Iowa State Journal of Research

Volume 59, No. 4 ISSN0092-6345 May, 1985
ISJRA6 59(4) 323-545 1985

PLANT SCIENCE LECTURE SERIES, 1984

"Plant Genetic Resources—Key to Future Plant Production"

IOWA STATE
JOURNAL OF RESEARCH

Published under the auspices of the Graduate College of Iowa State University

All matters pertaining to subscriptions, remittances, etc. should be addressed to the Iowa State University Press, 2121 South State Avenue, Ames, Iowa 50010. Most back issues of the IOWA STATE JOURNAL OF RESEARCH are available. Single copies starting with Volume 55 are $7.50 each, plus postage. Prior issues are $4.50 each, plus postage. Because of limited stocks, payment is required prior to shipment.

The IOWA STATE JOURNAL OF RESEARCH (ISSN 0092-6435) is published quarterly in August, November, February, and May for $20.00 per year (Canada, $21.00/ other foreign countries, $25.00) by the Iowa State University Press, 2121 South State Avenue, Ames, Iowa 50010. Second-class postage paid at Ames, Iowa 50010.

POSTMASTER: Send address changes to THE IOWA STATE JOURNAL OF RESEARCH, c/o Iowa State University Press, 2121 South State Avenue, Ames, Iowa 50010.

Printed by Graphic Publishing Co., Inc., Lake Mills, Iowa 50450.

IOWA STATE JOURNAL OF RESEARCH / MAY, 1985 323-324
Vol. 59, No. 4

FROM THE EDITORS

The Plant Science Lecture Series is held annually at Iowa State University. The focus each year is on plant or crop improvement and a series of lectures is constructed to center on a topical theme. The 1984 theme was Crop Genetic Resources—Key to Future Food Production. The papers in this issue of the *Iowa State Journal of Research* represent manuscripts prepared from lectures given at Iowa State University in 1984.

The collection, preservation, evaluation, and use of crop genetic resources, collectively called *germplasm*, is a vital activity and concern in our quest to produce food and other necessities obtained from plants for an ever-expanding population of humans. Over millenia, the ancestors of our important crop plants have evolved immense pools of genetic variants that support survival in diverse and changing natural environments. Modern plant breeding has developed techniques and strategies for utilizing this genetic variation to produce cultivars of crop plants that are high yielding, resistant to disease and insects, tolerant to edaphic and climatic stresses, and nutritious.

Many of the genetic variants in the germplasm of a crop species are subtle in their expression and present only in a few genotypes. Thus, it is necessary to maintain thousands of strains of a crop to assure that most or all of its genetic variation is available for plant breeders to use. Further, as mankind occupies more of the world's land area for living space and as new high-yielding crop cultivars are adopted, the land races and populations of wild and weedy relatives of crop plants are rapidly eroded into extinction. This makes the preservation of the germplasm of our crop plants a critical and immediate need because a genetic variant once lost is lost forever.

The papers in this volume were written by experts on germplasm. Dr. Te-Tzu Chang, who wrote the chapters on germplasm (a) principles, (b) collection, (c) preservation, (d) evaluation and documentation, and (e) enhancement and utilization, is Director of the Germplasm Evaluation and Utilization Program at the International Rice Research Institute at Los Baños, the Philippines. His chapter on "Crop History and Genetic Preservations . . ." is a case history of how a crop and mankind have coevolved. In all of his chapters, Dr. Chang has used rice as an example, but the principles he elaborates are applicable to all seed-propagated plants. Dr. Major M. Goodman and

Dr. Stanley L. Krugman provide chapters on germplasm evaluation. They stress how little of the germplasm of corn and forest trees has been utilized for mankind's benefit.

This compendium presents a partial record of the state-of-the-art of germplasm collection, research, and use in 1984 and gives insight to the work that needs to be done to assure mankind's food supply. It is an important reference for persons who work directly on germplasm and for plant breeders who utilize this natural resource.

Kenneth J. Frey, Coordinator
Plant Science Lecture Series

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PRINCIPLES OF GENETIC CONSERVATION[1]

Te-Tzu Chang[2]

ABSTRACT. Rapid increases in human population necessitate the conservation of natural resources of which plant germplasm is one of the components most vital to human welfare. Since the dawn of agriculture, plant germplasm has been continually dwindling. The erosion of crop germplasm was accelerated by recent progress in plant breeding. Farmers' adoption of F_1 hybrids, semidwarf wheats, and semidwarf rices has further reduced the genetic base of staple food crops. Conservation of the existing genetic resources and reinstatement of genetic diversity in major food crops are imperative to feeding the ever-growing population especially in the developing world.

The evolutionary history of conserving crop germplasm is retraced. Successful explorations and introductions led to the appreciation of sampling and acquisition of broader spectra of genetic resources. Large-scale replacement of the unimproved land races after World War II aroused the concern of crop scientists. Conferences and consultations preceded some of the significant strides in genetic conservation. Since the 1960s the international agricultural research centers (IARCs), including the IBPGR, have assumed major responsibilities for the systematic collection, preservation, evaluation, distribution, and use of the food staples.

This paper reviews the spectrum of genetic resources, the usefulness of different segments, conservation targets, conservation systems, and strategies for conserving and using the irreplaceable crop germplasm.

Index Descriptors: crop germplasm (or genetic resources), genetic conservation, plant exploration, plant introduction, genetic erosion, field collection, gene banks, base collection, active collection, spectrum of genetic resources, land races, wild species, weed races, conservation strategy, conservation systems.

INTRODUCTION

Importance and Scope of Conservation

A widely quoted definition of conservation describes it as "the management of human use of the biosphere (that is, all living things) so that it may yield the greatest sustainable benefit to present generations while maintaining its potential to meet the needs and

[1]Editor's note: A single **Literature Cited** for this and the other papers by Dr. Chang follows the last of the series. Appendices include a list of acronym definitions and a list of common names together with applicable scientific names of plant species mentioned in the papers.

[2]Principal Scientist and Head, International Rice Germplasm Center (IRGC), International Rice Research Institute (IRRI), P. O. Box 933, Manila, Philippines.

aspiration of future generations" (IUCN-UNEP-WWF, 1980). Thus, conservation includes preservation, sustainable use, enhancement, and restoration. As a means of development, maintenance of the ecosystems in the interest of human economies should be integrated with sound management (Holdgate, 1978; Prescott-Allen and Prescott-Allen, 1982).

Much of the public interest in biological conservation in the United States was aroused by Rachel Carson's 1962 book, *Silent Spring*, which was followed by *Since Silent Spring* (Graham, 1970). The books, together with many other publications of the past two decades, led to the widespread awareness that man's use or abuse of his natural environment could result in the destruction, conservation, or enhancement of the natural resources in ever-expanding dimensions.

The world is facing social, economic, and political decisions, both national and international, which are sorely needed to regulate and rationalize man's actions. These decisions will influence the future welfare of mankind.

Need for More Food from Plants

Plants furnish the base for all forms of life on earth. Among the higher plants, about 240,000 flowering species are found in the world, of which as many as 50,000 tropical species will be threatened or become extinct at the end of this century (Raven, 1976).

At least 3,000 species have been used for food at one time or another. The staple food crops are now reduced to fifteen species (Mangelsdorf, 1966). Presently, only 30 crops are produced annually in excess of 10 million metric tons. Seven of these crops—wheat, rice, maize, potato, barley, sweet potato, and cassava—are now widely grown and exceed 100 million metric tons each in gross annual production. In terms of edible dry matter, the 12 major crops are wheat, maize, rice, barley, potato, soybean, sugarcane, sorghum, sweet potato, oat, millet, and cassava (Harlan and Starks, 1980). All these crops originated from wild species by undergoing domestication, selection, dispersal, mutation, hybridization, and differentiation-selection cycles. Introgression has undoubtedly played an important role in the evolutionary pathway of several major cereal crops and enriched their gene pools (Harlan, 1961, 1965, 1975a, 1976b; Chang, 1976a, 1976b).

The sharp increases in the world's human population following the Neolithic Revolution (about 10,000 B.C.) and the Industrial Revolution

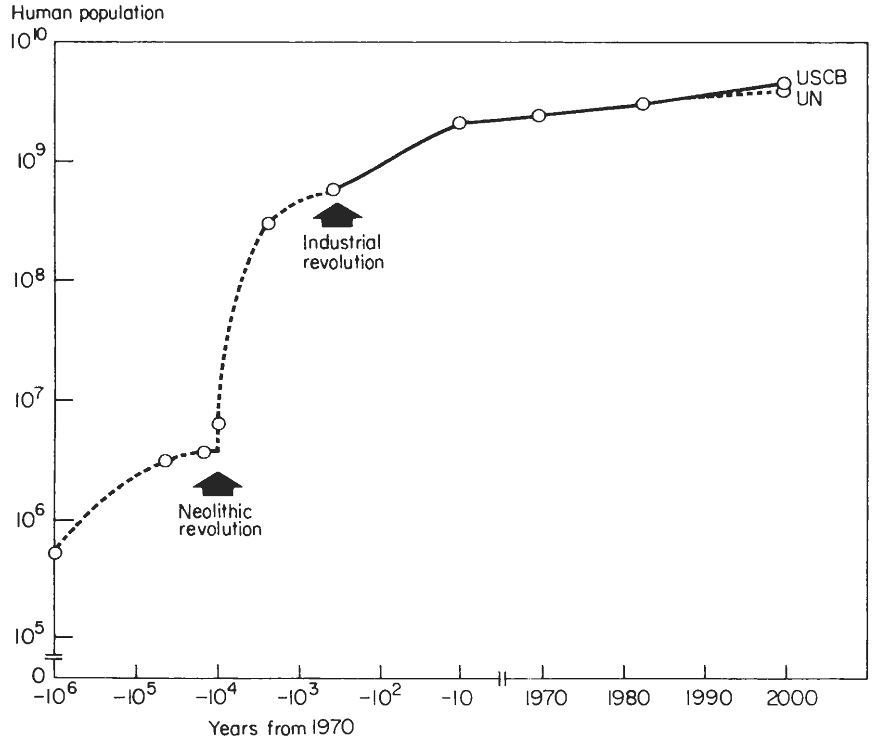

Figure 1. The growth of human population during the last million years (adapted and expanded from Bennett, 1971). Projections were based on August 1983 U. S. Census Bureau report and 1980 United Nations Population Studies No. 78.

(began about 1760 in England), and the continuing trend are depicted in Figure 1 (adapted from Bennett, 1971). The population explosion in the second half of this century has brought overcrowding and malnutrition to the populous nations in the developing world. Despite the "Green Revolution"in wheat and rice, the significant increases in food production have barely kept pace with the increases in human population, and mainly because of high population rates, the per capita food production in the developing countries has lagged behind demand since the early 1970s (IRRI, 1982a). By the year 2000 the world's human population will have risen from 4.72 billion in 1983 to between 6.12 billion (UN, 1981) and 6.34 billion (Chang, 1984a).

The prospects for quantum jumps in food production in the future appear less promising than those of several decades ago, because much of the arable land in monsoonal Asia has been developed and used. Undeveloped, but potentially usable land, is found only in Brazil and parts of Africa. Use of marginal land will destroy the existing ecosystems by deforestation or drainage. Efficient irrigation facilities have already been constructed. Future growth in food production will depend on further improvement in crop yield per unit of land and more efficient farming systems to produce more food per hectare per year. Production costs and the use of agricultural chemicals deleterious to the environment should be reduced.

Genetic Erosion of Crop Germplasm

Among the natural resources, the germplasm or genetic resources of crop plants have seen a sharp depletion in both the number of crop species and the genetic diversity expressed by the amount of genetic variation within a species since the beginning of scientific plant breeding (see papers by Frankel and Bennett, 1970b; National Academy of Sciences, 1972; Frankel, 1973, 1974; Harlan, 1975a). Along with the rapid pace of development during the last three decades, the genetic resources of crop plants have been dwindling or even vanishing at an alarming pace. The genetic base of the major food crops suffered a sharp reduction when the farmers, consumers, processors, and governments demanded genetic uniformity among the new varieties. The rapid spread of improved varieties has intensified the displacement of the traditional unimproved cultivars (land races) and accelerated their extinction. The trend toward greater uniformity has increased the potential genetic vulnerability of the major crops to epidemics of diseases and insects (Anon., 1969; National Academy of Sciences, 1972). Moreover, the broad genetic base required for further genetic improvement continues to shrink (Creech and Reitz, 1971). Paradoxically, genetic erosion is a by-product of successful plant breeding (Paddock, 1970; Hawkes, 1983).

Need to Conserve Genetic Resources for Future Needs

Plant breeders have been drawing heavily on existing reservoirs of genetic variation for the impressive record of progress achieved in the past century or so. Mutations, both spontaneous and induced, have provided additional, though small, genes to the pool.

Future plant breeding efforts will depend on a continuing and expanding supply of genetic resources. The urgent task facing all users of crop germplasm is rescuing and preserving the dwindling resources, which have not been properly conserved, to meet the following imminent needs:

1. To minimize damage by major diseases and insects.
2. To control new pests or new biotypes of a pest.
3. To tolerate adverse environments—drought, adverse soil factors, excess water, extreme temperatures, and pollutants.
4. To extend cropping into new areas—new environments, fauna, and flora.
5. To improve physical/nutritive quality.
6. To increase physiological efficiency in dry matter and grain production (Chang et al., 1979).

Meanwhile, measures should be taken to safeguard germplasm being maintained in various germplasm banks which are also facing the threat of genetic erosion through loss or neglect (Reitz, 1976; Mengesha and Rao, 1982; IBPGR, 1983a; Goodman, 1984). Genetic erosion is an irreversible process.

Finally, many national programs need to be strengthened to make full use of the available germplasm. Collaboration on national and international levels should be provided so that free exchanges are assured and crop scientists can adequately evaluate and use the gene pools. Cooperative and multidisciplinary efforts are also needed to provide security for the conserved stocks, either as *in situ* or *ex situ* collections. Thus, major portions of crop germplasm may be conserved for use by the present and future generations of mankind.

Thus, the preservation of genetic diversity is both a matter of insurance and investment for sustaining and improving future food resources. It is also a matter of moral principle to deter the extinction of useful plant species (IUCN-UNEP-WWF, 1980).

THE BEGINNING OF BIOLOGICAL CONSERVATION

Until the dawn of the neolithic era, sometimes known as the Neolithic Revolution, man depended entirely on the immediate environment for his food, which consisted of plants and animals in the wild obtained by hunting, trapping, fishing, and gathering. Within the radius of their travel on foot, the Advanced and Late Hunters maintained a kind of equilibrium among the human population, the sources of food available from wildlife, and the surrounding environment.

As rudimentary agriculture began to grow in several cradles of agriculture about 10,000 years ago, the Late Hunters settled on sites where the domestication of plants and animals was compatible with the surrounding environment. The settled life pattern led to the formation of communities. This socio-political change brought about a new awareness of the variable environment which determined the abundance or scarcity of food. Religious cults and customs related to environmental fragility are undoubtedly one of the products of this change.

Because populations grew faster in a settled life pattern than in a nomadic style, population pressure led to the recognition of the need to conserve biological resources so that a sustainable food supply within the community could be ensured. Soon after, human migration also took on a greater dimension to cope with the dwindling food sources.

In China the teachings of Confucius (551-479 B.C.) about the necessity of conserving animal resources during fishing and hunting of bird eggs indicates an early awareness of the need. During the Spring-Autumn and the Warring States Periods (722-221 B.C.), the Chinese governments established decrees to protect forests. Subsequent decrees included controls on hunting, fishing, grass cutting, burning of forests, and animal slaughter. Officers called Yu-Jen (meaning mountain officer) were appointed to manage the forests (Zhu, 1982). Similar measures were initiated in other old cradles of civilization. Soil conservation measures are a more recent outgrowth of biological conservation ethics.

Man's awareness of the need to maintain a balanced biotic environment to ensure a sustained supply of food, fiber, and other necessities signaled the advent of a higher state of civilization.

TRANSFORMATION FROM EXPLORATION INTRODUCTION TO GENETIC CONSERVATION

Plant Exploration and Introduction

Early migrants must have carried cereals and grain legumes with them while moving from one homestead to another. The grains served as both food and merchandise. For instance rice was introduced into Mexico from Spain in a cargo mixed with wheat (Lu and Chang, 1980).

The earliest form of plant introduction was partly done by traders, including the sea-faring ones who carried plants across oceans. Since the sixteenth century, some of the large trading companies of European countries took on massive introduction efforts to maintain and monopolize their hold on plantation crops (Brockway, 1979).

The earliest government-directed plant collection expedition was that sent by Egyptian pharaoh Sankhkere (about 4,500 B.C.) to the Gulf of Aden in search of cinnamon and cassia. A thousand years later, Queen Hatshepsut of Egypt sent ships to the coast of East Africa in search of new plants, and the Egyptian armies procured numerous introductions (Burgess, 1971; Moore, 1982).

The most massive effort was the importation of the Champa rices of central Vietnam by the Chinese emperor Chen-Tsung of the Sung Dynasty around 1010 A.D. The early-maturing and drought-resistant (perhaps drought escaping) rices have played a significant role in the rapid increase in rice production as well as in the population growth of China in the centuries that followed (Ho, 1956).

Many British, French, Spanish, and Dutch botanists actively explored and acquired little-used plants which later became export crops (Lemmons, 1969; Moore, 1982). Rubber, coffee, cocoa, banana, sugarcane, cotton, cinchona, spices, and ornamentals were the spoils of such exploitations. The United States Department of Agriculture (USDA) also sent plant explorers abroad who greatly enriched the cultivated crops and trees of North America. David Fairchild and Frank N. Meyer are giants among these plant collectors (Burgess, 1971).

Genetic Conservation Measures

Genetic conservation is a relatively young venture, although it had its roots in part in the pioneering studies on variability within a species by Charles Darwin (1868) and on plant origin, dispersal, and diversity by De Candolle (1882) and Vavilov (1926). Vavilov and his Russian colleagues made the most extensive collection of cultivated plants, followed by systematic studies (Vavilov, 1951, 1957). Vavilov's proposal of recognizing "centers of origin" (more appropriately, "centers of diversity") aroused great interest in plant exploration and botanical analyses.

A germplasm bank of unprecedented size (about 200,000 varieties and samples in 1940) was established at the All-Union Institute of Plant Industry in Leningrad (later named the N. I. Vavilov Institute of Plant Industry). The collections were reduced during World War II. New acquisitions were made after the war (Brezhnev, 1970). Some of the unadapted materials were probably maintained more like botanical specimens than living collections. Long-term seed storage facilities were not established until the 1970s (Plucknett et al., 1983). National interest in crop germplasm remains high (Reitz, 1976).

Although the need to conserve genetic stocks and land races was voiced before and during World War II by participants to the 1932 International Congress of Genetics (Wilkes, 1983) and by workers such as Harlan and Martini (1936) and Landauer (1945), the message was not heeded by many plant breeders at that time. It was from the mid-1950s to 1970 when the rapid disappearance of traditional cultivars in many areas of the world where scientific plant breeding had been successful, that worldwide interest in field collection for genetic conservation was stimulated (Harlan, 1956, 1961; Whyte, 1958; Wallace, 1961; James, 1961; Whyte and Julen, 1963).

Systematic and thorough collections were implemented by various teams on the following crops:

1. Races of maize in Central and South America, by the staff of Rockefeller Foundation (RF) country programs and their counterparts in national programs under the guidance of a U.S. NAS/NRC Committee on the Preservation of Indigenous Strains of Maize (see Brown, 1975; Timothy and Goodman, 1979).
2. Pasture species of the Mediterranean region, by a FAO-CSIRO team (see Whyte, 1958).
3. The common potato in South and Central America, by J. G. Hawkes and workers of Mexico and Peru (Hawkes, 1970) and the Rockefeller Foundation staff (International Potato Center, 1973).
4. Wheats of Iran, by Garibagli and Kuckuck (Kuckuck, 1970).

5. Sorghum and millet in India, by the Indian Agricultural Research Institute and Rockefeller Foundation staff (RF, 1970; Murty et al., 1976a, 1976b); sorghum in Ethiopia, by a RF-USDA team (Creech, 1970).
6. Wild relatives of wheat in Karakorum, Hindukush, Afghanistan, and Iran (Kihara, 1959) and wild relatives of rice in monsoonal Asia and West Africa, by the staff of the National Institute of Genetics, Japan, under a series of Rockefeller Foundation grants (Kihara et al., 1965; Oka and Chang, 1964). Other sizable collections of rice were made in Indo-China and Thailand by the Japanese Society of Ethnology (Hamada, 1965) and in South and Southeast Asia by the Tottori University Survey Team of Japan (Watabe, 1980).
7. Species of peanuts (*Arachis*) in South America from 1959 to 1967 and 1976 to 1983 (Gregory et al., 1973; Hammons, 1976; Simpson, 1984).
8. Safflower, by P. F. Knowles and co-workers (Knowles, 1969, 1977).
9. Wild species of tomato, by C. M. Rick and co-workers (Rick, 1973, 1977, 1979).
10. Traditional rice varieties of major producing countries in Asia by national and international teams (Love, 1954; Chang, 1970; Sharma et al., 1971; Chang and Perez, 1975; Nagamatsu and Omura, 1975; IRRI-IBPGR, 1978, 1983).

During the 1950s awareness of agricultural scientists of the large-scale replacement of land races and minor varieties by the improved (advanced) cultivars led to the establishment of large seedbanks equipped with refrigerated storage facilities. In the U. S. the National Seed Storage Laboratory (NSSL) of the USDA was built at Fort Collins, Colorado, in 1958 (James, 1961; Bass, 1979) to augment the storage facilities of the USDA at Beltsville, Maryland. This was followed by (1) the Japanese seed storage center built in 1965 at Hiratsuka (Ito and Kumagai, 1969) which was later moved to Tsukuba (Kumagai, 1979; Kawakami and Fujii, 1981), (2) the Italian seed bank at Bari, about 1972 (Porceddu, 1979), and (3) German seed bank (FAL) at Braunschweig (FRG), about 1974 (Hondelmann, 1979). Other major gene-banks of the world are listed by Chang et al. (1979) and Ng and Williams (1979).

Soon after several International Agricultural Research Centers (IARCs) were founded in the 1960s, each of the crop-oriented centers built and expanded its germplasm storage facilities. These centers under the CGIAR system are the IRRI (Los Baños, Philippines) for rice; CIMMYT (El Batan, Mexico) for maize; IITA (Ibadan, Nigeria) for African rice, cowpea, sweet potato, and other root crops; ICRISAT (Patancheru, India) for sorghum, millets, and grain legumes; CIAT (Cali, Columbia) for beans and cassava; CIP (Lima, Peru) for the common potato; and ICARDA (Aleppo, Syria) for broadbeans, barley, lentil and durum wheat. The above IARCs are located in the primary centers of crop diversity. A regional center, the AVRDC (Shanhua, Taiwan, China), has sizable collections of soybeans, Chinese cabbage, mungbean, sweet potato, tomato, and other vegetables (see Plucknett et al., 1983).

The FAO and IBPGR have made surveys of germplasm collections in different banks of the world (Gullberg, 1971; Ng and Williams, 1979; Ayad and Anishetty, 1980; Damania and Williams, 1980; Ayad et al., 1980a, 1980b; Toll et al., 1980; Croston and Williams, 1981; Acheampong et al., 1984). Additional information on crop collections may be found in recent reviews by Chang et al. (1979), Harlan and Starks (1980), and Plucknett et al. (1983). Recent information on Chinese crop germplasm may be found in a report of the Rockefeller Foundation (1980).

Beginning in the mid-1950s, a series of international meetings helped set the stage for a systematic approach to the conservation of plant genetic resources. The FAO was a prominent sponsor or cosponsor of such meetings (Whyte, 1958; Hawkes, 1983). The major conferences were:

1. 1961—Technical Meeting on Plant Exploration and Introduction, held at FAO, Rome (Whyte and Julen, 1963).
2. 1967—FAO/IBP Technical Conference on the Exploration, Utilization and Conservation of Plant Genetic Resources, held at FAO, Rome (Bennett, 1968; Frankel and Bennett, 1970a).
3. 1972—TAC/FAO *ad hoc* Working Group on the Collection, Evaluation and Conservation of Plant Genetic Resources (TAC/FAO, 1972).
4. 1973—FAO/IBP Technical Conference on the Conservation of Crop Genetic Resources (Frankel and Hawkes, 1975a).
5. 1981—FAO/UNEP/IBPGR International Conference on Crop Genetic Resources (FAO, 1981).

The 1961 meeting led to the creation of the FAO Panel of Experts on Plant Exploration and Introduction and the establishment of the Regional Crop Research and Introduction Center at Izmir, Turkey (see Hawkes, 1983). The 1972 TAC-FAO-UNDP-sponsored meeting at

Beltsville, Maryland (TAC-FAO, 1972), followed by the 1972 UN Conference on the Human Environment at Stockholm (see Frankel, 1972), led to the establishment of the International Board for Plant Genetic Resources (IBPGR) in 1974.

The Rockefeller Foundation (RF) also convened study groups in 1971 (Creech and Reitz, 1971; Anon., 1973; Brown, 1975). It has funded the exploration of wild wheats and rices by Japanese geneticists, the collection of potatoes in Latin America, and the collection of sorghums in India and Ethiopia. Its assistance also made possible IRRI's initial efforts on rice collection during 1972-74. The RF is assisting China in establishing a long-term seed storage facility in Beijing (Rockefeller Foundation, 1980).

After the outbreak of the southern corn leaf blight in 1970-71 in the U.S., many papers written by plant pathologists and geneticists together with the National Research Council Agricultural Board survey (National Academy of Sciences, 1972) focused on the need to reinstate genetic diversity in major crops. These papers were significant in arousing worldwide attention to the importance of maintaining genetic diversity in major crops. Concurrent developments led to the formalization of the National Plant Germplasm System (NPGS) in the U.S. (Anon., 1977) and the establishment of the National Plant Genetic Resources Board (Anon., 1979).

