet. 108:131–140.

Zhu, H., H.-K. Choi, D.R. Cook, and R.C. Shoemaker. 2005. Bridging model and crop legumes through comparative genomics. Plant Physiol. 137:1189–1196.

Zimmerer, K. 1996. Changing fortunes: Biodiversity and peasant livelihood in the Peruvian Andes. Univ. of California Press, Berkeley, CA.

Zizumbo-Villarreal, D, P. Colunga-GarcíaMarín, E. Payró de la Cruz, P. Delgado-Valerio, and P. Gepts. 2005. Population structure and evolutionary dynamics of wild-weedy-domesticated complexes of common bean in a Mesoamerican region. Crop Sci. 35:1073–1083.