Since its establishment in 1974, the IBPGR has redefined priorities for crop conservation in different geographic regions, assisted in the organization of international and regional networks, catalyzed associations of gene banks by crop or geographic region, formed a number of crop advisory committees, sponsored workshops, funded 250 field collection missions in more than 70 countries, supported research on seed physiology and tissue culture, published 37 descriptor bulletins for different crops and bibliographies, upgraded the seed storage facilities of several national gene banks, and assisted the training of young conservationists (Hawkes, 1983; IBPGR, [undated]; Wilkes, 1983).

The International Rice Research Institute (IRRI) is the oldest of the international agricultural research centers under the CGIAR system. IRRI established its rice germplasm bank at the beginning of its operations in 1961. Its rice collection, obtained in collaboration with many rice-growing countries and other centers, has surpassed 70,000 accessions at the end of 1983, of which about 36,000 samples were collected from farmers' fields since 1971 (Chang, 1983b). The International Rice Germplasm Center (IRGC) at IRRI conducts a comprehensive program of functions related to genetic resources conservation and thus qualifies as a crop-specific genetic resources center (Chang et al., 1975b; Frankel, 1975). The genetic resources program of IRRI is widely recognized as a model for other centers (Seetharaman et al., 1972; Frankel and Hawkes, 1975b; Frankel, 1977; Harlan, 1977; IBPGR, 1978, 1979a; Anon., 1984a).

GENETIC RESOURCES OF A CULTIGEN

Crop Evolution and Agricultural Origins

Crop improvement depends on the genetic variations accumulated during the long process of evolution and further enriched by mutation, natural hybridization, ecogenetic differentiation and maintenance by natural selection, and dispersal and selection by human beings. The genetic resources present in the unimproved and rather primitive cultivars—the land races—were extremely rich and largely undisturbed, until progressive agriculture began in the middle of the nineteenth century in the developed countries, or, in the case of China, until the government extended the introduced Champa rices in the eastern and southern provinces in the eleventh century.

The richest diversity was generally found in the primary areas of diversity (corresponding to Vavilov's "centers of origin") where additional variations were contributed by introgression from related wild and weed races as well as by selection under adverse conditons. After a primitive domesticate and its associated wild/weed relatives have been introduced into another area or the progenitor had a large noncentric distribution (Harlan, 1971), a secondary center of diversity might develop into another region of crop diversity. Such areas also represent centers of agricultural origins.

Adjacent to the main centers of agriculture, a number of minor centers of diversity may evolve through cultural diffusion (Hawkes, 1983). Rice varieties of Korea, Japan, and the USSR belong to this pattern (Chang, 1976b; Lu and Chang, 1980).

The papers by Vavilov (1926, 1935, 1951, 1957), Schiemann (1943), Zohary (1970), Harlan (1951, 1970, 1971), Zhukovsky (1970), Kupzov (1976), and Hawkes (1983) offer additional information on these "centers." An understanding of the different postulates on crop origin in relation to agricultural development would help a plant breeder to efficiently exploit existing genetic resources.

Spectrum of Genetic Resources

Figure 2 depicts the full spectrum of genetic resources that can be found in a cultigen of great diversity and ancient agricultural origin, such as rice and wheat (IBP, 1966; Creech and Reitz, 1971; Chang, 1976e; Chang et al., 1979). The major categories may be briefly described.

1. Related wild species and weed races in the same genus; related genera, found in the regions of primary or secondary diversity. This class may include undomesticated wild species which are consumed by man as food or for other uses, e.g., forestry species, medicinal plants, and pasture species for chemical industries.
2. Unimproved land races (folk varieties) and special-purpose types from the areas of diversity which are adapted to specific ecological niches or provide special dietary/religious needs. Inherent diversity is a unique feature of the land races. Many land races are varietal mixtures.
3. Pure-line selections or open-pollinated commercial varieties from old agricultural areas where production levels remain largely unchanged in the last half century.
4. Obsolete varieties which can be found only in germplasm collections. Ecostrains of obsolete cultivars may persist in other areas.
5. Advanced cultivars: modern elite varieties (HYV, MV) and F_1 hybrids developed by scientific breeding for and grown in areas of modern intensive agriculture. Composites and synthetics evolved through plant breeding also belong to this class.
6. Other products of plant breeding programs or genetical studies, which include breeding lines, breeding stocks, mutants, gene markers, genetic stocks, induced polyploids, aneuploids, intergeneric and interspecific hybrids, and cytoplasmic sources.

These categories also indicate first an evolutionary continuum linking prehistoric wild forms with present-day cultivars, and second an ecological continuum linking wild and partly domesticated taxa with domesticated forms (Frankel and Soule, 1981)

Genetic Diversity Among Segments of Germplasm

The evolutionary pathway from a wild species to a domesticate, either by direct descent or through natural hybridization, is inevitably

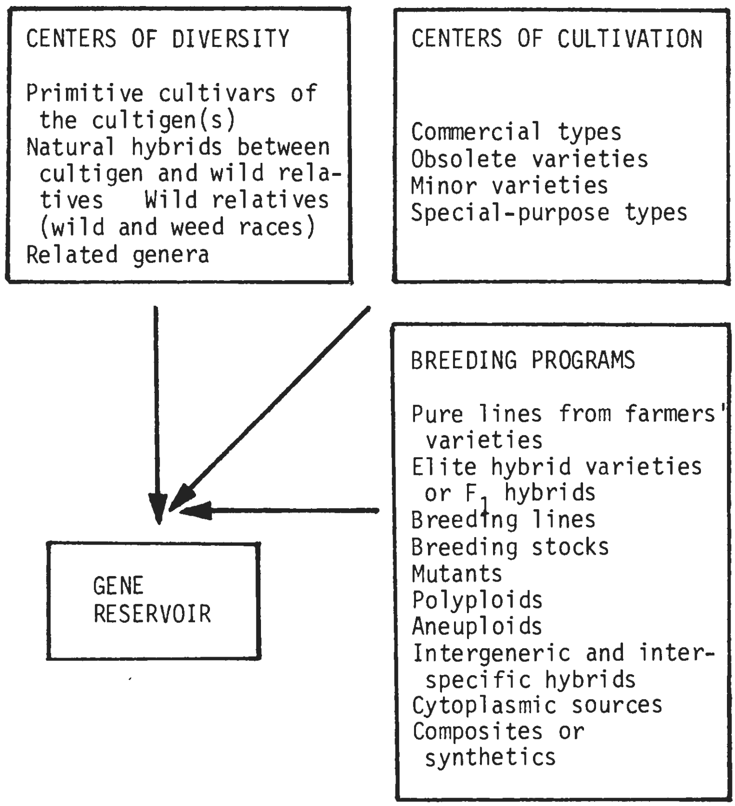

Figure 2. The full spectrum of germplasm in a crop species (cultigen) and its wild relatives. The sources are also indicated.

accompanied by a reduction in the number of species being retained and used and concurrently by an increase in intraspecific diversity. The process in the domesticates took a turn when intensive agriculture and scientific breeding greatly decreased the intraspecific diversity as the ecosystem changed from a generalized natural system to a specialized artificial one (Harris, 1969; Harlan, 1975a; Frankel, 1977).

The important relationship among wild and domesticated species and the dynamic changes in the diversity of the domesticate have been described by Frankel (1977). Such information is vital to both conservation and use.

Genetic diversity within a group confers potential for further improvement, whereas heterogeneity within a population offers low commercial or agronomic value in modern agriculture. A comparative listing of various segments in these aspects is in Table 1 (Chang, 1976c). The obvious choice in plant breeding is to use the modern cultivars as the base, adding the desired genes or gene-complexes from the land races, special types or wild species, depending on the need. In gene deployment, rotation, and pyramiding, even obsolete varieties can be re-used.

Perils of Genetic Uniformity

The following examples of the devastating effects of major epidemics during the last 150 years as a result of the diminishing genetic base point to the importance of maintaining genetic diversity in major crops:

1. The famine of the 1840s in Ireland due to the potato late blight (*Phytophthora infestans*) (see NAS, 1972).
2. The wheatless days of 1917 in the U.S. due to stem rust epidemics (*Puccinia graminis*) (see NAS, 1972).
3. The great Bengal famine of India in 1943 associated with the brown spot disease of rice (*Cochliobolus miyabeanus*) and a typhoon (see NAS, 1972).
4. The complete elimination in the mid-1940s of all oats derived from the variety Victoria in the U.S., due to the Victoria blight disease caused by *Cochliobolus victoriae* (see NAS, 1972).
5. The southern corn leaf blight epidemic (*Cochliobolus heterostrophus*) of 1970-71 on all U.S. corn hybrids carrying the T-type cytoplasmic male sterility (NAS, 1972).
6. The rapid shift of the rice brown planthopper (*Nilaparvata lugens*) from biotype 1 to biotype 2 during 1974-76, when

Table 1. Genetic composition, productivity level, and potential value in breeding of different gene sources.

Group	Diversity within group	Homogeneity within a strain or population	Agronomic or commercial value	Genetic potential in breeding
Modern elite cultivars	Low to moderate	Very high	Very high	Moderately high
Principal commercial types	Moderately low to moderate	Moderate to high	Moderately high	Moderate
Minor varieties	Moderately high to high	Moderately low to moderate	Moderate	Moderately high
Specialty types	Moderately low to moderate	Moderately high	Moderately low	High
Obsolete types	Moderate to high	Moderately high to high	Moderately low to moderate	Moderately low

(continued on the next page)

Table 1 (cont.). Genetic composition, productivity level, and potential value in breeding of different gene sources.

Group	Diversity within group	Homogeneity within a strain or population	Agronomic or commercial value	Genetic potential in breeding
Breeding stocks	Moderately low to moderately high	Moderate for lines; low for bulks	Most variable	Moderate to high
Mutants	Moderately low to moderate	Moderately high to high	Mostly low; few moderately high to high	Mostly low
Primitive types	Moderately high to high	Low to moderate	Moderately low	Moderately high to high
Weed races	Moderately high to high	Low to moderately low	Low	Moderate to moderately high
Wild species	Moderately low to moderate	Low to moderately low	Very low	Moderate to high

large areas in the Philippines and in Indonesia were planted to a few semidwarf rices (Chang et al., 1979). The cycle was repeated in 1982-83 when IR36 was widely grown and multicropped in the same areas (Chang, 1984a).

Although uniformity within a crop leads to genetic vulnerability, reinstatement of genetic diversity is one of the most effective means of protection against such vulnerability. On the other hand, the sequential release of varieties with vertical resistance based on major genes can only lead to 'boom and bust' cycles as described by Robinson (1976). Where the choice of pesticides is limited, integrated pest control measures and community efforts in cultural management should be adopted to supplement genetic resistance (Chang, 1979a).

The potential hazards of genetic uniformity leading to the vulnerability of crops are even greater today in some crops such as rice (Table 2) than in the early 1970s when the problem became widely recognized (Anon., 1969; Frankel, 1970a; Harlan, 1972a; NAS, 1972; Day, 1973). Recent epidemics in rice associated with the widely grown and multiple-cropped semidwarfs have been pointed out (Chang, 1979a, 1984a).

Genetic diversity, both genic and cytoplasmic, within a crop is needed to cope with the production constraints common to intensive and continuous monocropping in the tropics. Genetic diversity will help:

1. Slow down genetic changes in a major pest or pathogen.
2. Prevent evolution of a minor pest into a major pest.
3. Minimize yield reductions due to unusual climatic changes.
4. Counterbalance the epidemic-prone situation associated with continuous monoculture of a major crop in the tropics.
5. Provide the potential for further genetic improvement (Chang, 1976e; Chang et al., 1979).

Diversity in itself does not guarantee protection unless that diverse gene pool includes genetic resistance to, or tolerance for, the production problem concerned (Brown, 1983). Farmers, especially those in low-input areas, are conservative and individualistic in choosing different varieties, which helps to maintain some of the diversity in the crop (Chang, 1984a; Duvick, 1984).

Land Races, Wild Species, and Weed Races

Among the six categories of genetic resources, the land races and wild species deserve special mention because they offer the largest potential for use in plant breeding.

Table 2. Examples of crop uniformity for single traits (expanded from Day, 1973).

Crop	Trait
Beans	stringlessness
Maize	Texas cytoplasmic male-sterility high lysine content (*opaque*-2)
Rice	semidwarfism photoperiod insensitivity Cina cytoplasm in tropical semidwarfs Wild Abortive cytoplasm in Chinese hybrid rices
Sorghum	Milo source of cytoplasmic male serility
Wheat	semidwarfism photoperiod insensitivity cytoplasmic male-sterility from *Triticum timopheevi*

Land races evolved both by natural and human selection under conditions of low-input cultivation and were adapted to the local environment where they were cultivated for ages. Land races are marked by diversification among races, within a race between sites and populations, and within sites and populations. Their genetic diversity expressed over space and time is likely to provide improved protection against climatic extremes and epidemics (Harlan, 1975b). Moreover, land races have been shown to be capable of providing high yield potentials to plant breeders, if properly used in crosses. However, the main use of land races has been and will remain as donors of desirable genes (Frankel and Soule, 1981).

Up to the present, most germplasm collections are deficient in geographic coverage, number, and information on the potential of the land races. Land races also present challenges during field sampling, nomenclature, maintenance of genetic integrity, and systematic description (Kuckuck, 1970; Chang, 1972b, 1976c, 1980; Frankel and Soule, 1981).

The wild species and the weed races represent the highest level of genetic heterozygosity and heterogeneity among the different classes of germplasm. They generally have higher rates of natural outcrossing than the domesticates. *Oryza longistaminata* A. Chev. *et* Roehr., a perennial wild rice of Africa, is even self-incompatible.

The genetic variability provided by the wild species and weed races is a source of: (1) resistance to diseases and insects, controlled mainly by major genes; (2) tolerance for extreme environments such as salinity, desiccation, waterlogging, and frost; (3) high vegetative vigor in sugarcane and potatoes; (4) high protein content in cassava and oats, (5) greater fiber strength in cotton; (6) higher oil content in oil palm, (7) greater ecological adaptation in grapes; (8) stronger roots in pineapple; (9) short stature in wheat; (10) greater biomass growth rates and delayed senescence, which lead to higher yields, in three cereals; and (11) cytoplasmic male sterility and restorer systems in many crops. Summaries of these findings may be found in Harlan (1976b), Hawkes (1977), Frankel and Soule (1981), Prescott-Allen and Prescott-Allen (1981, 1982), and Frey (1983a).

For most crops the wild species and weed races are poorly collected, inadequately maintained, or both. Like the land races, the wild species of rice rapidly disappeared in the tribal reserves of India because of development factors (IBPGR-IRRI Rice Advisory Committee, 1982). On the other hand, field collection and maintenance of the wild species, as exemplified by the genus *Oryza*, also present special challenges (Chang, 1976e; IBPGR-IRRI Rice Advisory Committee, 1982; Oka, 1983; Sharma, 1983).

Targets of Conservation

Genetic conservation may be described as a formulation of policies and programs which will allow the long-term preservation of genetic resources either *in situ* or *ex situ*, in such a manner that the potential for continuing evolution or improvement would be sustained. Thus, conservation is more inclusive than preservation; the latter provides only for maintenance but not for evolutionary modifications under different environments.

It is of course impossible as well as impractical to conserve all of the available gene resources—vast resources had vanished before the advent of agriculture. The primary goal should be to conserve as many representative samples of existing germplasm as human resources permit. Priority should be given to those being threatened by extinction or displacement. Efforts should be extended to those collections being threatened by "genetic erosion" in inadequately managed germplasm or seed banks. Frankel and Soule (1981) called such an approach the "genetics of scarcity."

In genetic terms, the targets of conservation may be one or more of the following: (1) a nucleotide pair—a muton, (2) a desirable or favorable allele of a gene, (3) a gene-complex controlling a desirable trait, (4) a co-adapted gene complex, (5) a chromosomal segment, and (6) a cytoplasmic component or components.

Although exploration and collection for introduction purposes generally have specific objectives, genetic conservation partly covers the known genes and partly aims to save plant materials of yet unknown genetic potential. The latter category must necessarily be the primary responsibility of the conservationists because of the large number of species included. An effective conservation program should be planned to maintain such materials in reserve for unexpected needs.

The salient point in genetic conservation is that once a genetic component is lost from human control, it is impossible to reconstitute it by known scientific means. Hence, the term "irreplaceable germplasm" aptly describes the irreversible nature of genetic erosion (Harlan and Martini, 1936; Frankel, 1967).

Conservation Systems

A comprehensive genetic conservation program for a given crop, using *ex situ* preservation, should include the following components: (1) survey, (2) acquisition/exploration and collection, (3) maintenance/multiplication/rejuvenation, (4) evaluation, (5) documentation, (6) distribution/exchange, (7) preservation, (8) training, and (9) collaborative network.

Plant quarantine facilities and measures should form part of a large genetic resources center.

Methods of conserving plant germplasm were classified by Frankel and Soule (1981) as follows:

1. Conservation *in situ*—natural reserves (dynamic type).
   a. Preservation of vast tracts to conserve plants and animals in entire biomes—extinction of species is deterred, but this has little impact on useful plants.
   b. Wild—in natural communities.
   c. Domesticates—land races in their areas of cultivation.
2. Conservation *ex situ*.

a. Domesticates in mass reservoirs (Simmonds, 1962) or genetic reserves (Dinoor, 1976, 1978) under the dynamic type.
b. Forest reserves (provenances) in the wild.
c. Preservation of seeds, plants, plant parts, cells, tissues, and meristem cultures under a static environment (gene banks). Botanical gardens or parks also belong to this category as the last line of defense, but they also generate useful information and provide educational benefit (Frankel and Soule, 1981).

Seed preservation is by far the most efficient means of genetic conservation. Seed or germplasm banks may be organized on the basis of projected seed longevity and seed rejuvenation cycle. Two types of seed banks are designated by the FAO Panel of Experts (see Frankel, 1975; Hawkes, 1983):

1. Base collections—seeds of 5-6% moisture content are sealed and stored at between -10° and -20° C for long-term conservation; the scope is generally comprehensive. The seeds are distributed not for use but for rejuvenation (regeneration). A duplicate site is needed for security.
2. Active collections—seeds are dried to 8 ± 1% moisture content, sealed, and stored in medium-term storage (slightly above 0° C), from which samples are drawn for distribution, exchange, multiplication, and evaluation. Active collections complement the base collection and are often associated with plant breeding or plant quarantine stations. An active center should have seed rejuvenation capability. Records on origin, handling, and distribution of accessions should be maintained.

Working collections of plant breeders and other disciplines are not considered part of the genetic conservation system. Collections of parents and other materials are generally held in short-term storage and their maintenance is subject to the whims and fancies of the breeder (Reitz, 1976; Wilkes, 1983). The evaluation data should be made available to other interested workers for use in breeding programs. Therefore, promising breeding materials such as F_1 hybrids, F_2 and F_3 bulks, and composite crosses should also be carefully stored for a period of time in order to enable other breeders to be able to have access to the materials, if and when needed (Jensen, 1962). In addition to land races and wild species of rice, the IRGC at IRRI also preserves breeding lines used in crosses, advanced selections carrying specific genes, and promising entries in the nurseries of the International Rice Testing Program.

Strategies for Conserving and Using the Biological Heritage of Crops

The genetic conservation of a major crop encompasses such a complex task involving national agencies, international organizations, private companies and institutions, individual collectors and curators, and farmers, that no single person or team can manage and maintain the collection(s) with security at this development stage. A widely distributed crop poses additional problems in assembly and exchange. For many crops the time to define the objectives and perspectives in genetic conservation is long past. It is not too late to reexamine the conservation strategy on a global basis and to develop pragmatic and realistic approaches.

An overally strategy is to enlist the participation and help of all possible agencies and persons concerned with the cause. Action plans should be developed according to priority. At the organizational level, it involves international networks (IRRI-IBPGR, 1978; IBPGR, 1983b), regional networks (IBPGR, 1977, 1979b), national programs (Anon., 1977), crop-specific committees (IBPGR, 1979b; Jones, 1984), and individual workers. At the working level, multidisciplinary cooperation across national boundaries is indispensable. To have a continual and permanent base, the activities should be institutionalized and properly funded. Such a series of events has evolved from the process of plant explorations to national programs to international networks as described in "Preservation of Crop Germplasm," the third paper of this series.

The urgent questions are: when can the periled crop germplasm be adequately sampled and collected, and how can the collected materials be safely preserved? Equally vital are the areas of evaluation, documentation, distribution, and use, but these depend largely on the size of the conserved resources and supporting resources for implementation. All six aspects are related and interwoven into the science of crop improvement. Above all, the free and open exchange of germplasm and related information must be provided.

Participation in the conservation measures must stem from all sectors of the human society. Different groups in a society can help perform their own responsibilities at four levels: (1)professional—by the scientific community of both public institutions and private enterprises in planning, implementing, and coordinating their scientific activities; (2) political—by leaders of government and communities in d eveloping policies and providing support; (3) public—by educating the public sector on the importance of genetic conservation; and (4) social—by communication among scientists and interacting with other sectors of the society (Frankel, 1973, 1974; Swaminathan, 1983b; Anon., 1984a).

The world's population stood at 4.72 billion in 1982-83. At the prevailing growth rate of 1.75% per annum, the total population will reach about 6.34 billion by the year 2000 (Chang, 1984a). Even though the Green Revolution, which began in the mid-1960s, had stalled widespread famines during that period and spurred yield increases in wheat and rice (Borlaug, 1968, 1983; Chang, 1979a), food production per capita in the developing world has lagged behind population growth in recent years (IRRI, 1982a). The impending food deficit will surface in the most populous countries of Asia and many countries in Africa, where yield per hectare is among the lowest in the world.

Where and how can we provide food for the additional 1.62 billion human beings without damaging the already deteriorating ecosystems? Increases in arable land may be feasible in Brazil and some parts of Africa but not significantly so in the most densely populated countries of Asia. The major contributions will have to come from increased yields, higher production efficiency, more intensive use of the available land, and novel food source or production processes. Crop germplasm will again serve as the gene reservoir for the genetic inputs. Therefore, it is imperative that all of us strive very hard to save the available germplasm resources as a genetic base for providing a sustained supply of food for the rapidly expanding world population in the coming decades. In the face of dwindling resources, both physical and biological, crop germplasm is one of the few and true heritages of man. Let us conserve and use it wisely and efficiently.

IOWA STATE JOURNAL OF RESEARCH MAY, 1985 349-364
Vol. 59, No. 4

COLLECTION OF CROP GERMPLASM

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ABSTRACT. The initial step in genetic conservation is the assemblage of crop germplasm from farm fields and wild habitats. Successful collection operations require broad-based consultation and advance planning, adequate funding, a team of competent collectors, knowledgeable guides, and personal dedication of team members to the mission. Recent collections primarily involved general survey and sampling or recanvassing. This paper describes the preparations necessary for a systematic approach to field collection: survey, setting of regional and crop priorities, formulation of sampling strategy, field sampling, processing of collected samples, compliance with plant quarantine measures, and documentation. Experiences drawn from the field exploration of potato, tomato, and rice are incorporated in the discussions. A standard field collection form is provided.

Index Descriptors: exploration, introduction, field collection, recanvassing, survey of germplasm resources, regional and crop priorities for field collection, collection team, sampling strategies, sampling sites, sampling techniques, sample size, field collection form, processing collected samples.

INTRODUCTION

The initial step in genetic conservation is the assemblage of crop germplasm from farm fields and wild habitats. Exploration and collection represent the most difficult and challenging phase in the process because: (1) they are usually implemented in remote places where physical hardships and political-military-religious obstructions are common; (2) they require scientific expertise, team spirit, knowledge of host country and prevailing customs, versatility, and good human relationship; (3) they are expensive; (4) time is inevitably too short to carry out all the desired prospecting, collection, and recording; and (5) it is not always feasible to return to the same site at a later date and find its earlier population structure intact. There is also the problem of little information on specific crops and regions in scientific literature.

A good collector should have: (1) a broad knowledge of the crop and its companion plants (wild relatives, weeds, and other crop plants grown in mixture or in the community), (2) a keen grasp of the environmental factors prevailing in the ecosystem, (3) personal dedication to the mission of salvaging the crop germplasm, and

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(4) the capacity to absorb hardships and make the best out of unforeseen conditions. Glimpses of the delights and inspirations as well as the stresses of a collector's life in the field may be obtained from the writings of veteran traveler-collectors such as Fairchild (1938), Hawkes (1941), Vavilov (1957), Rick (1973), and Harlan (1975a).

Although the field collection phase was much advocated in several international meetings and sessions of the FAO Panel held between 1961 and 1972, little action of a systematic nature resulted from the meetings and related reports for a number of years (Harlan, 1975b). The earlier efforts of the Vavilov team and the RF country programs on maize races and the common potato mentioned in the paper on the Principles of Genetic Conservation (first paper of this series) remained historic landmarks until the early 1970s.

Systematic and coordinated collection programs on an international scale began to materialize when IRRI catalyzed the rice collection program in tropical Asia (IRRI, 1972; Chang and Perez, 1975) in the early 1970s, and the newly founded IBPGR began to re-examine crop and regional priorities, convened regional workshops and set up a few regional networks, and financed a number of collection programs in the late 1970s (IBPGR Annual Reports, 1975-1982; IBPGR, undated). Some of IBPGR's collection programs were implemented by the IARCs, such as the collection of rices and grain legumes by IITA in West Africa (Ng et al., 1983) and the assemblage of Asian rices by IRRI and collaborating national programs (Chang, 1980).

TYPES OF FIELD COLLECTION

Three kinds of approaches in field collection may be recognized, although one type may lead to another.

Exploration

Exploratory collection is a survey of remote areas for specific materials of expected value and the subsequent introduction of these materials into new areas for plant breeding, agricultural production, or industrial uses. Exploration and introduction lead to organized exchanges, scientific studies, and establishment of germplasm collections for preservation (Creech, 1970). In recent years the targets of exploration were largely: (1) the threatened or endangered species in the interest of conservation and (2) little-used new crops of the tropics (NAS, 1975).

General Survey and Sampling

A systematic collection of germplasm may be implemented over a large area without special emphasis on certain materials. This type of broad and general sampling will provide an understanding of the general variability in an area and could lead to recanvassing for special types at a later date.

Recanvassing

Following a series of observations, evaluation, and documentation, the need to re-explore in a previously collected area to enrich the gene pool of certain species or special segments may arise. This approach may also apply to a species which has suddenly become threatened or is facing extinction.

PREPARATORY COMPONENTS OF A SYSTEMATIC FIELD COLLECTION PROGRAM

The recent large-scale field collection programs are generally international, multidisciplinary, well-planned, and adequately financed. Setting up a systematic program embodies the following components and sequence: (1) survey of past efforts and current status of germplasm resources, (2) setting of priorities, (3) planning and seeking funds, (4) formation and training of collection team(s), (5) formulating sampling strategy, (6) implementing field sampling, (7) processing of collected samples, (8) compliance with existing plant quarantine measures, and (9) documentation.

Crops and regions share similar concern in assigning priorities. Major gaps in existing collections are examined on the bases of crop geography, biosystematics, crop ecology, and specific goals to meet human needs through agriculture and industry.

Survey of Germplasm Resources

An in-depth survey of germplasm resources is a prerequisite to efficient and rewarding collection efforts. A survey may assume a variety of forms: (1) tracing an earlier crop specialist's experience and writing, (2) holding informal gatherings of crop scientists sharing a common interest, often in the form of crop advisory committees, and (3) convening large conferences devoted to one crop (Varnell and McCloud, 1975; IRRI-IBPGR, 1978, 1983) or several related crops (PCARR, 1982). Repeated discussions are needed to update the assessments and to provide follow-up action. Periodic meetings and communication by correspondence are important in keeping the cooperation alive. Analysis of characterization and evaluation results also aids in revising target areas, goals, and procedure.

Several publications can provide useful information on germplasm resources under different categories:

1. On a global basis for many crops: Vavilov (1926, 1951), USDA Yearbooks (1936, 1937), Frankel (1973), Zhukovsky (1975), Zeven and Zhukovsky (1975), Harlan (1975a, 1977), Simmonds (1976).
2. For groups of crops: Purseglove (1968, 1972).
3. For geographic regions:
   a. Africa: Harlan (1973), Porteres (1976), Purseglove (1976), Harris (1976).
   b. Central and South America: Hernandez (1973), Leon (1973), Heiser (1979), CATIE (1979).
   c. Mediterranean: Bennett (1973), Porceddu et al. (1982).
   d. Near East: Kjellqvist (1973).
   e. South Asia: Singh (1973), Mehra and Arora (1982), Jain and Mehra (1984).
   f. Southeast Asia and Oceania: Williams et al. (1975), SABRAO (1977), IBPGR-PCARR (1977).
   g. East Asia: Matsuo (1975), Rockefeller Foundation (1980), Williams and Creech (1981).
4. For specific crops:
   a. Wheat: Kuckuck (1970, 1975), Zohary (1970), Witcombe and Rao (1976), Witcombe and Gilani (1979).
   b. Rice: Jeypore Botanical Survey I and II (Govindaswamy, 1956; Anon., 1957), Porteres (1956, 1976), Oka and Chang (1964), Hamada (1965), Chang (1970, 1972a, 1975, 1983b), Watabe (1972), Hakim and Sharma (1974), Nagamatsu and Omura (1975), Oka et al. (1978), IRAT-ORSTOM (1977), Bezancon et al. (1978), Oka (1978), Katayama (1978), Richharia (1979), Vaughan and Chang (1980), Morishima et al. (1980), Chang et al. (1982), Ng et al. (1983).
   c. Corn: Kuleshov (1929), Wellhausen et al. (1952, 1957),

Brieger et al. (1958), Timothy et al. (1961, 1963), Mangelsdorf et al. (1967), Brandolini (1970), Brown (1960, 1975), Brown and Goodman (1977), Paterniani and Goodman (1978), Timothy and Goodman (1979).

d. Potato: Hawkes (1970, 1978), Ochoa (1973, 1975), International Potato Center (1973, 1976).
e. Barley: Takahashi (1955), Harlan (1968, 1979), Witcombe and Gilani (1979).
f. Oats: Baum (1977).
g. Sweet potato: Yen (1970, 1974).
h. Cassava: Nestel and MacIntyre (1975).
i. Soybean: Bernard (1983), Hymowitz (1983), Nelson and Bernard (1983).
j. Sorghum: Murty et al. (1967a), RF (1970), Doggett (1970), Harlan (1972b), Gebrekidan (1979), Mengesha and Rao (1982), Acheampong et al. (1984).
k. Millets: Krishnaswamy (1951), Murty et al. (1967b), Rachie (1975), Rachie and Majmuder (1980), Acheampong et al. (1984).
l. Peanut: Varnell and McCloud (1975), Banks (1976).
m. Yam: Martin (1973, 1975).
n. Tomato: Esquinas-Alcazar (1981).
o. Tropical legumes: Rachie and Roberts (1974), NAS (1979).
p. Tropical vegetables: Grubben (1977).
q. Tropical fruit trees: Sastrapradja (1973, 1975), Ho (1973).
r. Underexploited tropical plants: NAS (1975), Jain (1983).
s. Oil seed crops: Princen (1983), Jones (1983).

An interested worker should consult (a) bibliographies, such as the *Bibliography of Agriculture*, *International Rice Research Bibliography*, and *Plant Genetic Resources Bibliography* (Hawkes et al., 1983), (b) abstracts, such as *Plant Breeding Abstracts* and *Field Crops Abstracts*, (c) periodicals, such as *Economic Botany*, *Euphytica*, *Crop Science*, and *American Naturalist*, and (d) newsletters, such as the *Plant Genetic Resources Newsletter*, *IBPGR Southeast Asian Regional Newsletter*, *Diversity*, *Australian Plant Introduction Bulletin*, and the *Canadian PGRC Newsletter*.

Setting of Priorities

The setting of priorities for a given crop or group of crops should be based on geographic area, economic importance in relation to other crops in the same area, degree of threat by replacement, extinction or widespread crop failure, and the needs of the breeders.

The FAO Panel, the IBPGR board members, and various crop committees of the IBPGR have studied the relative priorities among crops and regions. Four degrees of priorities have been adopted: 1—first priority, 2—second priority, 3—third priority, and 4—lesser priority. The first set of priorities has undergone some modifications (IBPGR, 1976a) and the 1981 revision (IBPGR, 1981) of high-priority crops is partly shown in Table 1.

Priority for IRRI's participation in a cooperating rice-producing country of Asia is based on: (1) the rate at which improved cultivars replace local or traditional varieties, (2) the richness of genetic diversity and the range of environments within countries or areas, (3) the time and extent of past collection and preservation efforts, (4) the accessibility of potentially rich germplasm areas to field collectors, (5) the extent of local (in-country) support for collection, and (6) funding from an outside source.

Thus, the high-priority areas for rice have been Bangladesh, Burma, India, Indonesia, Nepal, Philippines, and Sri Lanka. Fortunately, flexibility and opportunities in timing have enabled IRRI to work cooperatively with each of these countries (Chang, 1980).

Planning and Seeking Funds

Planning well in advance is absolutely essential. Allow for at least one year's lead time.

For field collection in a foreign country, it is essential to enlist the participation of national workers from governmental, research and educational institutions at the planning stage—it will also help implementation later. It is also desirable to hold the planning session in the host country to acquire a thorough knowledge of germplasm distribution, diversity, and availability. For specific areas, local scientists and extension workers can offer valuable information.

In recent years IBPGR has become the major source of funding for field activities within its prescribed priorities. There are many other sources, public and private, which are interested in supporting field conservation projects.

Table 1. Priority among regions and crops (IBPGR, 1976a, 1981).

Region	Priority	Crop priority within each region*
Mediterranean	1	1: wheat, broadbean, sugarbeet, lentil 2: chickpea
Southwest Asia	1	1: wheat, barley, groundnut, chickpea, lentil 2: chickpea, cotton
Central Asia	1	1: wheat
South Asia	1	1: wheat, rice (in tribal areas of India), finger millet, pearl millet, maize (in Himalayas), green gram, black gram, oil seed rape, sugarcane 2: chickpea, jute
Southeast Asia	2	1: rice (in Indochina), groundnut, soybean (in Indonesia), coconut, sugarcane, sorghum 2: cassava, sweet potato
East Asia	2	1: rice, maize, foxtail millet, soybean, oil seed rape and sorghum—all in China 2: groundnut, broadbean
West Africa	2	1: wild sorghum, pearl millet; *glaberrima* rice 2: sorghum
North Africa	1	1: pearl millet, barley
Brazil	2	1: maize, *Phaseolus* beans 2: cocoa
Andean zone	2	1: quinoa, lupin 2: potato, minor tuber crops
Pacific islands	3	1: yam, coconut
East Africa	3	1: *Phaseolus* beans 2: sorghum, cowpea, cassava
Southern South America	3	1: *Phaseolus* beans 2: groundnut, cassava, cotton

*Wild relatives included.

OPERATIONAL COMPONENTS OF A SYSTEMATIC FIELD COLLECTION PROGRAM

Tactics, logistics, preparations, and procedures may be found in the discussions of Whyte (1958), Bennett (1970), Williams (1978), IBPGR (1983a), and Simpson (1984), and the manuals of Chang et al. (1972a), Hawkes (1976, 1980), and CIAT (1979).

Formation and Training of Collection Teams

The number, size, and composition of collection teams depend on the scope of the mission. Generally speaking, a small team of two or three persons is preferred. For diverse environments, a multidisciplinary team would be more effective than a group of similar background. Team members should be well briefed and rehearsed for the collection job within a tight schedule. For large-scale operations, teams of extension workers or college students may be trained within a short period to cover many areas. Proper timing of travel is crucial to rewarding collection returns. Prior communication with local workers is essential.

Formulating Sampling Strategy

Because of the inherent variability in every biological entity, it is impossible to conserve every genotype of a species or even of a population. Therefore, proper sampling strategy will help in assembling representative segments and including the maximum amount of genetic variability (variousness) of the available gene pools.

The development of appropriate sampling procedure for any crop will depend on:

1. Mode of reproduction: A general guide is to increase the size and number of samples from apomitic plants to cross-fertilizers to self-fertilizers (Whyte, 1958).
2. Geographic distribution of variability: Prior knowledge of the geographic distribution of desired traits would be helpful in searching for morphoagronomic or special traits. Random sampling is generally recommended within a population. Subsequent planting and evaluating the collected populations would reveal site-specific characteristics by location: topography, climate, soil type, hydrology, and other environmental

factors. The information derived will help in recanvassing and devising an appropriate sampling method for special situations (Allard, 1970).

Based on seed samples of wheat and barley collected in Pakistan and Nepal, the amount of variation in qualitative traits in these Vavilovian centers of diversity was large. But variation in quantitative traits was found to be much smaller and largely determined by natural selection. Intensive collection within a Vavilovian center of diversity does not appear to be effective in capturing the maximum amount of genetic variation. On the other hand, collection made in areas of environmental extremes may be more advantageous (Witcombe and Gilani, 1979).

3. Sampling strategies: A generalized sampling strategy for seed crops is for a collector to capture the maximum amount of variability in the minimum number and size of samples. As many sites as possible should be sampled. The sites should include a representative spectrum of environments within the area of distribution of the target crop/wild taxa.

   Gene pools should be sampled nonselectively to supply, with at least ninety-five percent probability, one copy of each variant occuring in the target populations with a frequency greater than five percent. A collector should collect from fifty to one hundred individuals per site with fifty seeds taken from each plant (Marshall and Brown, 1975).

   A mixture of selective and random samples by both selective and non-selective methods may also be used (Bennett, 1970). Selective sampling would identify morphological variants whereas non-selective sampling may capture alleles for biotic and environmental stresses.

   For a population that has been extensively studied, sample sizes five to ten times larger than that recommended by Marshall and Brown (1975) and from separate sites may be used. The aim is to obtain interesting but rare recombinations (Qualset, 1975).

4. Extent of variability within a local population: Variability within a population is partly related to the mode of reproduction. However, polymorphism in various dimensions is common within land races and wild relatives. Considerable variability also exists in inbreeding populations.

For general purpose sampling, a coarse grid approach may serve as the initial effort, followed by resampling of areas of special interest on a fine grid (Allard, 1970).

5. Method of maintaining the variability after assembly: For heterozygous materials, it is more effective to collect sufficiently large samples and preserve the stock as a bulk population in cold storage. Rejuvenation should also be carried out as bulk. Some mixtures of variants within a population may be kept as subsamples. Only highly homozygous materials should be maintained as pure lines.

   The size and number of samples should be planned in relation to the method and capability of maintaining the collected samples. It would be meaningless to collect many samples when there is no provision for evaluation and conservation. Capacity in shipping the collections and related plant quarantine problems should be considered at the planning stage.

Implementing Field Collection Activities

1. Equipment and supplies: Adequate preparations with respect to proper timing; appropriate transportation means; knowledgeable local guide; detailed road, climatic, topographic, and soil maps; supplies for carrying and processing samples; record forms; scientific equipment and supplies; camping equipment; field clothes; medical supplies; and local travel documents and letters of authorization should be made in advance. See Hawkes' 1980 manual for useful suggestions.
2. Liaison and cooperation with local agencies and workers: Field collection in a foreign country will be facilitated by including a worker or workers from national/local programs. It pays to work through government channels in a hierarchical manner: national→state→district→township→village. After the local extension workers have been involved in the task and become knowledgeable with the procedure, they may continue the field collection in later years. Observance of local customs concerning harvest method and information on local environments and cultural practices may be aided by working with the local extension staff (Chang and Perez, 1975). The national plant quarantine service may be contacted regarding seed or plant requirements.

Collectors can obtain and study agricultural statistics and crop production data from the target areas and develop a more informed basis for setting priorities. Up-to-date information on the development of irrigation schemes or the imminent damming of a valley may aid in giving top priority to an area under sudden threat.

Local workers can help in planning effective itineraries in an agroecologically diverse area to allow the team to collect by following the local pattern of crop maturity (e.g., from drier to more humid sites; from upland to lowland, etc.). Their knowledge of appropriate travel methods and a suitable time scale for travel in the more remote germplasm-rich areas will be valuable.

A local extension worker in the team may help make collection from each site faster through introduction to and compliance of the farmers concerned. His local knowledge of the ecological and social background to crop diversity in little-known areas can lead the explorer to atypical or rare varieties which may be of evolutionary, genetic, or direct economic significance.

3. Choice of sampling sites for seed crops: Sampling sites range from fields (either standing or harvested) for cultivars, natural habitats for wild taxa, bins, markets, and stores. The collector's order of preference is from fields to bins to markets.

The small local markets, often held periodically in remote rural areas, can be useful sources of germplasm. In these markets where the farmers themselves often are the ones selling the material, there is the unique opportunity of observing regional variation in a crop. In contrast, market sellers or store owners may deliberately mix different varieties to meet consumers' demand. It is important, therefore, to know the geographic origin of the sample and the stage when artificial mixing was introduced.

The collector should make a careful survey of the locale before taking samples. By assessing the environmental conditions, he may relate the habitat to unusual opportunities in obtaining genotypes that are adapted to specific physico-chemical stress or can resist biotic enemies. Such an approach has led to the acquisition of useful wild species of tomato (Rick, 1973) and special types of rice (Chang and Perez, 1975; Chang, 1980).

4. Sampling frequency: The number of sites and distance between sites should be chosen on the basis of (1) ecological diversity in an area, (2) the pattern of distribution and density of individuals in the populations, especially in wild and weedy forms, and (3) detection of rare (or targeted) variants in the populations. For a widely scattered population with low density distribution, samples should be taken over a broad area so as to represent the population.
5. Sampling technique: The general sampling procedure is to randomly take samples over predetermined intervals and use the bulked samples to represent one site. The collector may make a series of transects through the crop walking across a field, either in the form of a cross (+) or diagonally in the form of an × or both. Sampling only from the borders of a field and collecting diseased or insect-infested plants should be avoided. Select healthy-looking plants from a site where a biotic stress, such as disease damage, or a physical stress, such as cool weather or adverse soil factors, exists.

   For wild and weedy forms, several plants may be collected in a small area and the sampling repeated over several areas within a broad belt. This is called the clustered sampling pattern. Wild species should be collected repeatedly over several years to compensate for climatic effects on population structure.

   To recanvass for desired individuals in a previously sampled area, a fine-grid approach may be used.
6. Sample size: What factors constitute an optimum sample size? The choice of an appropriate sample size depends on (1) the frequency of sampling or samples per site, (2) diversity in the crop population and ecological conditions at the site, (3) amount of plant material available for sampling and for leaving sufficient stock to perpetuate the wild population, and (4) number of parties involved in the joint collection activities. In general, more sites per target area is preferred to more seed per site.

   Sample sizes based on various theoretical considerations range from sixty to one hundred plants per site (Marshall and Brown, 1975) to two hundred plants per location (Allard, 1970) to five hundred plants (Qualset, 1975). A general proposal is to capture, with ninety-five percent probability, all the alleles at a random locus in the target population with frequency greater than 0.05 (Oka, 1969; Marshall and Brown, 1975). Oka (1975) has suggested different sample sizes for wild forms, land races, and advanced cultivars.

As a general guide, the following suggestion on a proportional scale for rice may prove to be workable (T. T. Chang and D. A. Vaughan, unpublished):

Population type	Sites/day	Plants or panicles/site*	Seeds/site
Slightly improved	20-40	20-30	300-450
Unimproved (land race)	10-20	30-50	300-500
Wild-growing	10-15	40-60	200-300
Outbreeding	10-15	50-100	200-400

*For a single-party collection team.

For small grains, one panicle per plant is preferred to several panicles per plant for the same sample size because the single panicles provide a broader intrapopulational sampling. When seeds are collected from farmers' bins or market places, large quantities are needed to compensate for reduced viability or losses due to insect infestation. Larger samples are also needed if the collected seed will be placed directly in medium- or long-term storage (see Hawkes, 1980). When a cultivar contains two or three morphologically distinct types, it is better to separate the mixture into subsamples with each subsample given different sample numbers.

7. Collecting root and tuber crops: Root and tuber crops are more difficult to collect than seed crops because (1) of the physical difficulty in obtaining samples by digging, (2) they are bulky, (3) they have to be harvested at the right stage of maturity, and (4) transport and storage are difficult. Random sampling in the field may not be effective because many populations were derived from a single clone.

Cultivars should be sampled selectively to obtain distinct morphotypes. Try to collect a complete range of morphotypes at every collection site. Supplement with seed collection when possible. Individual plants of wild species should be sampled at separate sites. Collect a single propagule from each of ten to fifteen individuals. Sample as many sites as possible over a broad environment. Take plant specimens if possible (Hawkes, 1980). Additional information may be found in Hawkes (1978).

8. Field collection form: A well-designed and preprinted record form is an immense aid to field collectors. As a minimum the following information should be recorded on the form: (1) collection (sample) number, (2) variety (or species) name and the translation of a vernacular name, (3) location—district, village, farmer's name, (4) maturation date and collection date, and (5) collector's team and name (in codes) (IBPGR, 1983b). To these, the collector may add other important items, namely, information on ecological factors, type of variety and its culture, grain or fruit characteristics, altitude, topography, sampling source (field, bin, or market), sample type (pure line, populations, or individual), sampling method, habitat of wild species, growing season, insect and disease in the field, plant community, companion crops, uses, soil type, and pH. The forms could be assembled in a loose-leaf form with a tear-off portion bearing the sample number which can be placed inside the sample bag. Some collectors prefer to have the field collection data stamped on the sample bag.

   An example of a comprehensive form recommended by the IBPGR is shown in Figure 1.
9. Herbarium specimens: Plants of wild species should be collected, recorded, and preserved in herbaria.

POSTCOLLECTION OPERATIONS

Processing of Collected Samples

Processing the collected samples consists of drying and dusting the collected panicle or seed samples with a fungicide and an insecticide, recording the data in notebooks, and properly packing the samples. If space is not a limiting factor, samples collected as panicles or spikes may be packed as such to facilitate careful comparison at the laboratory. Otherwise, threshed seeds may be packed. Recording

FIELD COLLECTION FORM

EXPEDITION/ORGANIZATION ______
COLLECTORS ______
SPECIES NAME ______
(if not *O. sativa*)
VERNACULAR/CULTIVAR NAME ______
______
LANGUAGE ______
MEANING ______
LOCATION: Lat. ______ N ______ S
Long. ______ E ______ W
Alt. ______ (m)

VILLAGE (or distance and direction from nearest settlement) ______
______
TOWN/CITY ______
DISTRICT/PROVINCE ______
GROWER'S NAME ______

COLLECTION SOURCE (circle one)

farmland	1	institute	6
threshing floor	2	bordering field	7
farmstore	3	wild	8
village market	4	others (specify)	9
commercial market	5		

STATUS OF SAMPLE

wild	1
weedy	2
primitive cultivar	3
others (specify)	4

TYPE OF SAMPLE
seeds 1 panicles 2 vegetative 3
HERBARIUM SAMPLE yes no
VARIETAL SAMPLE

single variety	1
varietal mixture	2

SAMPLING METHOD
random 1 non-random (specify) 2
ORIGIN
local 1 exotic (specify) 2 ______
VARIETY GROUP

indica	1
japonica or sinica	2
javanica	3
hybrid (intermediate)	4

FREQUENCY

abundant	1	occasional	3
frequent	2	rare	4

______
______
______
______

ACCESSION NO. ______
COLLECTION NO. ______
DATE OF COLLECTION ______
Photo No. ______
Map Sheet ______
CULTURAL TYPE:

irrigated	1
rainfed-lowland	2
deepwater	3
upland	4
tidal wetland	5

CULTURAL PRACTICES:

shifting	yes	no
terraced	yes	no
direct seeding	yes	no
double transplanting	yes	no
mixed stand	yes	no

SOWING DATE ______
TRANSPLANTING ______
HARVEST DATE ______
USAGE ______
______

TOPOGRAPHY:

swamp	1
flood plain	2
plain level	3
undulating	4
hilly	5
mountainous	6
others (specify)	7

SITE:

level	1	summit	3
slope	2	depression	4

SOIL TEXTURE:

sand	1	silt	4
loam	2	highly organic	5
clay	3		

DRAINAGE:

poor	1	good	3
moderate	2	excessive	4

NOTES: (pests/diseases, special plant characters, status of genetic erosion, grain characters, other observations)
______
______
______
______
______
______

Collection No. ______	Collection No. ______
Date ______	Date ______

Figure 1. Field collection form recommended by the IBPGR and adapted for use in rice (IRRI-IBPGR, 1983).

the daily harvests in an alphabetical listing will prevent the collection of duplicates.

Tuber and root crop samples should be properly packed in porous bags to provide aeration and minimize damage during transport.

For vegetables such as tomatoes, cucurbits, peppers, and potatoes, the seeds should be extracted from the fruits, washed, and dried between layers of absorbent paper.

Other postexploration measures during the plant introduction process may be found in the FAO Handbook on Plant Introduction in Tropical Crops (Leon, 1984) under the chapter on rice (Chang, 1984c). Wild species should be re-identified and given the appropriate name after planting and seed increase.

Plant Quarantine Measures and Shipping

It is advisable, and sometimes part of a contractual agreement in IBPGR-funded missions, to deposit a duplicate set of the collected samples with the appropriate national center of the host country. It is essential to observe local plant quarantine measures and export procedure. Compliance with local regulations will pave the way for continuing cooperation and assistance from local authorities in future collection activities. Seeds should be cleaned, properly treated, and selected to include only those free from discoloration, diseases, and insects.

Documentation

The collectors should keep a diary of their activities. The trip report should cover the itinerary, highlights of observations on local flora, cultural practices, and annotated maps showing collection sites and ecological features. Listings of collected samples and cooperating personnel should be included. The report should be as informative as possible to give subsequent collectors a firm basis for recanvassing and intensive collection.

A register of collected materials should be kept at the national center of the host country and at the collector's institution. This information should be later entered into computerized data systems.

IOWA STATE JOURNAL OF RESEARCH / MAY, 1985 365-378
Vol. 59, No. 4

PRESERVATION OF CROP GERMPLASM

Te-Tzu Chang[1]

ABSTRACT. The preservation of assembled germplasm is the core of genetic conservation. It links acquisition with evaluation and use. It also includes distribution and documentation.

Of the various forms of preservation, seed preservation by refrigerated storage is the most efficient means for most food crops. High-quality seed is a prerequisite for maximum seed longevity. Biological, physical, and human factors essential to safeguarding seed viability are enumerated. Storage conditions for orthodox (nonrecalcitrant) and recalcitrant seeds are separately described. Procedures, seed containers, and safeguards for attaining maximum seed longevity of orthodox seeds are discussed. Periodic monitoring of the viability of stored seed is essential.

Other preservation methods include storage of vegetative parts, *in vitro* culture of plant parts, mass reservoirs, and genetic reserves. Recent advances in *in vitro* culture for genetic conservation are reviewed.

Index Descriptors: preservation, gene bank, long-term seed storage, orthodox (nonrecalcitrant) seed, recalcitrant seed, preservation of population structure, hermetic seed containers, *in vitro* culture for storage/shipment, cryogenic storage, slow growth storage, monitoring of seed viability.

INTRODUCTION

Preservation is an indispensable operation which immediately follows the acquisition of crop germplasm either through exploration-collection or exchange. Preservation serves as a link between acquisition on one hand and evaluation and use on the other. It should, therefore, include distribution to serve its purpose. Documentation is also an integral component of preservation.

Preservation is achieved in a number of ways. The principal methods are: (1) long-term seed storage, preferably at duplicate sites, (2) cold storage of vegetative parts and recalcitrant seeds, (3) storage of meristems or other plant tissues, (4) establishment of mass reservoirs of composites or naturally mixed populations, and (5) establishment of genetic reserves.

For most field crops, seed preservation is the most efficient means of maintaining large numbers of accessions and making

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them available for distribution. Cold storage of vegetative parts and recalcitrant seeds provides a limited span of plant life. Cold storage of meristems or other kinds of plant tissues is still at the experimental stage. The establishment of mass reservoirs and genetic reserves has been discussed but yet to be implemented. Botanical gardens offer a limited scope in preserving some plants.

REQUISITES FOR MAXIMIZING SEED LONGEVITY

The goal in seed preservation is to maximize the longevity of the stored seed at minimal cost. To attain the objective, the crop scientist needs to consider both biological and physical factors in harvesting, selecting, and preparing seed for storage. Human factors also affect the security of crop collections.

Biological Factors

1. Physiological maturity: Most satisfactory results are obtained from seeds that have reached physiological maturity, although the seed moisture content may be as high as thirty percent when the seed enters this stage. Maximum dry weight is a general criterion for physiological maturity, although it is not always easy to determine (Harrington, 1972). Generally better quality seed is obtained from a slightly advanced harvest than from a delayed harvest.
2. State of seed health: Seed for preservation should be harvested from plants that are free from disease infection, insect infestation, frost or hailstone injury, and stress due to water deficit, water excess, or mineral deficiency in the field. The seed should also be free from microbial infection and insect infestation.
3. Freedom from mechanical injury: A single harvest operation will include both premature, mature, and overmature seeds. More than one harvest operation may be needed for a crop with an extended period of maturation to minimize harvest injury. Mechanical injury during threshing may be reduced by using a lower cylinder speed of the thresher, coating the beater bars with rubber bars, and threshing when seeds have appropriate range of moisture contents (Harrington, 1972).
4. Grain dormancy: Dormancy of various mechanisms generally helps prolong longevity. Hard or impermeable seed coats enable seed to resist water absorption even when it is buried

in soil (Barton, 1961). In rice, a crop planted in the wet season has stronger grain dormancy than that planted in the dry season (Chang and Yen, 1969).

5. Interspecific and intervarietal variation: Crop species vary greatly in their seed longevity (Barton, 1961; Harrington, 1972). Among rice cultivars, marked variation was found among varieties of different geographic origins (IRRI, 1981; Chang and Tolentino, 1983).
6. Some species have recalcitrant seeds: The seeds have limited storage life and are killed by drying (Chin and Roberts, 1980).

Physical Factors

1. Temperature: Temperature and humidity are the major factors that jointly determine seed longevity. As a rule of thumb, for each 5° C increase in seed temperature, the life of the seed is halved. This rule applies between 1 and 50 ° C. The adverse effect of high temperature extends from physiological maturity to harvest, during transport, drying, and from open-shelf storage to cold storage (Harrington, 1972).
2. Moisture: Most crop seeds are hygroscopic—they will absorb moisture from the surrounding air, and seed moisture content will reach equilibrium with the ambient relative humidity (RH) and temperature. The relationship among temperature, RH of the air, and seed moisture content is usually expressed in an S-shaped (sigmoid) curve called an isotherm. Different crops have slightly different isotherms (Harrington, 1972).

   Again, as a rule of thumb, for every one percent increase in seed moisture content, the life of the seed is halved. This rule applies to a range between five and fourteen percent (Harrington, 1972). More recently Roberts and co-workers have modified the factor to 2% (Roberts, 1979).
3. Temperature-moisture interaction: The two rules based on temperature and moisture apply independently. For instance, seeds with ten percent moisture and stored at 20° C will survive as long as those with eight percent moisture stored at 30° C (Harrington, 1972). Roberts and Roberts (1972), Roberts and Ellis (1977), and Ellis and Roberts (1980) have furnished predictions on seed longevity. It also appears plausible that various crop species react differently to changes in temperature and moisture.

4. Other factors: High oxygen content tends to hasten loss in viability, especially in seed with high moisture content. High CO_2 or N_2 content or a vacuum may retard deterioration. Seed exposed to ultraviolet light will deteriorate faster. Radiation can damage seed in storage (Harrington, 1970).

Human Factors

The management of a large seed bank requires continuity in personnel and administrative support; sustained funding; cooperation from collectors, other curators, users, and seed physiologists; and assistance from refrigeration engineers. Political instability, the vagaries of war or civil strife, and natural disasters such as earthquakes and flood also add to the vulnerability of germplasm collections (Reitz, 1976; IRRI, 1980b; Chang, 1984b; Goodman, 1984). Above all, the security of seed requires the dedicated care and vigilance of the bank staff who are frequently overburdened by a nonglamorous task (Chang, 1984b). Instances of gaps in personnel, management or funding which led to loss of valuable germplasm have been described by Larson (1961), Mengesha and Rao (1982) and Goodman (1984).

PRODUCTION OF HIGH QUALITY SEED FOR MAINTENANCE AND PRESERVATION

Freshly collected seed samples are frequently insufficient in quantity to be directly stored for preservation. One cycle of seed multiplication is needed to produce sufficient and viable seed. The seed increase operation should consider the need to preserve the genetic structure of the original population.

Quantity of Seed to be Produced

It is best to produce large quantities of seed sufficient for preservation and distribution in as few cycles as possible. Frequent rejuvenation (regeneration) of seeds in small plots should be avoided because it: (1) may lead to errors in identifying accessions and creating mechanical mixtures, (2) is possible that unadapted or susceptible accessions may be lost, (3) leads to changes in the genetic composition of an accession when population size is small, and (4) creates extra work loads and increases the need for fields and storage space (Chang et al., 1979).

As a rule of thumb, at least 3,000 to 12,000 seeds per accession are needed for entries in the base collection under long-term storage (IBPGR, 1976b). Larger quantities per accession are needed for the active collection which is stored under medium-term conditions for evaluation and distribution.

Most seedbanks rely on the breeding stations to furnish fresh seeds when the conserved seedstocks become depleted or low in viability. For land races and wild species, the ideal site of rejuvenation is the original habitat or locale having similar environments. However, most seedbanks find it difficult to enlist cooperators who can carry out the task. Genebanks of the IARCs generally rejuvenate the seedstocks on their farms or in isolated fields. Constraints to seed production under *ex situ* conditions are poor seed yields, possible loss of unadapted or susceptible accessions, and the need to have separate planting dates to match the photoperiod reaction of the varieties (Chang, 1980).

Measures to Preserve Population Structure

For self-fertilized cultivars, the seed should be sown thinly or transplanted in single-seedling hills to facilitate judicial removal of mechanical mixtures. Complete protection against diseases and insects should be provided. Soil fertilization is often needed, but fertilizers should be applied at moderate rates. Plant quarantine inspection for the initial planting of foreign introductions is necessary. Accessions of different maturity or photoperiodic responses should be planted on different dates for maximum seed production without selecting against unadapted individuals. A sample showing distinct morphologic variants, e.g., red versus white seed coats, may be separated into two accessions. Ecostrains of the same variety may also be kept as separate accessions. Other samples showing small variations which were inherent in the original population should be harvested *in toto* as a bulk. Harvested bundles should be transported and dried in cloth bags to minimize mechanical mixtures.

For wild species, it is important to provide environmental conditions similar to their home habitat. The planting of a wild population should be of sufficient size to preserve its genetic composition. For land races and wild species of rice, 20 to 100 and 4 to 6 plants per population are recommended for each, respectively (Oka, 1983). The individual panicles of wild rice should be bagged to reduce outcrossing and facilitate seed harvest. The harvested seed should be kept as a bulk. Oka (1983) made comparisons between the pedigree and bulk methods of seed multiplication.

For cross-pollinated crops, seed multiplication is carried out by one of the following means: (1) planting in an isolation plot, (2) selfing or sib-mating, and (3) compositing, as used in maintaining maize races (Timothy and Goodman, 1979). Problems in maintaining genepools in a cross-pollinated crop such as pearl millet were discussed by Burton (1976).

For perennial and rhizomatous wild species, measures should be taken to prevent the rhizomes of one population from invading the plots of adjacent accessions or becoming an obnoxious weed. Dropped seed will remain viable in soil for years.

Systematic characterization by morpho-agronomic characteristics may begin with the first seed increase.

Before planting the seeds, a small number of seeds should be taken from the original seedlot and placed in a "seed file." This file will prove its value later when the conservationist finds it necessary to verify the trueness of the multiplied seeds by comparing with the original sample. Additional suggestions on operational matters may be found in the *Manual on Genetic Conservation of Rice Germplasm for Evaluation and Utilization* (Chang, 1976e).

SEED PRESERVATION BY REFRIGERATED STORAGE

Seed Storage Behavior

Most crop seeds can be preserved under low moisture content and low temperatures. These are called the orthodox or nonrecalcitrant seeds. On the other hand, seeds of some tropical horticultural and plantation crops such as tea, coffee, cocoa, and rubber will degenerate rapidly and die shortly under such temperature and moisture regimes—this is the recalcitrant type. Vegetative parts also have a narrow range of tolerance for dehydration and chilling.

Storage Conditions for Orthodox Seed

Base collections should be preserved at duplicate sites under the most ideal conditions: low moisture content of seed, low temperature, low RH, and packing in hermetic containers. The FAO Panel of Experts initially stipulated -18 ° C and 5 $\pm$ 1% moisture content as the standard storage conditions. This set of conditions constitutes the long-term (LT) storage class. The projected seed viability under LT storage may exceed one hundred years (Roberts and Ellis, 1977).

However, this temperature regime is difficult to maintain, especially in warm regions. A higher level of -10° C has been suggested by the IBPGR Working Group on Seed Storage (IBPGR, 1976b). On the other hand, seeds stored at -10° C require rejuvenation twice as frequently as those kept at -18° C.

As an example, rice seeds preserved at IRRI under LT storage have a moisture content of six percent, are sealed in aluminum cans under partial vacuum (0.5 atmospheric pressure), and are stored at -10° C, 37-40% RH. Only a small number of gene banks in the world have LT storage conditions (Plucknett et al., 1983).

Storage conditions for many active collections fall under the medium-term (MT) category. The temperature ranges from 0 to 10° C, RH from fifteen to fifty percent, and seeds are stored in fairly airtight containers. The projected seed longevity ranges from ten to thirty years or longer (depending on a combination of factors). About thirty gene banks have such facilities (Plucknett et al., 1983). IRRI's earlier MT conditions were 8.5% seed moisture content, 2-3° C temperature, 60% RH, seeds stored in airtight glass jars containing silica gel. The present setup consists of six percent moisture content, vacuum canning, 2-3° C, and 40% RH.

The short-term category is widely used by plant breeders. The storage conditions vary so widely that the shelf life of seed in open-type containers or tight containers ranges from three (in the tropics) to more than ten years (in very dry environments).

Storage Conditions for Recalcitrant Seeds

Recalcitrant seed storage behavior occurs in seeds of some aquatic species, many large-seeded species, most tropical forest species, and a number of timber species. The economic crops having this behavior are coffee, tea, coconut, oil palm, rubber, and American wild rice. Recalcitrant seeds cannot be dried to low moisture content and are, therefore, not storable under 0° C. Some species are even damaged by chilling injury at 10 to 15° C (Roberts, 1975; Roberts and King, 1980). Moreover, desiccation injury (Harrington, 1972), microbial contamination, and germination during storage pose additional difficulties. A list of recalcitrant species has been provided by King and Roberts (1980).

Sealing the seeds after appropriate treatments (washing, heating, and fungicide application) in a thin polyethylene bag appears to be the most practical method to seal in the moisture without microbial growth or germination. The storage life may thus be prolonged, but the total span is still relatively short (from six months to a few years) as compared to the orthodox seeds. Immersion in liquid nitrogen may be an alternate method, although further studies are needed to perfect the technique (King and Roberts, 1980).

PREPARING ORTHODOX SEED FOR MEDIUM- AND LONG-TERM STORAGE

Selection of High Quality Seed for Preservation

Only high quality seed obviously free from heat injury, surface infestation by microbes, or insect infestation deserves MT and LT storage. The process consists of mechanical cleaning, fumigation, individual seed selection by visual inspection or electronic seed selector, and removal of weed seeds and off-types (see Chang, 1983c).

Drying Seed

To prepare seed for MT or LT storage, seed moisture content must be lowered from the level safe for short-term storage (10-13%). Equally important is to dry the seed slowly without high temperature heating. This approach can be attained in a dehumidified environment. Heating to above 50° C would markedly shorten seed longevity (Harrington, 1970).

The commonly used methods are:

1. Liberal amounts of a dehydrating agent, such as silica gel, are placed together with the seeds (wrapped in porous paper bags or fine-mesh cloth bags) inside an airtight container. After two to three weeks, the silica gel is replaced with a freshly activated lot. The seed moisture content can be lowered to eight to nine percent. This approach was used at IRRI from 1963 to 1978 and appeared to be a safe method.
2. The seeds are dried in a room which has dehumidified air. A combination of 15° C and 10-15% RH with good air recirculation is used by the Royal Botanic Gardens, Kew at Wakehurst Place, and at the National Vegetable Research Station, at Wellesbourne, United Kingdom (Cromarty et al., 1982). The Seed Storage Center at the National Institute of Agrobiological Sciences, Tsukuba, Japan, uses a slow drying process by placing

seeds in a room maintained at 25° C and 15% RH until the desired moisture content is reached (Kumagai, 1979).

3. Rice seeds of eleven percent moisture are dried inside paper coin envelopes to six percent moisture by heating the seeds at 38° C inside an oven supplied with air dehumidified to 8% RH and 13° C under forced ventilation. The process is completed in nineteen hours. Seeds for MT and LT storage are dried by this method at IRRI (IRRI, 1980b).

These methods may be modified but the conservationists should first consult an appropriate psychrometric chart and vapor pressure nomogram to determine the equilibrium relationships between seed moisture content and relative humidity at various temperature regimes. Crop varieties differ in the relative humidity equilibrium relationship, especially between low- and high-oil-content seeds. Curves for rice, wheat, soybean, and peanuts are provided by Cromarty et al. (1982). Because crops vary in seed size, the air ventilation rate and drying duration need to be individually computed. Helpful guidance may be found in Cromarty et al. (1982). Large seeds may require a two-stage drying process: The first stage is at 17-19° C, 40-50% RH; the second is at 30° C, 10-15% RH. Large seeds with high oil content, such as peanuts, may benefit from the two-stage drying process.

Storage of legume seeds with high oil content such as soybean require special care. Moisture content should be maintained below ten percent but not lower than six percent. The drying temperature should not exceed 43° C (Cartter and Hartwig, 1962).

Freeze-drying was recently reported as a new method to lower seed moisture to the two to five percent range by avoiding potential damage due to heat and overdesiccation. Seed storability at warm temperatures may be improved by this technique (Woodstock et al., 1983). However, the freeze-drying equipment is not generally available to seed laboratories.

Monitoring Seed Moisture Content and Germinability Before Sealing and Storage

Because any equipment may malfunction or fail, extra samples should be included in a large batch of accessions to be dried and seed moisture content determined at the end of the drying process. (Refer to the 1976 ISTA rules and its 1981 amendments for the procedure.) Cromarty et al. (1982) have given an excerpt of the procedure. Germination tests should be made at the initial period of setting up the drying process to ensure its safety in preserving viability.

Choice of Hermetic Seed Containers

Most seeds are hygroscopic, and refrigerated conditions, especially the RH factor, may fluctuate. Hence, the best insurance against changes in the seed moisture content is to use containers that are impermeable to moisture penetration—the hermetic type.

Hermetic containers are of three types: metal, glass, and plastic. Metal cans furnished with a sealable lid offer a relatively inexpensive and durable protection, provided that they are rust-proof (either made of aluminum or coated with a plastic film) and the lid has a high quality rubber gasket of the solvent-based type. Two-piece cans are preferred to three piece cans. Both require a double-seaming machine and preferably a connecting vacuum pump. Small metal cans with a screw cap and rubber gasket are suitable for MT use and can be reused if carefully handled.

Glass containers come in the form of vials, bottles, and large jars. Each type should have a screw cap and a gasket inside the cap. Rubber gaskets are better than the paper ones. To monitor the moisture level in the glass container, silica gel, both the plain (colorless) and indicating (blue, when dry; pink, when moist), can be placed inside the glass bottles. This dehydrating agent serves both as a maintainer of low moisture content and as an indicator of changes in moisture level. Strips of cobalt chloride paper may be used, but it is very sensitive to changes in moisture level and functions only at very low levels.

Plastic materials are available in the form of bottles, jars, envelopes, and aluminum foil-polyethylene-cellophane envelopes. The most common for small quantities of seed is the foil envelope. Foil envelopes should not be fully filled or used for seeds with rough surfaces.

All plastic containers tend to vary in quality when mass produced. Moreover, all kinds of plastic will warp, turn brittle, or develop invisible fissures (cracks) with time. Hence, plastic containers need testing for tightness before use and its impermeability periodically monitored. In IRRI tests, plastic bottles and foil envelopes remained airtight for about four years (Chang and Tolentino, 1983). Discussions on these seed containers may be found in Cromarty et al. (1982) and Chang (1983c).

Records

The accession number of each sample of seeds to be placed in MT and LT storage should be marked both on the outside and inside of the container. Stick-on labels and indelible ink are used. Numbers can also be stamped on paper by a numbering machine.

Records of the conserved stocks should contain: (1) accession number, (2) crop season/year grown, (3) date of packing, (4) viability of the sample or batch at packing, (5) seed quantity of the whole lot, (6) location (shelf) number, (7) scheduled date of rejuvenation, and (8) records on distribution or use in planting. A computerized inventory of this information should be set up at the beginning of the seed processing phase.

Requisites of an Efficient Refrigerated Seed Storage Facility

Medium- and long-term refrigerated seed storage facilities are costly to build, operate, and maintain. It is imperative that the design and equipment are carefully chosen to meet the needs of the crop or crops concerned. The following factors should be seriously considered to ensure efficiency and security:

1. Selection of site to provide security and efficacy of operation: The risk factors of flooding and earthquakes should be considered. A steady supply of electric power is essential.
2. Functionality of design: The facility should be designed to meet the specific requirements for temperature and RH levels. Space allocation for different areas, such as processing, packaging, and storage should follow the operational sequence. Dry and wet areas should be separated.
3. Effective insulation of the cold rooms and stepwise cooling and dehumidification from a warmer area toward a cooler area will cut running and maintenance costs. Leaks should be promptly sealed.
4. Uniform cooling of all parts of the storeroom is essential.
5. Reliable hermetic containers will guard against failures in temperature/humidity control. The duration of open storage before canning or bottling should be cut to a minimum.
6. Choose simple, reliable, and fool-proof devices and steps of operation. Provide extra units of equipment to cope with equipment failure.
7. Good maintenance will pay off in the long run.

8. Mobile shelves will increase usable space.
9. Tests on the seed containers, seed moisture content, and accuracy of monitoring instruments should be periodically made.

These aspects have been discussed in detail by the IBPGR Working Group on Long-term Seed Storage (IBPGR, 1976b), Cromarty et al. (1982), and Chang (1983c). For small collections, home-type food freezers may be used to good advantage (Ellis and Roberts, 1982). Again, hermetic containers will provide protection.

Adjuncts to Effective Long-Term Seed Preservation

Even in orthodox seeds, long-term storage requires a number of vigilant efforts to maximize its useful potential. The deterioration of seed viability is subject to the effect of many factors and is hardly detectable except by direct checks on viability. Crop conservationists should include the following operations in the program:

1. Periodic monitoring of seed viability: A test of seed viability involves the destruction of conserved seeds. Germination tests may involve hundreds of seeds per test. Test size may be reduced by using the tetrazolium test or the sequential testing method (Roberts, 1983). Indirect tests on the tightness of the seed container and RH of the ambient air may help minimize seed loss. The task, however, is complicated by the differential seed longevity within a crop species such as rice (IRRI, 1981).
2. Threshold level for seed rejuvenation: A crucial question is the choice of a viability level at which rejuvenation should begin. Roberts (1975) has suggested that when seed viability drops to eighty-five percent, rejuvenation is warranted. However, this stipulation appears impractical for most conservation programs. A forty to fifty percent level may be more realistic (IRRI, 1976a; Kawakami and Fujii, 1981).
3. Genetic stability of preserved seed: Some findings indicate that aged seeds have shown markedly higher frequency of mutations or chromosomal aberrations than fresh seeds (see Roberts, 1975). These may be isolated cases for certain crop species. In the case of ten-year-old temperate zone rice cultivars with a fifty percent viability or below, no visible increase in mutation rate was detected at IRRI.
4. Dependability of refrigeration equipment: As safety measure, there should be extra units of refrigeration equipment on hand.

An emergency generator for the medium- and long-term storerooms is also necessary.

OTHER TYPES OF PRESERVATION TECHNIQUES

Cold Storage of Vegetative Parts

Potato tubers can be kept at 4° C up to nineteen months (Hawkes, 1970). This period, however, falls within the short-term range. Therefore, it is preferable to store seed as long as the maintenance of fixed genotypes is not a requirement. Potato seed has as good storability as most orthodox seeds (Grahl, 1983).

Yam tubers may be stored between 15 and 20° C. Small tubers have better storage life. The longevity of aerial tubers may last more than two years (Martin, 1975).

In vitro Culture of Plant Parts

Recent studies have made it possible to use tissue culture of shoot meristems of potato, cassava, sweet potato, and yam for the maintenance of clonal materials and for protection from disease and insect attacks, climatic changes, and soil problems at low cost. Moreover, this method is also desirable for international shipment (Roca et al., 1979). Nodal cuttings facilitate clonal propagation in large numbers. The meristem cultures can be continuously maintained by regular transfer of nodal cuttings to fresh medium. By changing the medium, single- or multi-meristem cultures can be obtained. Storage under minimal growth condition may extend the transfer interval in cassava to four years (Roca, 1984). At the CIAT over fifty percent of the 3500-accession cassava germplasm collection have been introduced in an *in vitro* bank under slow growth conditions (W. M. Roca, personal communication). Cryogenic storage also appears to have some promise, especially with cassava and potato (Henshaw and Roca, 1976; Grout and Henshaw, 1978).

In vitro tissue cultures may include single cells and protoplasts, anthers and pollen, meristems, embryos, calli, and cell suspensions. Some or all of these cultures may be stored, depending on the plant species. For meristems, the process consists of: (1) choosing suitable material, (2) isolation of healthy specimens, (3) development of methods for meristem isolation and plant regeneration, (4) optimization of culture conditions for regeneration of plants from meristems, (5) storage of cultivars in minimal nutrient medium or at a reduced temperature (e.g., 6-9° C° C) or by freezing in liquid nitrogen at -19° C, and (6) regeneration of plants from stored meristems (Withers, 1980; Wilkins et al., 1982). Although *in vitro* culture requires relatively little space and maintenance is simple, inexpensive, and capable of maintaining a pathogen-free condition, it may also pose problems: when regeneration is difficult, cultures become genetically unstable in storage, the morphogenetic potential may get lost, or the culture may contain many abnormal cells (D'Amato, 1975). Thus, cryogenic storage in liquid nitrogen with the help of suitable cryoprotectants has additional benefits. Progress is being made with the technique but its usefulness for many species remains to be tested (Henshaw, 1975; Withers, 1984). It requires periodic replenishment of liquid nitrogen at sixty-day intervals but no electrical power.

In a recent review, Withers (1980) concluded that much physiological/biophysical research is needed to understand the phenomena accompanying cell establishment and operation during pregrowth before freezing and recovery growth after freezing in relation to cryodamage. When such aspects are worked out, tissue culture storage may become a routine operation or amenable to exchange operations. It can be envisaged in the future that for plants adapted to *in vitro* storage, a base collection may be maintained under cryogenic storage and an active collection under slow growth storage (W. M. Roca, personal communication).

Mass Reservoirs

Mass reservoirs are panmictic populations derived from many crosses of a wide array of materials including locally adapted types in combination with introduced primitive and wild types which have shown promise as adjuncts in plant breeding (Simmonds, 1962; Frankel, 1970b). No information is available regarding the feasibility and outcome of this approach.

Genetic Reserves

Genetic reserves consist of providing organized protection to endangered communities of wild species, forages, and forest trees under ecosystems nearest to their native or adapted ecosystem to ensure survival as well as potentials for continuing evolution (Frankel, 1974, 1984; Jain, 1975). Frankel (1974) has described a time scale for the categories of wild species of concern to man and the elements of the genetic system for *in situ* preservation. Some efforts have been initiated to set up genetic reserves but their management and successful use remain to be elucidated (Prescott-Allen and Prescott-Allen, 1981).

IOWA STATE JOURNAL OF RESEARCH / MAY, 1985 379-397
Vol. 59, No. 4

EVALUATION AND DOCUMENTATION OF CROP GERMPLASM

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ABSTRACT. Evaluation is a prerequisite for the use of conserved stocks; conserved accessions that do not undergo evaluation remain curiosities. Evaluation may accompany initial seed increase. Documentation should be an integral part of systematic evaluation.

Evaluation efforts must meet crop improvement goals. Mass screening techniques should be developed to expand the scope of evaluation. Initial findings need to be verified through critical tests. A multi-disciplinary approach to systematic evaluation holds the key to success. Effective communication between the conservationists and the users is essential.

The formulation of an efficient evaluation procedure which also provides conservation opportunity is discussed. A systematic and comprehensive evaluation program, taken from IRRI's GEU program, is also described. Computer programs can be developed to meet the specific needs of the crop scientists. Components of a computer-based documentation system are illustrated. International and interinstitutional cooperation is needed at all levels of evaluation and documentation.

Index Descriptors: preliminary evaluation, systematic evaluation, characterization, mass screening, multidisciplinary teams, maintenance of genetic integrity, GEU program, data files, descriptors, descriptor states, updating of data.

INTRODUCTION

Types of Evaluation Methods

Evaluation is the essential link between conservation and use. The role of documentation, which extends across all phases of conservation, becomes more imperative at this stage because its availability or unavailability will influence the breeder's interest in using the evaluated germplasm. Free exchange of evaluation results will also lead to enhanced exchange of germplasm.

The evaluation process may involve some of the following steps:

1. Seed multiplication and preliminary evaluation: During the initial cycle of seed multiplication, the breeder or curator usually takes notes on some morphoagronomic features,

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disease and insect incidences, and other notes of interest. At this stage, too, obvious duplicates are removed and promising samples are entered into intensive evaluation experiments.

Observing plant quarantine needs should be part of the initial process of seed increase and preliminary evaluation (Kahn, 1970; Hewitt and Chiarappa, 1977).

2. Systematic morphoagronomic characterization: For base collections maintained by national or international centers, complete notes are taken from the entire collection on a staggered schedule. For instance, the IRGC staff at IRRI records 45 traits (descriptors) on the *Oryza sativa* accessions. These kinds of voluminous notes are obtained during the seed increase cycles and are manageable if executed by a competent team.
3. Mass screening for selected traits: For assessing economic and other traits of potential importance, mass screening procedures adapted to field or greenhouse or laboratory testing are prerequisites to efficient evaluation. The approach is usually empirical, but the emphasis is on simplicity, speed, dependability, capacity, and low cost.
4. Critical tests for selected traits: The value of promising accessions identified by mass screening or other means is ascertained by more refined tests to establish the bases for their use or further study. Specialized equipment and the control of environmental factors are often needed in the critical tests. By this time the number of entries has been reduced to a small manageable size.

   New genetic materials which survive these series of tests generally offer potentials in one or a few characters. They are suitable as donors of desired traits rather than as candidates for immediate commercial use.

   Many economic traits are controlled by multiple genes or polygenes and are subject to marked environmental effects. Reproducibility of findings is essential.

Team Approach in Systematic Evaluation

Evaluation efforts during the period before the 1950s were largely carried out by breeders or crop-curators on relatively small segments of plant introductions or local collections. The approaches were generally empirical and limited, the findings filed in unpublished reports, and the seeds conserved haphazardly without provisions for continuity and security. Many of the useful and potentially useful materials disappeared after the breeder or curator changed his job, interest or retired (Larson, 1961; Reitz, 1976; Chang, 1980, 1984d; Goodman, 1984). This kind of descriptive and empirical evaluation is still going on at some of the smaller centers or stations.

Systematic evaluation of large collections requires a multidisciplinary team and an interdisciplinary approach. Interaction among members of a multidisciplinary team would lead to more rewarding findings and greater potentials for further research than any one discipline can offer. Moreover, the traits being sought are becoming increasingly complex and multifaceted and only a multidisciplinary group could unravel the underlying mechanisms. Crop physiologists and chemists have recently joined the traditional team composed of a breeder, geneticist, agronomist, plant pathologist, and entomologist.

Crop scientists recognize that the lack of systematic evaluation efforts and the dearth of evaluation data in the germplasm banks have discouraged plant breeders to seek and use the "raw" germplasm. Insufficient information about a collection cannot help the crop researchers to identify gaps in the existing collection and plan further collection efforts. Evaluation efforts for specific traits frequently discontinue once a resistant or tolerant source is found (Anon., 1984a).

MAJOR OBJECTIVES IN SYSTEMATIC EVALUATION

Systematic evaluation operations are expensive and time-consuming. It is imperative to select those traits of high priority among economic traits and to devise screening procedures based on available resources in physical facilities, manpower, and funds.

Although the ultimate goals of crop improvement are primarily higher yield potential, increased yield stability, higher productivity per hectare per day, and improved nutritional or industrial quality, the most commonly sought traits in exotic germplasm are disease and insect resistance, tolerance for ecoedaphic stresses, and nutritive factors. Some of these traits are rather simply inherited but often tightly linked with undesirable traits. For complex traits such as yield potential, the trait is the end result of a long process of plant growth, development, and interactions. It may be more profitable to first analyze the underlying mechanisms, identify relative contributions from different components, and concentrate on the more effective component or components than to tackle a complex end product (Chang and Oka, 1976).

The principal goals in exploiting useful genes from exotic germplasm vary greatly among crops and among different ecological zones within a crop. We draw examples from six crops to illustrate the breeder's needs.

1. Wheat: Stable resistance to the races of wheat rusts; new sources of resistance to *Septoria tritici*; new sources of semidwarfism; improved quality, greater tolerance for drought and cold temperatures; earliness; additional sources of cytoplasmic male sterility; tolerance for aluminum toxicity in acid soils; and other factors related to wide adaptability (Krull and Borlaug, 1970; CIMMYT, 1976, 1984).
2. Rice: Higher yield potential, especially in the cloudy monsoon season; improved yield stability through multiple resistance to pests and tolerance for adverse hydrologic and edaphic factors; higher nitrogen use efficiency; wider adaptability to marginal production areas; and improved nutritive quality (Beachell et al., 1972; Hargrove, 1978; Khush, 1980; Brady, 1982; Swaminathan, 1983a).
3. Corn: Additional sources of cytoplasmic male sterility; resistance to southern corn leaf blight, downy mildew, stalk rots, root rots, and maize dwarf virus; resistance to European corn borers and earworm (CIMMYT, 1976; Hallauer and Miranda, 1981).
4. Potato: Resistance to virus diseases, round-cyst and rootknot nematodes, bacterial diseases; stable resistance to late blight; broader adaptation; and improved nutritive quality (Howard, 1978; Ross, 1979).
5. Sorghum: Earliness; short stature; drought resistance; bird tolerance; compact and long heads; weathering resistance of grain; strong root system; and disease and insect resistance (Quinby, 1974; Miller, 1982; ICRISAT, 1982).
6. Tomato: Tolerance for extreme temperatures, water deficits or excesses; disease and insect resistance; contents of soluble solids; acidity and flavor; thick pericarp; jointless pedicel (Rick, 1982, 1984).

PRINCIPLES RELATED TO PROCEDURAL MATTERS

Although evaluation will remain in the domain of the problem-area disciplines such as plant breeding, plant pathology, entomology, crop physiology, and soil science, it is important to consider a number of general principles which relate evaluation to genetic conservation.

Providing Conservation Opportunities at the Earliest Stage

Sufficient seed or other propagative material should be produced for storage, further evaluation, and distribution. The pitfalls of frequent seed rejuvenation in small plantings have been pointed out in the preceding manuscript of this issue, "Preservation of Germplasm." Small seed quantity may also pose as a limiting factor in evaluation.

Adequate Sample Size

The appropriate sample size to represent a population should be determined by the inherent genetic variability within an accession or population, heritability of the trait concerned, extent of control of the environment, and degree of precision needed. An efficient experimental design and increased replications may help the researcher cope with environmental variability.

Representativeness of Testing Environment(s)

A common pitfall in evaluation is the lack of a representative environment on the experiment station ground so as to produce useful information. Tests in off-station and endemic sites may yield results that justify the efforts. Areas where a biotic factor, such as a plant pathogen, frequently appears are called "hot spots." Mass screening may be efficiently implemented at hot spots.

Nature of Duplicate Accessions

In the course of varietal development and subsequent dispersal, one or more events may lead a cultivar to develop strains showing some discernable differences in characteristics while the same variety name was retained. Morphologic variants differing in one or a few morphologic features such as glume color, awning, and seed coat color may result from spontaneous mutations or accidental outcrossing. Ecostrains are products of natural and artificial selection after one cultivar has been transported to another geographic area and grown under different ecosystems. Semidwarfs of rice have often appeared in tall cultivars due to mutations at the height loci. Other duplicates may have resulted from errors in harvesting and labeling or natural out-crossing so that the accession name no longer applies to the characteristic designated by name: color of plant parts, type of endosperm, awning, or maturity. This category of duplicate accessions should be assigned new accession numbers and individually evaluated.

Splitting vs Pooling in Maintenance

Plant breeders and other germplasm users generally demand highly homogeneous plant populations. On the other hand, land races collected from farmers' fields and wild species gathered from natural habitats are inevitably heterogeneous and heterozygous. It is not advisable for the curator to carry out subjective selection and purification just to attain superficial uniformity. Otherwise, some of the useful genes in the population may be inadvertently discarded during purification.

Although it will cause inconvenience and time delay for the evaluator to fix the desired plants on a family basis, the evaluator is in a better position to do so. The selected strains can be given a subnumber or another accession number to distinguish them from the original population. The parent population should be conserved in its original structure. Discussion on this important aspect of handling populations has been provided by Frankel (1970b), Chang (1976e), and Oka (1983).

Maintenance of Genetic Integrity

Care should be taken to minimize labeling errors and to reduce mechanical mixtures during the planting of the collection. Harvested plants, panicles, or heads of each plot should be transported and dried in cloth bags.

For self-pollinated crops, a sufficiently large number of plants (about fifty to one hundred) should be harvested and the seeds bulked. Plants of rows bordering other accessions should be discarded. If any doubt should arise, the seed file and the characterization data should be consulted.

For cross-pollinated crops, the population can be treated as a monoecious or dioecious species. Under each method, three sampling procedures are possible: (1) control of both female and male gametes, (2) control of only the number of female gametes, and (3) no control of either female or male gametes. See Hallauer and Miranda (1981) for a discussion of effective size for maize populations resulting from each of these procedures.

A cross-pollinating crop may be efficiently maintained by growing a reasonably large sample of the original population in isolation plots. For maize, about eighty to two hundred plants appear adequate (Omolo and Russell, 1971). For land races of rice, each seed plot at IRRI contains at least sixty plants.

Verification of Evaluation Data

Disease- and insect-susceptible accessions may be recorded as such without retesting, whereas resistant or tolerant populations from the first test need to be retested under more precisely controlled conditions to establish the validity of preliminary evaluation.

This step should also apply to the evaluation of other traits, especially those subject to the effect of variable environments or planting density in field trials. The sampling of environment variance and the genotype × environment component will add scope to the evaluation experiments.

Planning and Managing Evaluation Tests

Every evaluation test should be a scientific investigation: it should embody well-defined objectives, the experimental design should be efficient, and there should be judicial choice of treatments and control varieties, control of the environment if necessary, and complete statistical analysis. Data should be entered in computerized data files for easy retrieval and monitoring. Results from repeated tests should be compared with previous data before entering the information into the files for updating purposes.

Communication Among Conservationists, Problem-Area Scientists, and Plant Breeders

Open and continuous communication among conservationists, problem-area scientists, and plant breeders is essential to sustain evaluation efforts. At IRRI the three groups of scientists under the Genetic Evaluation and Utilization (GEU) program meet every month to exchange ideas and information. These frequent exchanges are followed by an annual program review and a five-year review. Many crop advisory committees of national centers and of the IBPGR also meet periodically to sustain the cooperation.

Newsletters and scientific journals are other avenues for scientists with a common interest to communicate information, which frequently leads to germplasm exchange. The publication process in scientific journals, however, has become increasingly slow and expensive.

AN EXAMPLE OF A SYSTEMATIC AND COMPREHENSIVE EVALUATION PROGRAM

Organizational Scheme

The evaluation activities of IRRI's large-scale GEU program are excerpted below to serve as an example of multidisciplinary cooperative and intensive efforts on a single crop, rice. IRRI's evaluation efforts date back to 1962 when it began its research operations. Resistance to rice diseases and insects along with grain quality were the main thrusts (Juliano, 1972; Chang et al., 1975a). Successful efforts in identifying pest resistance within the first decade of operation prompted many national rice research programs to evaluate their indigenous cultivars (Pal, 1972; Zaman et al., 1972). IRRI's GEU Program was streamlined in 1974 to expand, systematize, and coordinate the ongoing evaluation activities and to extend its scope to unfavorable rice-growing environments in which additional production contraints exist (Brady, 1975). Such unfavorable factors affect about three-fourths of the rice growers in the tropical areas.

The problem areas of evaluation and research were organized into eight task forces as follows: (1) Agronomic and physiological traits related to grain yield: plant physiologists and agronomists; (2) Disease resistance: plant pathologists and biochemists; (3) Insect resistance: entomologists and biochemists; (4) Drought: plant physiologists, agronomists, biochemists, climatologists, and irrigation engineers; (5) Temperature tolerance: plant physiologists, (6) Deepwater and submergence tolerance: plant physiologists and agronomists; (7) Grain quality and nutrition: cereal chemists, agronomists, and biochemists; and (8) Adverse soil factors: soil chemists, plant physiologists, and agronomists.

In addition to the problem-area scientists, the conservationists, statisticians, geneticists, and breeders contribute their expertise to each of the areas. An operations committee coordinates some of the interdisciplinary activities. Meetings and field visits are frequently held.

Scope of the Evaluation Efforts

The scope of evaluation may be shown by the total of 30,000-50,000 accessions screened by the different teams per year from 1976 to 1983. The number of individual experiments conducted each year may be indicated by the number of requests for seeds received by the Germplasm Center, which ranges from 190 to 340 during 1975-83 period.

Some GEU tests are accelerated when the IRGC staff feeds newly harvested seed of accessions reported to have special characteristics to the concerned GEU scientists to speed up the evaluation process. These special characteristics include tolerance for temperatures, extreme drought, deep water, salinity, and other adverse soil factors (Chang, 1980; Chang et al., 1982a).

During 1975 the international dimensions of the GEU Program were expanded by the establishment of the International Rice Testing Program (IRTP), under which many international nurseries under both favorable and unfavorable conditions have been grown in more than seventy-five countries in the world (IRRI, 1980a).

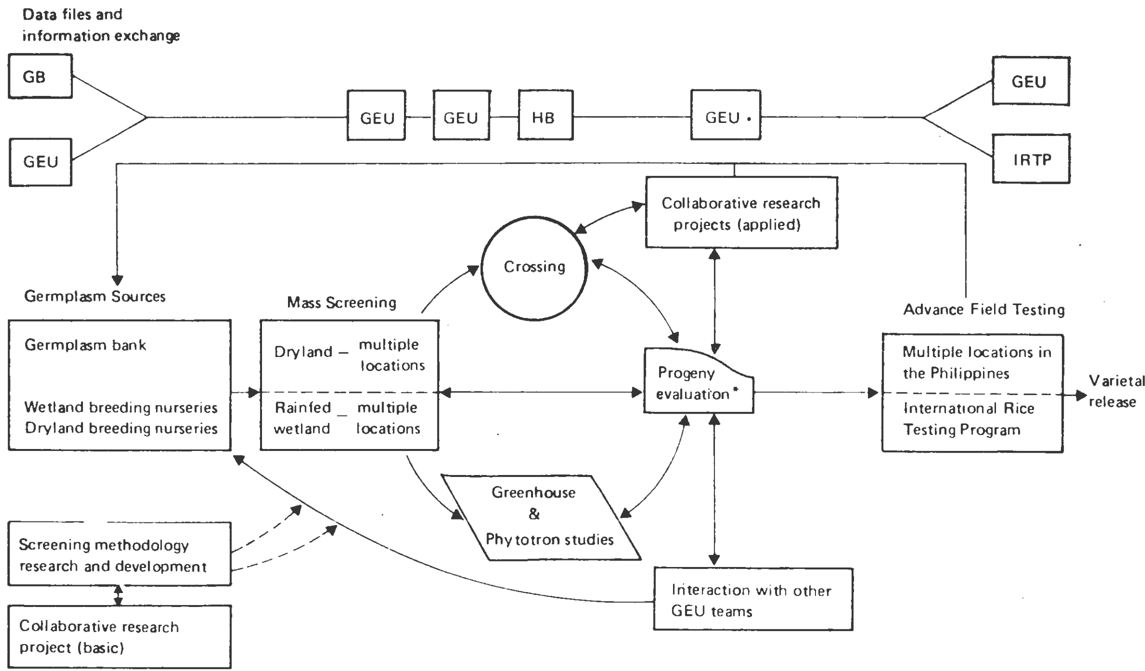
For traits that require sophisticated research methods and equipment, such as the biochemical nature of insect resistance and salinity tolerance and the physiological basis of drought resistance, IRRI staff collaborates with scientists in developed countries. The operational procedure of the GEU program exemplified by breeding for drought resistance is shown in Figure 1.

Other IARCs also cooperate with advanced research institutions in developed countries to tackle those research problems that require investigations of a fundamental nature (Henshaw and Roca, 1976; Interantional Potato Center, 1983; Mujeeb-Kazi and Jewell, 1984).

Outstanding Sources of Agronomic Traits and Resistance/Tolerance Identified from the Germplasm

Chinese semidwarfs with the improved plant type was the most useful trait identified from IRRI's germplasm collection. It led to the development of IR8 (see Chandler, 1968) and many other high-yielding semidwarfs (Chang and Li, 1980).

The second stage of development involving disease and insect resistance and grain quality was contributed by several land races such as TKM6, Mudgo, PTB18, PTB20, and N22 of India, Tadukan of the Philippines, and Gam Pai 15 of Thailand. *O. nivara*, a wild relative from northern India, furnished the useful source of grassy stunt virus.



*Including mass screening under different hydrologic-edaphic-cultural regimes

Figure 1. Flow diagram of related activities under the drought resistance component of IRRI's GEU program (modified from Chang et al., 1982b).

Deep-and-thick roots were found in Japanese upland varieties and other upland varieties of Southeast Asia and West Africa.

Tolerance for salinity was found primarily in land races of Sri Lanka and India. Varieties tolerant of iron toxicity in wetland soils came from Sri Lanka and Vietnam. Sources able to withstand aluminum toxicity in aerobic soils were identified from the upland varieties of Brazil, West Africa, and the Philippines.

Varieties able to withstand deep water or to tolerate submergence under flash floods came from Bangladesh and India. Tolerance for cool night temperatures was found in varieties originating in China, Indonesia, and Nepal as well as in upland varieties. Detailed information may be found in Chang et al. (1982a).

Impact on National Rice Research Programs

Evaluation of native rice germplasm and foreign introductions began in Japan and the USA around the mid-1920s. After World War II major rice-growing countries in tropical Asia and Latin America also began to implement evaluation programs. But the operations were largely carried out by rice breeders, sometimes with assistance from a related discipline, and the scope was limited to a few priority breeding objectives. A survey of the evaluation results was provided by Chang et al. (1982a).

When the enormous returns from IRRI's evaluation efforts became apparent, several national rice improvement programs in tropical Asia also implemented extensive and coordinated evaluation projects. The All-India Coordinated Rice Improvement Project was started in 1966. In recent years national evaluation programs patterned after the GEU Program have been established in Bangladesh, South Korea, Indonesia, Thailand, and China.

Lessons Learned from the GEU Program

The remarkably rich rice germplasm and the intensive multidisciplinary evaluation program not only have given rice researchers enormous gene pools to exploit for varietal improvement and research but also broadened the dimensions of rice research. The research aspects are described in the sixth article of this issue on rice history and conservation.

Equally important are a number of lessons gained from the evaluation efforts which would aid further collections and evaluation.

1. Ecological impact on varietal adaptation: The ecological conditions of the rice-growing environment greatly influence the kind of land races that could have evolved under specific ecological niches to resist certain diseases and insects or to tolerate physicochemical stresses. For instance, the majority of land races resistant to the brown planthoppers came from South India and neighboring Sri Lanka, where multiple and continuous cropping of rice has been practiced for centuries in a humid and tropical environment without the use of insecticides. Other sources resistant to insects such as the gall midge and whitebacked planthopper were isolated from land races of those areas where the pest had been endemic for many decades. This aspect was pointed out earlier by Leppik (1970).

   The same relationships apply to tolerance for submergence, adaptiveness to deep water, drought resistance, tolerance for aluminum toxicity, and tolerance for salinity. In the case of tolerance for cool night temperatures, high altitude or latitude is not the only moving force in the differentiation process—the dryland (upland) environment had also contributed to the process. This was shown in Silewah, the most cold-tolerant cultivar, which was collected at an elevation of about 1,300 m in the upland rice area of north Sumatra (3° lat. 05′N). A refined characterization of the rice-growing environments in different geographic regions would benefit germplasm collectors and users.
2. Intrapopulational variability: The inherent variability within a land race or a wild population is amply demonstrated in the initial identification of sources resistant to biotype 1 of the brown planthopper and the grassy stunt virus. About eighty percent of the seedlings in the Indian cultivar Mudgo were resistant to the plant hopper while the other twenty percent were susceptible. The sole source of resistance to the grassy stunt virus, a strain of *O. nivara* collected from northern India, contained three resistant plants among a test sample of about thirty seeds. If rigorous and subjective purification and severe roguing were done during seed multiplication and characterization, rice workers might not have access to these two resistant sources, each of which has contributed untold millions of dollars to rice production. Therefore, the conservationists should carry out purification with great caution.

3. Ecostrains: The rice plant contains so much genetic plasticity that after a rice cultivar is introduced into a foreign area, it soon develops enhanced adaptation to adverse factors in the new ecosystem. In the deep-and-thick root systems, the most outstanding accessions were frequently found in the African upland varieties belonging to *O. sativa*, which were introduced from tropical Asia into West Africa only a few centuries ago. This finding points to the importance of conserving ecostrains which bear the same name and have many identical morphological features.
4. Co-adapted gene complexes: The existence of co-adapted gene complexes is best indicated by the drought-avoiding upland varieties and the floating rices that can withstand rising water depth up to 5 m. The drought-avoiding complex consists of a small number of deep and thick roots, low tiller number, tall plant height, gently droopy leaves, thick leaf blades, fixed growth duration, long panicles, full panicle exsertion, and large and bold grains. On the other hand, these upland varieties are susceptible to zinc deficiency and water-logging. The deepwater rices are tolerant of water deficit at the seedling stage, able to produce tillers and adventitious roots at the higher nodes, and capable of rapid internode elongation when the water depth rises quickly.
5. Unexpected findings: One of the sources of high resistance to the tungro virus is HBJ-DW8, a floating variety. The tungro disease is not prevalent or serious in the deepwater areas. The Indian variety TKM-6, on the other hand, showed susceptible reaction to the brown planthopper biotype 1, but many resistant progenies were found in its crosses. It soon became obvious that TKM-6 carries an inhibitor to the resistance gene. Thus, it requires systematic evaluation of parents and progenies to isolate the desired genotypes.
6. Component analysis: Much insight has been gained from the study of complex traits by separating and studying the individual components. The nature of resistance to the brown planthopper has been elucidated by designing experiments which differentiate between preference, tolerance, and antibiosis. The mechanism of virus resistance became more apparent when resistance to the insect vector was separated from resistance to the virus. Similarly, studies on drought resistance have been aided by investigating individual components: escape, avoidance, tolerance, and recovery ability. Growth

duration can be partitioned into the basic vegetative phase, the photoperiod-sensitive phase, and the critical photoperiod.

7. Control of environmental conditions: A classical case of genotype × environment interactions in breeding for disease resistance was the varietal reaction to cabbage yellows pathogen under different soil temperature regimes (Walker, 1957). Although such a dramatic instance has yet to be experienced in rice, the GEU scientists are aware of the complicating effects of daylength and ambient temperatures on the growth and development of rice cultivars from different geographic areas. IRRI staff makes use of the facilities in the phytotron where controlled environments are available for critical studies.

   Detailed information may be found in: (a) general: Chang (1971, 1976e), Chang and Li (1980), Chang et al. (1982a); (b) climatic: Chang et al. (1969), Chang and Vergara (1972), Chang and Oka (1976), Vergara (1976), Vergara and Chang (1976); (c) disease and insect resistance: Ou (1972), Ling (1972), Chang et al. (1975a), Pathak (1977), Khush (1977b); (d) drought resistance: O'Toole and Chang (1979), O'Toole (1982), Chang et al. (1982b); (e) tolerance for adverse soil factors: Ponnamperuma (1977b, 1982); and (f) issues of IRRI's annual report.

Evaluation results can be profitably used for recanvassing in a germplasm-rich area where extreme environmental stresses have led to the differentiation of stress-tolerant ecotypes (O'Toole and Chang, 1979) or marked interpopulation and intrapopulation diversity have developed (Ng et al., 1983).

OTHER LARGE-SCALE EVALUATION PROGRAMS

The first systematic effort in collaborative evaluation of the U.S. dates back to the uniform wheat rust nurseries of the 1930s which comprised a cooperative research program between the USDA and the state agricultural experiment stations of different wheat-growing states. Disease nurseries of other cereals such as barley and oats were set up after World War II. An extension of the U.S. uniform disease nurseries were the international rust nurseries of the Rockefeller Foundation Program in Mexico, which later became the CIMMYT. The series of International Wheat Yield Nurseries of CIMMYT began in 1960. The international rice nurseries began in 1975. The ICRISAT also coordinates international yield trials of sorghum and millets.

DOCUMENTATION

Importance of Document Systems

Documentation is such an essential component of genetic conservation that it is needed in every facet of the program and provides a connecting link between different facets. Full documentation of conserved material and free exchange of the information would stimulate germplasm exchange, evaluation, and use. This process will indirectly aid in the preservation of valuable germplasm at duplicate sites.

Unfortunately, the documentation of useful information from different crops was so fragmented and unavailable to interested researchers that it became a bottleneck in national germplasm systems. The most serious problem was the users' lack of interest in exotic germplasm when the potential usefulness of such agronomically poor materials was not made known to crop scientists.

Because documentation provides links to different facets of genetic conservation and use, the process needs to be set up as a comprehensive system so as to effectively serve the full spectrum of conservationists and users. The functions of a documentation system serving a genetic resources center have been illustrated by Rogers et al. (1975).

Components of a Documentation System

A documentation system should include: (1) operational components—data files on collections, evaluation results, inventories, and uses, (2) standardized information formats—descriptors (traits) and descriptor states (absolute or coded values), and (3) computer programs for storage, retrieval, statistical analyses, and collation.

The evolution of IRRI's germplasm data system was described by Chang (1984d).

Data Files

For the entire crop collection, the minimum entries are accession number, accession name, other designations, country of origin, seed source, breeding history, and, if applicable, collection site, ecological data on the site, and special use, if any. Such information is frequently referred to as passport data.

Postcollection information consists of (1) characterization (morphoagronomic) data, (2) evaluation data on reactions to biotic and climatic-hydro-edaphic stresses, quality characteristics, and industrial characteristics, (3) ethnobotanical and bibliographic data, and (4) information related to seed storage, rejuvenation, viability, and distribution. IRRI has three files for each crop category (Asian cultivars, African cultivars, and wild species): basic (morphoagronomic), GEU traits (disease reactions, insect reactions, etc.), and seed files (storage, distribution, rejuvenation, etc.).

For accessions being used in breeding programs, a data file on their use in the development of improved cultivars of germplasm should be set up. This facet requires different breeding centers to make available the hybridization records of each year or period. Private breeding enterprise may not be willing to furnish such information except for the registered varieties. In IRRI, a genetic monitoring network of international scope has been initiated. One file records the crosses made for each crop season at IRRI. Another file consolidates the information obtained from international nurseries and provides periodic analyses and summaries. The IRTP of IRRI provides such a service.

Descriptors and Descriptor States

Efforts to standardize crop research records and related information such as the morphoagronomic traits and growth stages of cereals began in the 1940s (Feekes, 1941) and came into worldwide adoption in the 1960s (Large, 1954; Chang and Bardenas, 1964; Hanway, 1966; Hanway and Thompson, 1967; Konzak and Dietz, 1969; McNeal et al., 1971; Zadoks et al., 1974; Seidewitz, 1974). The decimal codes have been widely used by all disciplines in international rice nurseries (IRRI, 1970, 1976b).

The first varietal catalog printed directly from computer-printed sheets of standardized code was the rice catalog (IRRI, 1970) based on standardized codes (Chang and Bardenas, 1964). Because printing catalogs is a laborious process and catalogs become quickly outdated by the increase in both accessions and evaluation data, IRRI no longer prints catalogs, but provides a computerized retrieval service for rice researchers (see Chang, 1984d).

Since its establishment, the IBPGR has assisted in the development of many descriptor lists for different crops by crop committees. However, descriptors for cultivars may not suit the needs for wild species.

Department of Statistics, IRRI

Germplasm Bank Information Retrieval Request Form

Form GB 1

Operator	
< less than	> greater than
= equal to	≠ not equal
≤ less than or equal to	
≥ greater than or equal to	

Researcher T. T. Chang Department IRGC
Date Submitted 5/8/79 Date Needed ASAP
Purpose of retrieval: To fill foreign seed request

Character	Criterion Operator	Criterion Value	Output
1. ACCNO			X
2. VARNM			X
3. DESIG			
4. SS			X
5. ORI			X
6. VG			
7. SDHT			
8. LLT			
9. LWD			
10. BLPB			
11. BLCO			
12. LSCO			
13. LA			
14. LFA			
15. LIGLT			
16. LIGCO			
17. LIGSH			
18. CCO			
19. AUCC			
20. HDG			
21. CULT	≤	100	X
22. CUNC			
23. CUAN			
24. CUDI			
25. INC[illegible]			
26. [illegible]ST			
27. FLT			
28. PTY			
29. BR			
30. FEX			

Character	Criterion Operator	Criterion Value	Output
31. PA			
32. PSH			
33. PTH			
34. AWPR	≤	1	X
35. AWCO			
36. APCO			
37. STCO			
38. LPCO			
39. LPP			
40. SLCO			
41. SLLT			
42. SPKF			
43. 10[illegible]			
44. GRLT	>	7.5	X
45. GRWD	<	3.5	X
46. SCC[illegible]			
47. ENDO			
48. SNT			
49. SEN			
50. MAT	>119&<136		X
51. *BP	≤	3	X
52. *BL			
53. *SHB			
54. [illegible]			
55. [illegible]			
56. [illegible]			
57. *BPH1	≤	3	X
58. *BPH2			
59. *BPH3			
60. *GLH	≤	3	X

Character	Criterion Operator	Criterion Value	Output
61. SBSD			
62. SBSW			
63. SBYD			
64. SBYW			
65. RWM			
66. *WBPH			
67. *ZLH			
68. RLF			
69. PRTD			
70. PRTW			
71. AMY			
72. GEL			
73. DRT1			
74. DRT2			
75. DRT3			
76. DRT4			
77. DRT5			
78. DRT6			
79. *DRT7			
80. *DRT8			
81. *DRT9			
82. ALK			
83. SAL			
84. ZNC1			
85. ZNC2			
86. FI[illegible]			
87. F[illegible]			
88. [illegible]			

Figure 2. Information retrieval form used at IRRI, showing the 50 descriptors entered under the GB-basic file and the 38 descriptors grouped under the GEU-traits file. The abbreviated descriptors (characters) along with their coded values are explained on the backside of the form. This form was completed and submitted to the statisticians of IRRI. The retrieved data are shown in Table 1.

Table 1. Specimen of a printout of the computer-retrieved data from two data files (BG-Basic and GEU-Traits) based on the specifications given in Figure 2.

Accessions with culm length < or = 110 cm, grain length > 7.5 mm, grain width <3.5 mm, awn presence < or = 1, maturity >119 and < 136 days, bacterial leaf blight < or = 3, bph-1 < or = 3, and glh < or = 3.

Accession Number	Variety Name	Seed Source	Origin	Culm Length	Grain Length	Grain Width	Awn Presence	Maturity	Bact. Blight	Bph-1	Glh
08511	DJ 9	113-1	113	98	8.5	3.2	0	120	2	1	3
08816	DV 29	113-1	113	96	8.5	3.2	0	130	2	3	1

Summary of retrieved information	
No. of accessions satisfying query	= 2
No. of accessions in the data bank	= 40757
Last accession no. in the data bank	= 40768

Computer Programs

As long as the biological scientists can communicate with the programmer on the scientific needs of a data file, there is no barrier to developing relatively simple and highly efficient computer programs to meet different needs (Gomez et al., 1977). The information retrieval system of the rice germplasm at IRRI has been published (Gomez et al., 1979). A sample form of IRRI's Information Retrieval Request Form is in Figure 2 to illustrate a user-oriented approach. A summary of retrieved data follows in Table 1.

Screening data from repeated testing of the rice germplasm at IRRI is updated by one of the following means: (1) establishing a subfile for the additional data of certain traits, (2) entering the most susceptible reaction for some diseases and insects, and (3) entering the average value over all tests made and the number of tests (K. A. Gomez, personal communication).

The processing of plant disease data was described by Loegering (1968). Fribourg (1968) discussed forage crop data processing. Thompson and Baum (1978) devised an information retrieval system for barley cultivars. Blixt (1984) described the data management systems of the Weibullsholm Plant Breeding Institute and the Nordic Gene Bank in Sweden.

The Ministry of Agriculture and Forestry of Japan and the USDA have each set up a national network of germplasm resources information (Suzuki and Kumagai, 1981; Anon., 1984b).

International and Interinstitutional Cooperation

International and interinstitutional cooperation is needed at all levels of operation: (1) to develop descriptor lists, (2) to use standard recording codes, and (3) to channel data into international/national data banks for research and exchange.

IRRI serves as the international data center for rice. The International Rice Research Newsletter (IRRN) published by the IRRI serves as a channel for rice researchers to quickly disseminate and share their research findings. Such collaborative efforts have led to an increased use of the germplasm maintained by the IRGC at IRRI (Chang, 1983b).

IOWA STATE JOURNAL OF RESEARCH / MAY, 1985 399-424
Vol. 59, No. 4

GERMPLASM ENHANCEMENT AND UTILIZATION

Te-Tzu Chang[1]

ABSTRACT. The use of and benefits derived from conserved germplasm is the sole criterion for assessing the genetic conservation program for a crop. Although mission-oriented plant introduction programs have had the largest impact, the use of land races and wild relatives in certain crops has yielded spectacular results. Extent of use and derived benefits varies from crop to crop. The more impressive results have been obtained in wheat, rice, tomato, surgarcane, and tobacco. This paper reviews the progress attained in some selected crops.

Before use by plant breeders, the exotic germplasm (land races and wild species) must undergo a series of steps to facilitate its incorporation into agronomically acceptable backgrounds: conversion and enhancement (prebreeding). Hybridization and cytogenetic techniques to expedite the tranfer of genes from related wild species are described. Additional tools recently offered by genetic engineering are also discussed.

Contributions of the exotics to crop production are summarized, and recent expansions in use-oriented conservation programs are noted. Both a greater awareness of the need for genetic diversity in major crops and potential constraints on germplasm exchange are evident; these are assessed. Prospects for meeting future food needs through genetic conservation and crop improvement are discussed.

Index Descriptors: exotic germplasm, conversion, prebreeding, germplasm enchancement, breeding techniques, cytogenetic techniques, *in vitro* and cellular approaches for plant breeding, yield increases in major food crops, cost-benefit relationship of genetic conservation, Plant Varieties Rights Act, role of IARCs, population growth vs food increase.

INTRODUCTION

The ultimate criterion for assessing the success of a crop-oriented germplasm conservation program is the use and benefits derived from its conserved genetic resources. Based on this criterion, introductions of a slightly improved cultivars have scored very high. Varietal improvement based on the use of land races is also impressive in many crops. The wild species remain the least conserved and exploited category, although impressive advances in crop improvement have been attained in some crops such as wheat, rice, tomato, sugarcane, and tobacco with genes contributed by the wild taxa. The

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extent of evaluation and initial use (enhancement) among the three categories of germplasm is nearly proportional to the degree of usage.

Most plant breeders use breeding materials that already have the desired agronomic background. The practice is dictated by economic and temporal needs. On the other hand, crossing a commercial variety with a very primitive land race or a wild species would introduce many undesirable genes into the breeding program and retard the progress of conventional breeding. Seed scarcity and the lack of evaluation data on the exotic germplasm, which appears to have no immediate usefulness, are another barrier in using the land races and wild species. Crossability between two distant species often poses technical difficulties in recombining the desired traits. Hallauer and Miranda (1981) viewed exotic germplasm as "all germplasm that does not have immediate usefulness without selection for adaptation to a given area."

However, not all land races and wild species carry undesirable gene-complexes. Many land races have contributed to yield increases (see Frankel and Soule, 1981) and pest resistance (see Harlan and Starks, 1980). The Turkish, Kenyan, Australian, and semidwarf wheats have greatly improved U.S. wheat production (Vogel et al., 1963; Reitz and Craddock, 1969; Burgess, 1971). Wild species of *Avena* have also enhanced yield levels by contributing greater vegetative growth rates (Helsel and Frey, 1983; Frey, 1983a).

To prepare exotic germplasm for greater use by plant breeders, it is often necessary to break up the tight linkage between the desired genes and the undesirable alleles. Transporting land races from their native habitats to a favorable production area with a different climatic pattern, photoperiod, and temperature may require supplementary seed increase and selection at a site similar to native habitat of the land races or many more cycles of disruptive selection. For wild species, particularly the putative progenitors, either a naturally introgressed population or an artificially directed back-crossing program would enhance their usefulness in breeding programs. These preparatory measures are known as conversion or germplasm enhancement or prebreeding. In all cases, longer periods are required to make use of the exotic germplasm than the well-adapted elite germplasm (Knott and Dvorak, 1976; Brown, 1982; Frey, 1983a; Chang, 1984b).

SUCCESSES OF PLANT INTRODUCTIONS

Although mission-oriented plant introduction efforts of the past century or so do not constitute genuine genetic conservation measures, the enormous contributions of foreign introductions to the agriculture of each agriculture-based nation cannot be overlooked. The phenomenal contributions of the foreign introductions were particularly significant to the developed countries in the northern hemisphere which were poor in native crop germplasm. The crop production of the U.S. draws its strength from crops introduced from foreign lands, experimenting with their culture, improving the genetic potentials, and developing expanded or new uses. Among the food crops, only sunflower, the small berries, and pecans originated in the North American continent (National Plant Genetic Resources Board, 1979).

Many countries in the developing world have also expanded their agricultural bases by planting introduced crops for food or for industrial uses. Recent and notable examples are Brazil and Argentina which now grow soybean and Bangladesh which today produces wheat.

Interesting accounts on the impact of foreign introductions on U.S. agriculture may be found in the USDA Yearbooks of Agriculture (1936, 1937), Norman (1963), Quisenberry and Reitz (1967), Burgess (1971), Creech and Reitz (1971), and the monographs on individual crops published by the American Society of Agronomy (Coffman, 1961; Quisenberry and Reitz, 1967; Hanson and Juska, 1969; Hanson, 1972; Caldwell, 1973; Sprague, 1976).

EXAMPLES OF GERMPLASM CONVERSION PROGRAMS

Sorghum

Short-statured sorghums (1.5-1.75 m) are required for mechanized harvesting but traditional sorghums (*Sorghum bicolor*) in many areas of the world are tall. To use genes from the two contrasting gene pools of climatic adaptation, the joint Texas Agricultural Experiment Station-USDA Project of Sorghum Conversion program was established (Stephens et al., 1967). The tall and late (photoperiodic) sorghums of the tropics have been crossed as male parents with U.S. sorghums and backcrossed to the temperate-zone sorghums, except for the last backcross, in which the tropical parent was used as the female parent. The crossing and backcrossing were conducted in Puerto Rico during the winter whereas selection for short and early progenies was made during long days in Texas. By substituting up to eight genes which were known to control height and maturity (see Quinby, 1975), many useful lines have been obtained after four backcrosses. Among the new materials, new sources of disease and insect resistance, other important traits that contribute to yield level and yield stability, and superior kernel characteristics have been identified. The diversity of converted germplasm is greater than that of the parents. Some of the converted materials maintain high and stable yields in the tropics due to lower base temperatures during seed germination. Thus, the conversion of *S. bicolor* germplasm not only has broadened the adaptive range but has also provided opportunities to select for highly specific adaptation to a locale (Eberhart, 1970; Miller, 1982).

Corn

Corn breeders in Hawaii have made use of its tropical environment at 14°N latitude to incorporate resistance to maize mosaic virus, common rust, and earworm from tropical races. The tall stature and late maturity of the tropical races were modified into earlier genotypes by backcrossing, while the maturity of Corn Belt germplasm has been lengthened by a week. Endosperm characters were also included in the conversion program (Brewbaker, 1974).

EXAMPLES OF GERMPLASM ENHANCEMENT PROGRAMS

Wheat

Interest in the evolutionary genetics of the wheat species has stimulated the numerous cytogenetic studies on *Triticum*, *Aegilops*, *Agropyron*, and other wild relatives. Moreover, the ease in manipulating individual chromosomes of hexaploid wheats has led to additional studies, some of which have benefited prebreeding or germplasm enhancement efforts.

Aegilops umbellulata was first crossed with *T. dicoccoides* and an amphidiploid progeny was obtained. The amphidiploid plant was crossed to *T. aestivum* but the F_1 plant turned out to be male sterile; the latter was backcrossed to *aestivum* twice and the progeny tested for rust resistance. A resistant plant carrying 21 bivalents and an added *umbellulata* isochromosome was identified. The pollen of this plant was irradiated to pollinate *aestivum* cv. Chinese Spring. Pollen having the *umbellulata* isochromosome rarely functioned and was eliminated. In other rust-resistant progenies, forty plants were found to carry translocations involving a part of the isochromosome to a part of a wheat chromosome. Only one of the intercalary translocations involving wheat chromosome 6B had normal pollen transmission (Sears, 1956). The line was later named Transfer and was widely used (Knott and Dvorak, 1976).

The induction of homoeologous pairing and crossing over between wild and cultivated species has been used to facilitate interspecific gene transfer. The *Ph* gene in tetraploid and hexaploid wheats allows only homoeologous chromosomes to pair at meiosis. This gene can be induced to mutate to an inactive state (*ph*). By a series of chromosomal manipulations, wheat plants with the *ph* gene and single doses of an alien chromosome and of a related wheat chromosome can be obtained. Pairing between the two nonhomoeologous chromosomes is made possible. Cross-overs would lead to the transfer of desired genes from the alien chromosome to wheat. The *ph* mutants have facilitated the transfer of genes from *Aegilops* and *Agropyron* (Sears, 1976).

Another approach is to use the suppression of the *Ph* gene by the 5B chromosomes of the B genome such as *Aegilops speltoides* and *A. comosa* (Riley and Chapman, 1958). An amphidiploid developed from *T. aestivum* and *A. comosa* was backcrossed to hexaploid bread wheat to produce a plant with all of the wheat chromosomes and a single, simple *comosa* chromosome carrying the desired gene for yellow rust resistance (Yr_8). When this plant was crossed with *A. speltoides*, the rust-resistant progeny carried single doses of the wheat and *speltoides* genomes as well as the *Yr*-bearing chromosome. Pairing between the *Yr* chromosome and the related wheat chromosome is now possible. After further crossing with wheat and selfing, a resistant line (Compair) having the same chromosome as wheat but carrying a modified chromosome pair contained segments from both species and included the Yr_8 alleles (Riley et al., 1968).

Other elegant cytogenetic methods to achieve intergeneric and interspecific transfers involve addition lines and substitution lines (see Morris and Sears, 1967). The substitution approach was successful in obtaining genes for disease resistance from *Agropyron* species (Knott, 1961, 1964; Sears, 1972, 1976, 1981; Knott et al., 1977).

Wild species have also been used by Canadian and U.S. breeders as source of improved winterhardiness, short stature, and cytoplasmic male sterility (see Knott and Dvorak, 1976; Stalker, 1980).

CIMMYT breeders have made numerous wide crosses to improve the spring bread wheats. Parents include spring and winter wheats, barley, *Agropyron* species, *Aegilops* species, *Secale cereale*, *Haynaldia* species; and *Elymus* species. Taxa of *Agropyron* possess genes for resistance to rust and barley yellow dwarf virus and salt tolerance. *Elymus* species have shown tolerance for drought, salt, cold, or heat as well as resistance to leaf-spotting diseases such as *Helminthosporium* and *Fusarium*. The *Aegilops* species are also potential sources of resistance to the leaf-spotting diseases. Spring × winter crosses have produced selections resistant to *Septoria tritici* (CIMMYT, 1983). CIMMYT workers have succeeded in using prepollination or postpollination, or both, and manipulating the embryo culture media to overcome the crossability barriers in intergeneric crosses (Mujeeb-Kazi and Jewell, 1984). CIMMYT staff have made good use of collaborating stations in Mexico, Brazil, and Pakistan to extend testing and selection under diverse environments and to carry out "shuttle breeding" (CIMMYT, 1979, 1984).

Rice

Six genomes have been identified from sixteen out of the twenty-two species in the genus *Oryza*. The Asian and African cultigens share the basic genome A, but the two cultigens and their immediate wild species differ sufficiently from one another that they belong to two subgenomes or primary gene-pools.

The most promising trait in the wild species of Asia identified to date is virus resistance (see Chang et al., 1982a). Crosses between the cultigen and the annual wild relative (*O. nivara*) have been generally fertile and, in one case, even exceeded the fertility of some inter-varietal crosses (Dolores et al., 1979).

The crossability between the Asian and the African cultigens is partly affected by the direction of crossing. More viable F_1 plants were obtained when *O. glaberrima* was used as the female parent than by the reciprocal cross. Attempts made at IRRI to transfer the resistance to green leafhopper in *O. glaberrima* to *O. sativa* have not produced desirable progenies.

Chinese workers have crossed rice with sorghum, bamboo, reed, 'gu,' corn, and wheat. Although fertile progenies were obtained, their usefulness in crop improvement has not been demonstrated (see Chang et al., 1982a).

Corn

Annual teosinte (*Zea mexicana*) and *Tripsacum* have been used by several workers to improve maize productivity. Reeves (1950) used backcrossing to introgress teosinte genes into corn inbred 127C. Some derived lines yielded twenty percent more than 127C in topcrosses. Reeves and Bockholt (1964) later isolated fertile lines from backcrosses of Tx203 × diploid *Tripsacum* that yielded higher than Tx203 or in hybrid combinations. Efron and Everett (1969) developed thirty-six synthetics by crossing twelve single or double crosses adapted to New York State with pollen mixtures from Mexican maize and teosinte. The synthetics were selected, randomly mated for four generations, and later mated to four tester stocks. Stover production from the five best topcrosses of the derived populations exceeded that from the five checks whereas grain yield of the best topcrosses equalled that of the checks. Harlan (1976b) found distinct vegetative heterosis in backcrossed lines from corn × *Tripsacum* hybrids when crossed to Corn Belt inbreds.

Hybrids containing exotic germplasm from Mexico or Brazil, either wholly or in parts, yielded higher than those containing only Corn Belt germplasm (Griffing and Lindstrom, 1954).

Introgression of germplasm from West Indian races has increased both genetic variability and higher yielding ability to Corn Belt germplasm (Goodman, 1965; Brown, 1982). Stuber (1978) has provided additional information concerning evaluation of a broader array of materials.

Two diallel series of matings involving Corn Belt and semi-exotic populations (including the West Indian races) were compared for grain yield. The better semi-exotic populations appeared promising for temperate zone corn improvement (Eberhart, 1971).

Inbred lines containing exotic germplasm of Tuxapeno, Cuban Flint, and Coastal Tropical Flint, as well as other races or cultivars from Brazil, Columbia, and Peru have provided wide adaptation to the southern U.S. conditions, excellent combining ability, and drought and disease tolerance (Nelson, 1972).

Resistance to corn rootworm, leaf aphids, and to the northern leaf blight has been identified in *Tripsacum* species. Resistance to northern leaf blight has been transferred from *T. floridanum* to dent corn after many years of breeding by Hooker (Galinat, 1977).

Resistance to anthracnose, *Fusarium* stalk rot, northern corn leaf blight, southern corn leaf blight, and Stewart's bacterial blight has been transferred from tetraploid *T. dactyloides* (R. R. Berquist, see de Wet, 1979).

Cuban flint has been used to transfer earworm resistance into central Corn Belt inbreds. Introduction of small increments of the exotic germplasm into adapted types appeared effective in using the alien races. Similarly, genes from a recently discovered wild teosinte, *Z. diploperennis*, have provided resistance to or tolerance for several virus diseases without other undesirable features associated with the wild germplasm (Seifert, 1981, see Brown, 1982).

The findings suggest that incorporating small increments of exotic germplasm into the adapted inbreds may be the most effective way of using the exotic races (Brown, 1982). But, the profitable use of exotic germplasm in U.S. hybrid production should be weighed against the steady increase in corn yield over the past fifty years during which adapted germplasm has been used almost exclusively (Frey, 1971; Russell, 1974, 1984; Duvick, 1977). Many corn workers, however, agree on the need to expand the genetic base of U.S. corn germplasm by using exotic races.

CIMMYT workers have crossed maize with sorghum, but the attempt to obtain a hybrid by sexual means was unsuccessful. More recent efforts have been to make use of *Tripsacum* for broad adaptation, tolerance for waterlogging, and drought and pest resistance in the wild relative. Some progress has been attained with the use of tetraploid *Tripsacum*. CIMMYT and the University of Illinois scientists are cooperating on the use of annual tripsacoid maize plants and a "transforming DNA technique" to facilitate the transfer of *Tripsacum* genes into maize (Mujeeb-Kazi and Jewell, 1984).

Potato

There are more than 140 species in the genus *Solanum*, ranging from diploids to hexaploids. The cultigen *S. tuberosum* ($2n=4x=48$) is a tetrasomic polyploid. Haploids of the cultigen are easy to obtain through $4x \times 2x$ crosses. Chromosome differentiation between the cultigen and wild relatives is small and makes gene transfer easy. Moreover, the sets of chromosomes are easy to manipulate.

Two breeding schemes are used by scientists of the Inter-regional Potato Introduction Station at Sturgeon Bay, Wisconsin, and the University of Wisconsin. One is to hybridize the 2n gametes of haploids ($2n=2x=24$) originating from first division restitution in $4x \times 2x$ crosses to produce haploid-species hybrids ($2n=24$). The 2n gametes of the hybrids are then crossed with a cultivar ($2n=4x=48$) to produce a tetraploid hybrid. The other is first to make crosses of (1) haploid × wild and (2) cultivar × haploid and to cross the 2n gametes from the two diploid hybrids to produce tetraploid hybrids. These schemes have led to yield increases and transfer of resistance to virus, late blight, nematode, and bacterial wilt from a wild germplasm such as *S. demissum* (Peloquin, 1981, 1984).

An alternative approach is to use a bridging species that has desirable genes and sufficient number of crossable genotypes. Prebreeding efforts can accumulate many useful genes in the bridging species before the cultigen is crossed with a remotely related wild species having valuable genes. This circuitous approach has advantage over the use of 2n gametes in certain crosses because the unreduced gametes may create a barrier to further crossing (Hermsen, 1979).

Wild species in the genus *Solanum* provide high levels of resistance to the potato leaf roll virus at the International Potato Center (CIP). Crosses between two wild species immune to potato leafroll virus were made to complement another resistant interspecific hybrid. Three Mexican wild species were used as new sources of late blight resistance. Resistance to three nematode species of *Meloidogyne* and race 1 of *Pseudomonas solanacearum* has been transferred from *S. sparsipilum*. The aphid-repelling glandular trichomes of *S. berthaultii* have been transferred to tetraploid types with potato virus Y immunity (International Potato Center, 1983).

Tomato

The nine, wild relatives of the cultigen *Lycopersicon esculentum*, including its wild form (var. *cerasiforme*), are diverse in their adaptive habitats, breeding systems, variability pattern, and traits desired in commercial production. Their crossability with the cultigen is variable but manageable. The germplasm collection is comprehensive, well-maintained, and available for use (Rick, 1979).

Some of the tolerances for environmental stresses such as drought, waterlogging, salinity, and freedom from diseases and insects were observed in the native habitats of the wild taxa. These provided clues about their useful features (Rick, 1973). Subsequent evaluation and research have identified drought resistance in *L. pennellii* and *L. chilense*; waterlogging tolerance in var. *cerasiforme*; high salinity tolerance (up to full seawater strength) in *L. cheesmanii*; resistance to root rots in *cerasiforme*; and resistance to insects and mites in *L. hirsutum*, especially *f. glabratum* (Rick, 1984). A long list of resistances to different diseases has been identified among the wild taxa (see Rick, 1982). New variants isolated from backcrosses also contribute potential attributes in crop improvement (Rick, 1982, 1984).

Soybean

The soybean cultivars of the U.S. had a narrow genetic base. Up to the early 1960s, six strains from northeast China (Manchuria) formed the exclusive background of varieties grown on ninety-five percent of the total acreage (Johnson and Bernard, 1963). In a comparison between two-way and three-way crosses involving foreign introductions, the population means of the three-way combinations of [(adapted × exotic) × adapted] produced higher yields and greater genetic variances than those of two-way crosses (Thorne and Fehr, 1970). A series of germplasm populations was later developed from plant introductions by intermating among forty PIs and forty U.S. cultivars and breeding lines. The percentage of exotic parentage in the populations ranged from one hundred to zero percent in five populations (AP 10 to AP 14). The genetic variability in seed yield among two hundred random lines of each population was similar for AP 10 to AP 13 and about twice larger than that of AP 14. AP 14 produced the highest yield and AP 10 the lowest. The seed yield showed a linear regression on the percentage of PI germplasm and a negative association with lodging susceptibility. Selected lines from the populations showed a similar trend. Populations derived by recurrent selection of the high-yielding lines in each original population showed the same relationship as that of the parental lines. Obviously short-term yield improvement would likely not come from the use of PI germplasm (Vello et al., 1984). In another series of PI × high-yield cv. or line populations, AP 3, which has fifty percent PI germplasm, produced acceptable mean yield and high genetic variability (Schoener and Fehr, 1979).

Several workers who made crosses between the cultigen and *G. ussuriensis* found no genetic barriers. The progenies tend to have the small seed size and prostrate growth habit of the wild parent. High-protein progenies were obtained in two studies. In general the species crosses have shown little promise in soybean improvement except for high-protein content and resistance to stem canker in the wild species (see Johnson and Bernard, 1963).

In recent years U.S. soybean researchers have organized a collaborative scheme of screening foreign introductions (PIs) and of making crosses for different breeding objectives and genetic studies. Recessive alleles that controlled the lack of the Kunitz trypsin inhibitor in soybean seed proteins have been found in PI 196172 and thus removed a major antinutritional factor (Orf and Hymowitz, 1979). Three PIs (171451, 227687 and 229358) and their progenies have shown promise in their resistance to various insects such as Mexican bean beetle, velvetbean caterpillar, and southern green stinkbug. A Brazilian line, IAC 74-1832, originating from Hill × PI 274454, has resistance to velvetbean caterpillar, southern green stinkbug, and corn earworm (see Proc. National Soybean Breeders Workshop, 1984).

Sorghum

The evaluation and use of sorghum germplasm by different breeders have been described by Doggett, House, Gebrekidan, and Webster in the ICRISAT publication, *Sorghum in the Eighties, v. 1* (ICRISAT, 1982). Principal traits being transferred are insect and disease resistance, grain quality as human food, high lysine content, cytoplasmic male sterility, and high yield potential. The discovery of apomixis by workers in India (Rao and Naryana, 1968) and in Texas (Hanna et al., 1970) provides the possibility of using apomitic hybrids.

EXAMPLES OF SUCCESSFUL USE OF LAND RACES AND WILD SPECIES

A number of outstanding successes in the use of exotic germplasm are enumerated to show the enormous contributions of exotic gene pools to crop improvement and food production.

Wheat

Hayes et al. (1920) used durum and emmer wheats to improve the rust resistance of a *T. aestivum* cultivar, Marquis. A rust-resistant hard red spring wheat, Marquillo, was bred from Marquis × Iumillo (a durum variety). Thatcher was later developed from (Marquis-Iumillo) × (Kanred × Marquis) (see Clark, 1936). McFadden (1930) crossed Yaroslav emmer (*T. dicoccum*) with Marquis. The use of conventional breeding techniques produced the stem rust-resistant spring wheats H-44 and Hope (Clark, 1936). A Turkey wheat (PI 178383) collected by J. R. Harlan in 1948 has provided multiple resistances to stripe rust, common bunt, and dwarf bunt. It has usable tolerance for snow mold and flag smut and is a source of excellent seedling emergence. It has been profitably used by wheat breeders of Washington, Oregon, and Montana during the 1960s (Burgess, 1971).

Cytogenetical studies by U.S., U.K., and Canadian workers have led to the transfer of various sources of disease resistance from *Aegilops* and *Agropyron* species (Riley et al., 1968; Sears, 1972, 1978; Knott et al., 1977).

Another group of land races from Turkey, collectively known as Turkey wheat, not only helped establish the wheat industry in the hard red winter areas during the 1920s (Quisenberry and Reitz, 1974), but also entered the parentage of the Japanese dwarf wheat, Norin 10 (Reitz and Salmon, 1968) and the Korean semidwarfs (Dalrymple, 1980). The dwarfing genes in Norin 10 (Rht_1 and Rht_2) have given the world the first series of CIMMYT-Mexico semidwarf wheats, which brought on the Green Revolution in wheat. The semidwarfing genes have also entered the wheat breeding programs of several states in the U.S., with cv. Gaines of Washington State as the first one in the series (Vogel et al., 1963).

Wheat breeding using wide crosses in the USSR was summarized by Brezhnev (1978). The widely grown durum wheat Kharkovskaya 46 came from a cross involving three wheat species: *T. durum*, *T. turgidum*, and *T. dicoccum*. *T. timopheevi* and *T. aephiopicum* were widely used in breeding durum wheats. *T. timopheevi* also served as the most important source of disease resistance in improving the bread wheats.

Improved wheats of European countries frequently carry the wheat/rye translocation between chromosomes IB and IR. A higher frequency is found in the wheats of Eastern Europe than in those of Western Europe (Ralph Riley and C. N. Law, personal communications).

Rice

A weedy plant of *Oryza sativa* f., *spontanea* was used by Chinese workers in the 1920s to develop Yatsen-1 which had tolerance for low air temperature and acid soil (Ting, 1933). Later it was used to breed insect-resistant varieties such as Bao-tan-ai and Bao-xuan 2 (see Chang et al., 1982a).

The Green Revolution in rice was triggered by the spread of cultivars carrying the semidwarfing gene sd_1. The gene was provided by unimproved short-statured varieties grown in Taiwan and in Kwangtung Provinces of China. Taichung Native 1 was first bred in

Taiwan from the semidwarf Dee-geo-woo-gen during the period 1949-56. On mainland China the cv. Ai-zai-zhan and Ai-jiao-nan-te (a spontaneous mutant) served as the parents for the first series of semidwarfs which were initially released in 1959. Dee-geo-woo-gen was also used to develop IR8 (named in 1966) and later releases of the IR series (see Chang et al., 1982a). The sd_1 gene is such a readily mutable locus that several induced semidwarfs carried the same gene (Chang and Li, 1980). Improved cultivars carrying the sd_1 gene are now grown on more than forty percent of the rice area in Asia.

A strain of *O. nivara* collected from the Uttar Pradesh State of India has provided tropical Asia with the sole source of resistance to the grassy stunt virus (Chang et al., 1975a). Progenies of this heterozygous population have reduced damage by the destructive virus by several million dollars. Varieties developed by IRRI, beginning with IR28, carried the *Gs* gene (Khush, 1977a).

On Hainan Island of China, a sterile plant probably belonging to the *O. sativa* f. *spontanea* (*fatua*) weed race (named Wild Abortive) has provided the most useful source of cytoplasmic male sterility in hybrid rice production (Chang, 1979b; Lin and Yuan, 1980). Since 1980 hybrid rices have been grown on more than five million hectares of riceland in China.

Many land races of South and Southeast Asia have provided rice breeders with resistance to drought and to major diseases and insects, tolerance for adverse soil factors, ability to withstand deep water, and cold tolerance. Their use by rice breeders in national and international programs was summarized by Chang et al. (1982a).

Ecotypes of Asian cultivars after centuries of cultivation and selection in West Africa have led to deep-and-thick roots, tolerance for iron toxicity, or rice blast resistance. Asian rices selected in Brazil have been found to have high levels of tolerance for aluminum toxicity. These sources are now used by breeders in Asian nations and at IRRI (Chang et al., 1982b).

Corn

Zapalote Chico, a white dent maize from Mexico, was used to provide resistance to corn earworm. Ladyfinger popcorn of Peru has served as a useful source of resistance to northern corn blight (Burgess, 1971).

CIMMYT maize breeders have made good use of four race-complexes (Tuxapeno and related Caribbean and U.S. dents, Cuban Flint, Coastal Tropical Flint, and ETO Flint of Colombia) in developing open-pollinated varieties and hybrids. These materials are widely used in the lowland tropics (Wellhausen, 1978).

Current efforts at CIMMYT involve continuous improvement of 29 gene pools by half-sib selection. The breeding goals include earliness and resistance to downy mildew, stunt, streak, fall armyworm, borers, and earworm. A parallel breeding program aims for quality protein by making use of the opaque-2 gene (Paliwal and Sprague, 1981; Vasal et al., 1982; Mujeeb-Kazi and Jewell, 1984).

Corn breeders of Pioneer Hi-Bred International and of CIMMYT are collaborating on the maintenance and use of the exotic races. Some of the races have been used in the production of commercial hybrids (William L. Brown, personal communication).

Sorghum

Four variants from the Kaura land race (*Sorghum bicolor*) of Nigeria have contributed their yellow endosperm to many U.S. sorghum hybrids (Burgess, 1971).

Sorghums of the U.S. were based on Kafir, Milo, and small amounts of Hegari and Feterita introduced from Africa. Growth duration was found to be controlled by four independent genes, short stature by four other genes. Genetic manipulations of such genes have produced early and short hybrid sorghums suitable for combine harvesting (Quinby, 1974, 1975). Knowledge of the genetic control of height and maturity thus has greatly aided the conversion of tropical germplasm into earlier and shorter genotypes for the temperate zone.

Peanut

Several wild species of *Arachis* were found immune to peanut rust. Peruvian sources of *A. hypogaea* have been used to incorporate rust resistance into improved lines. The cross of *A. hypogaea* × *A. cardenasii* has produced lines resistant to Cercospora leaf spot (Wynne and Gregory, 1981). *A. monticola* is freely crossable with *A. hypogaea* and has been used to develop Spancross (Hammons, 1970). ICRISAT workers have bred promising lines from diploid wild species by overcoming barriers to intersectional hybridization by manipulating the ploidy level and backcrossing (Moss, 1984).

Oats

During the 1920s and 1930s when *Avena sativa* was crossed with red oats, *A. byzantina*, for disease resistance, the genetic diversity brought in by the cross increased grain yield nine to fourteen percent over pureline selections (Browning et al., 1964). This change marked the first improvement in yield over the past forty years (Langer et al., 1978).

The next phase was the introgression of genes from the wild species *A. sterilis* in the 1950s. *A. sterilis*, a wild red oat, is the putative progenitor of both cultigens. It also provided eight genes for crown rust resistance. Rust resistance genes were transferred into the improved cultivars by backcrossing. Many of the backcrossed progenies showed unusual vigor and in one resistant source the isolines showed distinct yield superiority over the recurrent parents. From additional crosses, eleven lines ranging from BC_3 to BC_5 showed twenty percent or more yield improvement over a commercial cultivar. The good agronomic characters of the recurrent parents were unaffected. The yield increase was first interpolated from an increase in vegetative growth rate (Takeda and Frey, 1976). Evaluation experiments showed a greater leaf area and slower leaf senescence which, in the *sterilis*-derived lines, resulted in higher leaf-area duration. The greater leaf area before and after anthesis resulted in increased seed number and heavier grains (Helsel and Frey, 1983; Frey, 1983a). The *sterilis* cytoplasm was also found to have contributed to higher yields. Progenies with higher protein or oil contents were obtained (Frey, 1983a).

Resistance to mildew (*Erysiphe graminis* f. sp. *avenae*) has been successfully transferred from the tetraploid wild oat, *A. barbata*, into the cultivated oat by induced translocation (Thomas and Aung, 1978).

Sugarcane

The use of wild species in improving the cultivated *Saccharum officinarum* (2n = 80) dates back to the late 1800s. The first wild cane used to introduce sereh disease resistance into noblecanes was *S. spontaneum*. Cultivar 49-5 of Hawaii included germplasm contributed by five wild species in the genus *Saccharum*. Most commercial varieties today include three to five species in their pedigrees. Their chromosome numbers may range from 100 to 125. Because sugarcane is vegetatively propagated, aneuploid chromosome numbers do not affect yield. Higher chromosome numbers are considered desirable in incorporating genes from the wild species (see Price, 1963; Stevenson, 1965).

Tomato

The tomato is an outstanding example of using valuable genes from exotic materials to improve the crop. Among the wild tomato species, *Lycopersicon pimpinellifolium* has provided resistance to bacterial wilt, bacterial canker, Fusarium wilt, late blight, Septoria leaf spot, grey leaf spot, and spotted wilt virus. *L. hirsutum* was the source of resistance to bacterial canker and Septoria leaf spot, *L. esculentum* var. *cerasiforme* conferred resistance to leaf spot and verticillium wilt, *L. peruvanium* provided resistance to tobacco mosaic virus and root-knot nematodes, and *L. peruvanium* var. *dentatum* and var. *humifusum* to curly top virus. *L. peruvanium* has augmented the vitamin-C contents in cv. Hi-C and Doublerich. *L. hirsutum* has contributed to increased levels of betacarotene (see Rick, 1982).

Forage Grasses and Legumes

There is little difference between modern cultivars and ecotypes of traditional grasslands because of the short breeding history and long-time use in wild habitats (Frankel, 1977; Chang et al., 1979). A review on the wide intervarietal crosses, interspecific crosses, apomixis and interspecific crosses, and intergeneric crosses has been provided by van Dijk (1979). Interspecific crosses between *Medicago* species, as early as 1910, led to forty percent yield increase in alfalfa (Waldron, 1920).

Induced tetraploids of both annual and perennial ryegrass (*Lolium* spp.) have been bred in several European countries. The potential of producing desirable forages from autoploidy appears limited. Amphidiploids may offer greater potentials (Dewey, 1980).

Triticale

Triticale is a unique example of intergeneric hybridization which led to the development of the first man-made cereal. Its development in the early 1970s by the University of Manitoba-CIMMYT team was preceded by the attempts of many workers to cross hexaploid wheat with rye. The first fertile hybrids were reported as early as 1875 (Zillinsky, 1974; Hulse and Spurgeon, 1974; Muntzing, 1979). In just two decades triticale yields have doubled and are now comparable with the best bread wheats in favorable environments. It has a yield advantage over wheat in certain marginal areas characterized by cold temperatures, acid or sandy soils, and heavy disease pressure (Borlaug, 1983). Efforts to improve the triticale varieties especially on test weight and straw strength and maturity are being continued (CIMMYT, 1983).

Strawberry

The cultivated strawberries represent a crop derived from an accidental crossing between *Fragaria chiloensis* and *F. virginiana* in a botanical garden (Jones, 1976).

TECHNIQUES TO OVERCOME BARRIERS IN DISTANT CROSSES

For most of the agricultural crops, reproductive barriers encountered in distant crosses are mainly related to differences in ploidy level, structural alterations of chromosomes, loss of chromosomes, incompatibility in cytoplasmic components, hybrid breakdown, genic imbalance, and seed dormancy. Successful hybridization in wide crosses depends on the use of appropriate cytogenetic and physiological approaches and effective means of hybridizations to overcome barriers in sterility, aberrant segregation, and distorted recombination. Some of the approaches are more crucial in the interspecific transfer of genes than in intervarietal crosses.

Hybridization and Breeding Methods

Direct hybridization between two parents having the same chromosome number is the simplest means of overcoming reproductive barriers. Sometimes the use of reciprocal crosses may overcome cytoplasmic incompatibility (see Harvey et al., 1972). Cytoplasmic effects may also be expressed by different plant traits including yield (Frey, 1983a).

For intervarietal or interracial crosses, difficulties encountered in single crosses may be alleviated by the use of three-way or multiple-parent crosses. A bridging parent may be used in the three-way cross. Double crosses followed by intermating of F_2 and F_3 progenies are more effective than single crosses in releasing the total variability in the gene pool (Hanson, 1959; Chang, 1976f; Kenworthy, 1980).

Backcrossing F_1 hybrids to the adapted cultivar is the conventional means of transferring gene or genes from a wild species. Recent findings in oats point out the need to use the most efficient number of backcrosses and alternate use of the recurrent parents to derive the maximum progress from introgressive hybridization (Frey et al., 1984).

Variations of the recurrent selection method can be used to break tight linkages and obtain the desirable recombinations in wide crosses and to further improve plant populations. The subject has been discussed by Hull (1945), Hanson (1959), and Jensen (1970, 1978a).

For often open-pollinated crops such as sorghum and millets, wild germplasm could be introgressed into existing or newly created random-mating populations (Frey et al., 1984). Methods of managing heterogeneous populations were discussed by Burton (1979) and Frey (1983b).

Cytogenetic Techniques

For intergenomic or intergeneric transfer of genes, a number of cytogenetic and cellular techniques have been developed to facilitate the use of desired genes in alien germplasm. Three categories of techniques are outlined below.

1. Artificial allopolyploidy.
   a. Direct utilization: amphidiploids, partial amphidiploids, and some somatic fusion of protoplasts.
   b. Indirect utilization: genetic bridges, genome construction, genome extraction.
2. Chromosome manipulation.
   a. Additions and substitutions.
   b. Translocations.
   c. Recombination system.
3. Cytoplasmic manipulation.
   a. Male sterility.
   b. Cytoplasmic substitution.

Detailed discussions about these techniques have been provided by Riley and Lewis (1966), Sears (1975, 1976, 1981), Sanchez-Monge and Garcia-Olmedo (1978), Robbelen (1979), Stalker (1980), and Morris (1983).

In Vitro and Molecular Approaches—Genetic Engineering

Genetic engineering is defined as "genetic manipulations (bypassing the sexual cycle) by which an individual having a new combination of inherited properties is established" (Rieger et al., 1976). The method consists of:

1. Cellular approaches: *in vitro* culture of haploid cells and somatic hybrids.
2. Molecular approaches: direct manipulation of DNA through protoplasmic DNA uptake and DNA recombinant molecules via plasmids.

In vitro culture technique has been used to select for tolerance for salinity, aluminum toxicity, herbicides, fungicides, and antibiotics; such technique has also been used for selection for disease resistance and amino acid analog. Anther or pollen culture hastens the attainment of homozygosity from F_1 hybrids. Embryo culture has been proved to be a useful tool in obtaining viable F_1 plants when the endosperm collapses. Cell cultures treated with salt or disease toxins have produced tolerant sources after proper selection (see Ladd and Paule, 1983).

Variants arising somatically from cells in cell or tissue culture offer another source of novel variation (see Meins, 1983). Such somaclonal variation may be found in plants regenerated from cultures of homogeneous materials or interspecific hybrids. When detection of somaclonal variation, cellular selection, and early rapid screening of regenerants are combined into an efficient process, it offers another tool for crop improvement (Scowcroft and Larkin, 1982).

Protoplast fusion was first attained in *Nicotiana* species (Carlson et al., 1972). Fusion between *Petunia* and *Parthenocissus* cells was also obtained, but the *Petunia* chromosomes, except for some genes, were lost in the resulting cells. This approach remains at an experimental stage (Ladd and Paule, 1983). Initial success in gene transfer within the genus *Nicotiana* and cytoplasmic hybridization in *Brassica napus* × *Raphanus sativus* crosses has been demonstrated (see Cocking, 1984).

Recombinant DNA techniques permit specific gene addition or modification from widely different sources. The technique depends on the ability to fractionate and join fragments of DNA from divergent sources. The donor fragment, the vector, must carry the appropriate genetic information to allow the DNA to be incorporated into a host cell and to be capable of replication as if it were a part of the cell's genotype. The process consists of splicing, identifying a vector, transformation, and propagation (see Ladd and Paule, 1983).

The techniques offer powerful tools to: (1) attain gene transfer or modification of much greater dimension than conventional means, (2) assist development of viable hybrids, (3) enhance the nitrogen fixation of associated microbes or the beneficial functions of mycorrhizal association with crop plants, (4) control viruses and viroids through the snythesis of antibodies and recombinant DNA clones, and (5) increase the efficiency of plant improvement efforts. Some of the bottlenecks facing genetic engineers in applying the techniques to plant breeding are: (1) difficulty in regenerating plants from protoplasts, (2) shortage of vectors for genetic transformation in the monocots, (3) lack of effective DNA probes to detect specific genes in plant populations, and (4) lack of detailed and precise chromosome mapping to permit implantation of isolated genes and tightly linked markers. More sufficiently detailed information is available only in corn and wheat. A more important problem is the lack of knowledge of the biochemistry of metabolic processes and their intermediate products as well as of information on gene regulation, repeated DNA sequences, and expression of economic traits under different environments for proper planning, directing, and monitoring of the breeding procedure (see Rachie and Lyman, 1981; Swaminathan, 1982; Phillips, 1983; IRRI, 1984b). Workers in molecular/cellular biology, biochemists, geneticists, breeders, and other affiliated disciplines must work together to pave the way for the effective use of genetic engineering techniques.

For the plant breeders to use the cellular and molecular manipulations, the final steps must be relatively simple, while promising to provide a unique or improved solution to a problem and evident yield effects on a crop in a farmer's field (Carlson, 1983). Although the useful applications of genetic engineering may be several years or decades away even with assured funding and manpower, the breeders should view the ongoing research with avid interest and active participation (Carlson, 1983) and as useful adjuncts to, rather than a replacement of, conventional plant breeding approaches (Sprague et al., 1980; Simmonds, 1983). After all, the ultimate responsibility of the plant breeder is to develop cultivars which will be accepted by the growers, processors, and consumers. Conventional plant breeding, at least for the time being, will remain the major line of defense to cope with increasing food needs and will require sustained funding (Sprague et al., 1980; Borlaug, 1983). Meanwhile, a greater demand than ever before for exotic germplasm sources to improve crop germplasm can be anticipated. Issues related to patents or rights are expected to adversely affect the immediate application of certain useful research developments.

CONCLUDING REMARKS ON THE USE OF CROP GERMPLASM IN RELATION TO ITS CONSERVATION

Assessment of the Use of Germplasm in Crop Improvement

This survey of major food crops has revealed the following:

1. Use of plant introductions: Many plant breeders have made profitable use of introductions that have been incorporated into the improved germplasm of every country in the world. This is particularly true in developed countries deficient in indigenous germplasm. The economic returns are enormous in relation to costs (Burgess, 1971).
2. Use of exotic germplasm: The successful use of land races and wild species varies from crop to crop and from country to country. The exploitation of useful genes and cytoplasm in the exotic germplasm has been more extensive in the developed countries than in the developing world, partly because the developed countries started plant breeding earlier. The most extensive use of exotic germplasm may be found in tomato, sugarcane, tobacco, wheat, and rice.
3. Breeders' interest in the exotics: Many innovative plant breeders, assisted by geneticists, cytogeneticists, plant pathologists, entomologists, and crop physiologists, have taken the opportunity to make use of the desirable traits in the exotic materials, although the extent of use has been highly variable and dependent on the ease of incorporating useful traits into desirable agronomic types. Outstanding instances of team approach have been demonstrated by the work on wheat (Evans and Peacock, 1981), tomato (Rick, 1984), potato (Peloquin, 1984), and rice (Chang et al., 1982a). A similar trend may be found in other crops.
4. Obstacles in the use of exotics: Many plant breeders have been reluctant to devote much of their resources to the exotics. This was a common phenomenon when the potential value of the exotic germplasm was not fully known to the breeders or when the breeding process was envisaged as a long-range venture (Alexander, 1975; NPGRB, 1981; Brown, 1982; Frey,

1983a). Insufficient germplasm enhancement, lack of communication between curator and user, and little feedback from users were cited by the National Plant Genetic Resources Board (1981) of the U.S. as reasons for the continuing inertia. It was also feared that increased programs would entail so much additional funds that substantial funding by the public sector will be needed (Anon., 1984a).

5. Yield increases through conventional breeding methods: Current plant breeding programs in the U.S. using nearly entirely well-adapted germplasm have continually contributed to steady yield increases in wheat, corn and soybean: about fifty percent in U.S. wheats, fifty to sixty percent in hybrid corn, and thirty to forty percent in soybean (Frey, 1981). Varietal improvement of wheat in the U.K. led to an increase of about forty percent over a thirty-year period (Silvey, 1978; Austin et al., 1980). In eight Asian countries, the semidwarf rices and other improved varieties have contributed about 23.32% production increase during 1965-80 (Herdt and Capule, 1983). The enormous contribution of semidwarf wheats to the world food supply was recently reviewed by Borlaug (1983).
6. Have crop yields reached a plateau? In most food staples, it does not appear that a yield ceiling has been reached (Frey, 1971; Evans, 1984) although such concern for wheat in the U.K. (Austin et al., 1980) and in New York State (Jensen, 1978b) has been expressed. A major constraint of on-farm yields may be economic rather than scientific. However, the experimental yield ceiling of rice and wheat has not shown a marked increase since the semidwarfs were bred in the mid-1960s, mainly due to no increase in crop biomass (Evans, 1984). Moreover, there is a wide gap between potential crop yield and experiment station yield (Yoshida and Parao, 1976; Riley, 1981) as well as between yield in experiment stations and on-farm production (Barker et al., 1977). A long-range analysis would show that the yield increases have evolved as a series of steps. Each stepwise improvement to a new plateau is usually associated with the exploitation of a new source of germplasm or trait such as the semidwarf plant type or the adoption of a new variety type such as hybrid maize (Frey, 1981). Efforts from all research disciplines are needed to move crop productivity off the existing, although temporary, plateau toward a higher potential (Frey, 1971; Evans, 1984). Connections between fundamental and applied aspects must

remain strong (Riley, 1981).

7. Breeders' view and action on genetic diversity: Plant breeders in the U.S. today are more aware of the importance of genetic diversity than a decade ago. The genetic base of major food crops in the U.S. remains confined to a relatively small number of favored cultivars, but the genetic base of elite germplasm pool is wider and contains more useful diversity than is usually recognized. U.S. breeders have a high regard for the national germplasm repositories. The life span of successful cultivars gradually and continually shortens, largely due to the increased breeding activity of the private sector, especially in self-fertilized species, and may increase the magnitude of genetic diversity available to farmers (Duvick, 1981, 1984; Brown, 1983).

   Elsewhere in the developing world, rice breeders are also aware of the need for genetic diversity (Chang, 1984a), but broadening the genetic base is a long process and requires special efforts.

   Considerable hidden diversity may be found in superficially uniform improved germplasm such as the U.S. Corn Belt breeding stocks. Sources of disease resistance may surface from elite materials when intensive evaluation is carried out (Duvick, 1984).
8. Potential contribution from exotic germplasm: There is sufficient evidence that the exotic germplasm has served a highly visible role not only in supplying disease and insect resistance but also in providing wider adaptation through tolerance for adverse environments and increments to yield potential. Introduction of new alien germplasm may further advance the yield potential as demonstrated in oats (Frey, 1981). Efforts in this direction should be recognized as medium- to long-range projects of collaborative research programs rather than as a low-priority adjunct to plant breeding, as was frequently the case in the past.
9. Potentials in new crops: There is also a large, unexploited area of using the genetic potentials in new or little known crops (Strobel, 1980).
10. Support for plant genetic resources programs: Expanded and intensive use of exotic germplasm appears more tenable when the entire process of conservation, evaluation, and exchange is strengthened and assuredly funded. Greater support by both the public and private sectors is needed (Anon., 1984a).

Improved communication between the conservationists and users can markedly enhance the breeders' use of germplasm (NPGRB, 1981; Chang, 1984b). The team approach is essential (Brady, 1975; Frey, 1981; Riley, 1981).

11. Application of advances in genetic engineering: Techniques available in genetic engineering can serve as a powerful tool in expanding the horizons of plant breeding. Tissue cell and protoplast cultures may act as a bridge for molecular/cellular biology to serve plant breeding. Hence, these will not be substitutes for traditional plant breeding methods in the final selection of promising genetic materials (Sprague et al., 1980). Usable products from genetic engineering may not be forthcoming until one to two decades later (NPGRB, 1981; Phillips, 1983).
12. Training: Genetic conservation is a relatively new development, hence few scientists have been trained to manage the myriad aspects of the task. Only the University of Birmingham in the U.K. provides graduate training on germplasm conservation (Hawkes, 1983). But the number of trained young workers falls short of current and projected needs.

Measures Needed for Strengthening Conservation Programs

Germplasm conservation requires considerable and sustained technical as well as financial inputs. It is liable to suffer cutbacks during time of financial restraints (Reitz, 1976). Yet time is almost running out in salvaging the remnant unconserved germplasm in their areas of primary or secondary diversity where modern plant breeding has made its impact. This urgent task must be accomplished within the next decade or so. Additional inputs in evaluation, documentation, exchange, preservation, and training are sorely needed to safeguard the conservation phase and to enhance the utilization phase. Consolidation of the holdings of a common crop in major gene banks is necessary to eliminate redundancy, while duplicate sites of preservation are also essential. Both international and institutional collaboration on a sustained basis need to be intensified and supported (Anon., 1984a). Considerable progress has been made in this direction in wheat, rice, corn, sorghum, and the common potato, partly due to the role of the international agricultural research centers (IARCs) under the CGIAR system. Much of the cooperative efforts came from the crop scientists themselves (IRRI, 1972;

Anon., 1973, 1977; Marshall and Brown, 1981). Many national programs have yet to make full use of the genetic materials generated by the international networks.

In recent years, many developed countries have added funds to strengthen evaluation programs or to build gene banks. One instance is the recent establishment of the Nordic Gene Bank by several countries in western Europe (Anon., 1983), although the total input still falls short of the needs (Plucknett et al., 1983; Jones, 1984). Operations related to germplasm use also require expanded funding (Anon., 1984a).

Potential Constraints on the Exchange and Use of Germplasm

Since the 1950s a marked increase in the exchange of crop germplasm between countries and among crop scientists has taken place. The trend was further boosted by the establishment and coordination of the international agricultural research centers (IARCs). The IBPGR has also played a useful role in promoting cooperation. FAO plans to convene an intergovernmental meeting in 1984 to assure the free flow of germplasm from one country to another. Restrictions on exchange posed by existing plant quarantine laws of many nations also need to be reviewed and modified (IBPGR, 1983a).

Persons outside of the agricultural circles (Mooney, 1980, 1983) have expressed concern that the Plant Varieties Rights Act of the developed countries and the recent takeover of many seed companies in the U.S. by multinational corporations may hamper the free exchange and use of germplasm, which may lead to a narrowing of the genetic base. Such fear has also been expressed by some of the germplasm-rich countries in the developing world (Jain, 1982). It is the consensus of knowledgeable sources that although such concern is justified on social and moral grounds, the objections are rather weak on technical aspects (Sneep and Hendriksen, 1979; IBPGR, 1983c). Improved germplasm of the developed countries will also benefit the developing countries (Anon., 1984a; Smith, 1984). Much of the crop improvement work for major food crops in the developing countries has been and will continue to be implemented by the public (governmental) agencies. The IARCs have contributed substantially to the collaborative generation and exchange of improved germplasm. The restrictions on exchange and flow may apply only to hybrids of high-value cash and industrial crops. The plant breeders' rights may affect plant breeding activities more in the developed countries than in the developing world (Barton, 1982). Private breeding activities in the U.S. have sharply increased since the passage of the Plant Variety Protection Act (Perrin et al., 1983).

Prospects

During the past decade, increased funding and intensified activities on germplasm conservation, evaluation, documentation, and use were provided to the IARCs and the national research centers of almost all developed countries, especially the U.S. (Plucknett et al., 1983; Jones, 1984; Williams, 1984), even though the total inputs are still short of current and future needs (NPGRB, 1981; Wilkes, 1983; Goodman, 1984). Unfortunately, the national centers of most developing countries have not received increased support. It would be a mutually profitable venture for the germplasm-deficient countries of the developed world to assist and cooperate with the germplasm-rich countries in the developing world to expand efforts in safeguarding the dwindling genetic resources for use in the future. Both public and private sectors of the developed countries will benefit from such investments.

Meanwhile, all sectors of the human society should assume their respective responsibilities in conserving and protecting the most important biological heritage of mankind (Frankel, 1974; Chang, 1983b, 1984a; Swaminathan, 1983b; Anon., 1984a). Combined efforts of different sectors will enable mankind to better conserve and use the biological treasure which was partly molded by farmers of the past millenia. Crop scientists in particular should face the challenge and make use of the available genetic potentials with their scientific expertises for the benefit of the future generations of *Homo sapiens*.

The impressive record of reaping immense benefits from the use of rice and wheat germplasm during the past two decades (Dalrymple, 1978, 1980; Herdt and Capule, 1983; Borlaug, 1983) will assure the crop scientists of even greater returns in the future when population pressure will confer a higher priority on food production.

Meanwhile, population growth in the populous countries of the developing world must be arrested to allow a real improvement in human nutrition. Crop production statistics and population figures taken from the mid-1950s through the mid-1970s showed that the index of agricultural production per capita has remained stagnant in the developing countries (IRRI, 1982a; Hsieh et al., 1982) despite the gains of the Green Revolution in wheat and rice. Different sectors of the society need to work together to attain broad-based improvement in human welfare.

IOWA STATE JOURNAL OF RESEARCH / MAY, 1985 425-455
Vol. 59, No. 4

CROP HISTORY AND GENETIC CONSERVATION: RICE—A CASE STUDY

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ABSTRACT. This paper retraces the antiquity, evolution, dispersal, differentiation, and ecogenetic diversification of one of the world's food staples—rice. Unique features that enabled rice to become a widely grown crop are discussed. The evolution of rice culture in different geographic areas is described. Processes leading to the enormous diversity in the Asian and African cultigens are enumerated and compared.

Events that led to the conservation of the rich genetic resources are documented. The composition and security of rice collections at different gene banks are discussed. Timely conservation efforts on an international scale have saved the crop from a genetic wipeout during the rapid spread of the semidwarf rices and added rich gene pools for use by rice researchers.

Valuable sources of useful traits evaluated and identified from the conserved stocks, primarily by IRRI, are enumerated. Intensive studies on the broad-based germplasm have not only aided varietal improvement efforts (nicknamed Green Revolution) but also have had an impact on many areas of rice research.

A multidisciplinary approach to the understanding of crop history and diversification has also helped the mapping of genetic conservation strategies and the search for desired genes. The experience gained from rice can serve as a model for other crops.

Index Descriptors: *Oryza*, *Oryza sativa*, *Oryza glaberrima*, rice, semiaquatic species, subsistence crop for the humid tropics, Gondwana origin, parallel evolution in Africa and in Asia, dispersal and diversification, cultural types, hydroedaphic-seasonal regimes, genetic diversity, field collection, gene banks of rice, exchange of germplasm, GEU program, use of wild rices.

ECONOMIC IMPORTANCE OF RICE

Rice and wheat share equal importance in feeding the world's human populace. The bulk of the rice crop is produced by *Oryza sativa* L., the common or Asian cultigen. The African cultigen, *O. glaberrima* Steud., occupies a much smaller acreage in West Africa where it is being continuously replaced by *O. sativa*.

Although rice is generally considered a semiaquatic species associated with a monsoonal climate, its present cultivation spans from 53°N to 40°S latitude (Lu and Chang, 1980). The crop can be

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grown under a wide range of physiographic-hydrologic-edaphic regimes (O'Toole and Chang, 1979).

Among the food staples, rice is the only crop that can tolerate prolonged waterlogging. Thus, rice is the natural choice for many subsistence farmers in the low-lying areas of the humid tropics. Moreover, the rice plants can derive nitrogen in a flooded soil through biological nitrogen fixation in association with several microbes (see Lu and Chang, 1980; De Datta, 1981). Submergence of certain unproductive soils increases nutrient availability and reduces soil toxins (Ponnamperuma, 1977a). Thus, rice growers continually obtain low yields of rice from poor soils without fertilization.

World production of rough rice (paddy) during 1980 and 1982 ranged from 397 to 418 million tons per year, harvested from about 144 million hectares. The planted area in Asian countries totalled 127 million hectares in 1982 (IRRI, 1984a).

Rice provides twenty percent of the calories and thirteen percent of the proteins for human consumption on a worldwide basis. Rice is a major staple for more than two billion people. Most of the rice consumers are in the most populous countries of Asia. The demand for rice is also rising rapidly in Latin America and Africa (Lu and Chang, 1980; IRRI, 1982a).

As a food staple, brown rice packs more calories per gram than wheat. One hectare of rice can sustain 5.63 persons annually, whereas wheat and maize can only support 3.67 and 5.06 persons, respectively (Lu and Chang, 1980).

Between 1968 and 1981, total rice production in Asia increased by forty-two percent, average yields rose by about twenty-nine percent, and total land devoted to rice production increased by about eleven percent (IRRI, 1984a). Unfortunately, the population grew by thirty-one percent during this same period (IRRI, 1984a). During the last decade the food production per capita has lagged behind total food production in the developing countries. Future prospects appear grim because attainable increase in rice area is limited and the people in the populous rice-consuming countries such as Bangladesh, India, and Indonesia will continue to grow at almost two percent per annum (IRRI, 1982a). Further increasing the supply of rice will thus be a major challenge to agricultural scientists.

BIOSYSTEMATICS OF THE GENUS *ORYZA* AND EVOLUTION OF THE CULTIGENS

The genus *Oryza* belongs to the tribe *Oryzeae* under the subfamily Pooideae in the grass family Gramineae (Poaceae). The genus includes twenty wild species and two cultigens. Most of the species including the two cultigens are diploid (2n = 24); seven species are tetraploid. Table 1 presents the species name, ploidy level, genome group, and geographic distribution (updated from Chang, 1976a). Maps on their distribution in Africa, South Asia, and Southeast Asia have been compiled by Chang (1975) and Harlan (1975c).

Areas of Origin and Putative Progenitors of *O. sativa*

The twenty-two species of *Oryza* have such a wide pantropical distribution (Africa, Malagasy, South Asia, Southeast Asia, East Asia, Oceania including Australia, and Central and South America) that rice botanists and geneticists have been confused by its disjunct geographic pattern. The distributional pattern has led to conflicting views on the progenitor of *O. sativa.*

Since the days of de Candolle (1882), workers have proposed a divergent series of native homes and putative progenitors for *O. sativa.* As many as ten workers have considered "*O. perennis* Moench" an ambiguous designation used differently by various workers and which also included the annual weed races as the progenitor (see Chang, 1976c). As recently as 1974, Oka and coworkers yet maintained that "*O. perennis*" was the progenitor of both *O. sativa* and the wild perennial forms of Asia, Oceania, Africa, and South America (Oka and Chang, 1961; Oka, 1964, 1974). Even the tetraploid *O. minuta* Presl et Presl was suggested as a possible ancestor by Roschevicz (1931) and Chevalier (1932), and the former postulated that Africa was the center of the Section *Sativa* Rosch., to which *O. sativa* and *O. glabberima* belong.

The controversies and confusions may be traced to a number of factors:

1. Botanical studies and nomenclature of the past were based on very limited samples, and the type-specimens of different workers were deposited in herbaria of various countries or have been lost. Only Tateoka (1964) has been able to visit nearly all of the herbaria and made a definitive study.

Table 1. Species of *Oryza*, chromosome numbers, genome symbols and geographical distributions.

Species name (synonym)	x = 12 2n =	Genome group	Distribution
O. alta Swallen	48	CCDD	Central and South America
O. australiensis Domin	24	EE	Australia
O. barthii A. Chev. (*O. breviligulata*)	24	A^gA^g	West Africa
O. brachyantha A. Chev. & Roehr.	24	FF	West and central Africa
O. eichingeri A. Peter	24, 48	CC, BBCC	East and central Africa
O. glaberrima Steud.	24	A^gA^g	West Africa
O. grandiglumis (Doell) Prod.	48	CCDD	South America
O. granulata Nees & Arn. ex Hook f.	24	---	South and Southeast Asia
O. glumaepatula Steud. (*O. perennis* subsp. *cubensis*)	24	$A^{cu}A^{cu}$	South America and West Indies
O. latifolia Desv.	48	CCDD	Central and South America
O. longiglumis Jansen	48	---	New Guinea
O. longistaminata A. Chev. & Roehr. (*O. barthii*)	24	A^lA^l	Africa
O. meridionalis N. Q. Ng	24	---	Australia
O. meyeriana (Zoll. & Morrill ex Steud.) Baill.	24	---	Southeast Asia, southern China
O. minuta J. S. Presl ex C. B. Presl	48	BBCC	Southeast Asia

Table 1. (Cont.)

Species name (synonym)	x = 12 2n =	Genome group	Distribution
O. nivara Sharma & Shastry (*O. fatua*, *O. sativa* f. *spontanea*)	24	AA	South and Southeast Asia and southern China
O. officinalis Wall. ex Watt	24	CC	South and Southeast Asia, southern China, New Guinea
O. punctata Kotschy ex Steud.	48, 24	BBCC, BB (?)	Africa
O. ridleyi Hook f.	48	---	Southeast Asia
O. rufipogon W. Griffith (*O. perennis*, *O. fatua*, *O. perennis subsp. balunga*)	24	AA	South and Southeast Asia and southern China
O. sativa L.	24	AA	Asia
O. schlechteri Pilger	---	---	New Guinea

2. Differences in naming and renaming the wild relatives of *O. sativa*.
3. Typical specimens of the wild relatives are no longer available in nature as a result of hybridization and introgression with the cultigen and the annual weed race (*O. sativa* f. *spontanea*).
4. Restricted sampling base of experimental studies based on recent "naturally occurring" populations.
5. Errors in interpreting biogeography and crop history by Sampath and Seetharaman (1962), Watson (1971), Nayar (1973), and Huke (1976).
6. Failure to use the multidisciplinary approach to explore the complex subject (Chang, 1976b).

Rice workers are not alone in such a quandary. The unravelling of the crop evolution process is difficult and commonly speculative (Harlan and de Wet, 1973).

A Unified Postulate on the Origin and Evolutionary Pathway of the Two Cultigens of *Oryza*

By pooling all available information and evidence from earth sciences (especially the plate tectonics), archaeology, anthropology, biogeography, biosystematics, evolutionary biology, and agricultural history, Chang (1976a, 1976b, 1976c) has postulated that the two cultigens evolved from a common, distant progenitor in the Gondwana (Gondwanaland) supercontinent before its fracture and drift beginning in the early Cretaceous period. The process was a parallel series involving three primary species and a highly heterogeneous weed race for each of the two cultigens (Fig. 1). Harlan and de Wet (1971) have termed such groups as primary gene-pools.

What kinds of evidence can be offered to support this postulate which implies that rice is older than the Himalayas? The answers are as follows:

1. The fracture and drift of Gondwana into South America, Africa, Australia, Antarctica, South Asia and the associated portion of mainland Southeast Asia, and Malagasy beginning in the early Cretaceous period is a well-established fact in the earth sciences (Hallam, 1973). Approximate dates of the Gondwana components reaching their present positions have been provided (Smith and Hallam, 1970; Raven and Axelrod, 1974). The first split between Africa and South America began about 130 million years ago. The breakaway of Australia and Antarctica followed about 110 million years BP. The South Asian plate was the last major component to raft away from the west Gondwana component, Africa, at 85-90 million years BP. The rise of Himalaya followed the collision of the South Asian plate with the old mainland Asia plate (Laurasia), primarily China, at 45 million years BP. That explains the pantropical distribution of the twenty wild species of *Oryza* in the humid tropics of southern hemisphere.
2. The pantropical distribution of the *Oryza* species in the southern hemisphere is nearly identical to the northern boundary of the Glossopterid line (Melville, 1966). *Glossopteris* is a genus of fossilized seed-ferns which is generally recognized as the progenitor of the angiosperms.
3. Figure 2 shows that the known genomes of sixteen *Oryza* species have a reasonably good fit with the Gondwana components in geographic distribution (Chang, 1976d).

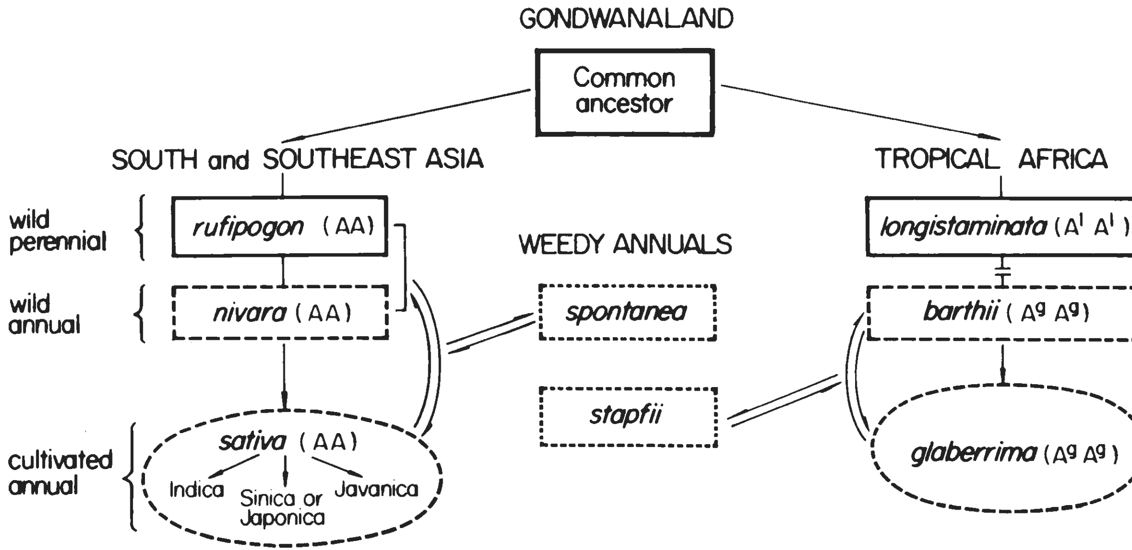

Figure 1. Evolutionary pathway of two cultigens. Taxa boxed by solid lines are wild perennials. Taxa boxed by broken lines are annuals. Arrow with solid line indicates direct descent. Arrow with broken line indicates indirect descent. Double arrows indicate introgressive hybridization (adapted from Chang, 1976c).

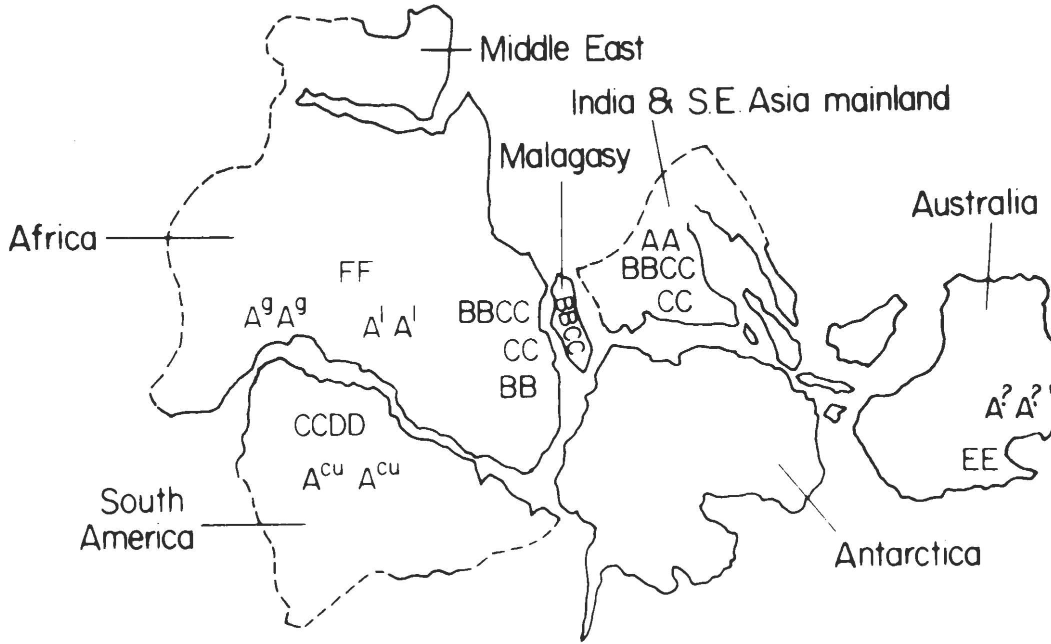

Figure 2. A reconstruction of the Gondwana components, showing the genomes of wild species found in different areas. (Paleo-geographic distribution of 16 species of *Oryza* by their genomic designations (Chang, 1976d). Reconstruction of the Gondwanaland components adapted from Melville (1966)).

Table 2. Contrast in diversification: *Oryza sativa* vs *glaberrima*.

Factor	Asia	W. Africa
Latitudinal spread	10°S - 53°N	5°N - 17°N
Topography	hilly	flat
Population density	high	low
Movement of people	continuous	little
Iron tools	many	none or few
Draft animals	waterbuffalo and oxen	?

4. After the union of the South Asian plate and China, China was pushed northward 10-13 degrees latitude (Wu, 1980). Remnants of the Gondwanic *Glossopteris* flora and Triassic fauna have been found on the northern slope of Himalaya, the Mount Jolmo, inside present-day Chinese territory (Yin and Kuo, 1978). This can explain the later formation of the temperate race (sinica, 'keng' or japonica) on the north side of the Himalayas (Chang, 1983a).
5. The general trend in crop evolution is: wild perennial→wild annual→cultivated annual→domesticated annual (Whyte, 1972; Simmonds, 1976). The cultivated rices of China represent the true domesticates in the sense that human care is essential to the perpetuation of a tropical species in the temperate zone.
6. Ecogenetic diversification of *O. sativa* is much richer in Asia than in Africa because of the greater crop dispersal and human movements in Asia (Table 2). The wild perennials of South America (*O. glumaepatula*) and Australia (*O. meridionalis*) have never been domesticated to become cultigens in the absence of an agricultural beginning in those areas.

This collation hopefully resolves most of the century-old questions about the place of origin and evolutionary pathway of *O. sativa*, although some of the evidences are still fragmentary and many questions about species relationships yet require study (Chang, 1976c).

Appearance of the Annual Cultigen in Asia

Annual ancestral forms of the Asian cultigen began to appear in the Neothermal age (10,000 to 15,000 BP) at the periphery of the wild annual progenitors, mainly on the southern borders of Himalaya and, to a lesser extent, in south and southwest China. Alternating periods of drought and pronounced variation in temperature during the period presumably accelerated the development of the annual forms in northeast and east India, northern Southeast Asia, and southern regions of China.

The early cultigens are of the indica ecogeographic race (Chang, 1976c, 1983a). These generally matured earlier than their wild progenitor. Thus, they flourished under drier and fluctuating climates and produced more seeds, which enabled them to move farther northward than the perennial form. Increasing aridity on the northern border of Himalaya and its associated mountain ranges in mainland Southeast Asia also forced the early settlers in China to move into more humid areas toward the east and to the south. The movement of people and the dispersal of rice plants greatly accelerated the ecogenetic diversification process (Chang, 1976b).

Inside the present boundaries of China, which included fragments of the South Asian plate along a branch of the Brahmaputra River (Hsiangchuan R.), a temperate-zone race, sinica (keng), evolved from the primary tropical indica race (Chang, 1976c, 1983a). This temperate-zone race became widely known as japonica after the Japanese workers (Kato et al., 1928) coined the term, although the Japanese people initially obtained their rices from the Chinese about 2,300-3,000 years ago (Morinaga, 1967, 1968; Akazawa, 1983).

From the eastern coast of South and Southeast Asia, the tall and large-grained forms were brought to the Indonesian islands and became differentiated into the javanica race.

The geographic dispersal and subsequent diversification of the Asian cultigen into three ecogeographic races—indica, sinica, and javanica—is shown in Figure 3 (Chang, 1976c).

History of the African Cultigen

Porteres (1956) has postulated that the African cultigen (*O. glaberrima*) originated in the Niger River delta. The primary center of diversity for *O. glaberrima* is in the swampy basin of the upper Niger River, and two secondary centers are to the southwest near the

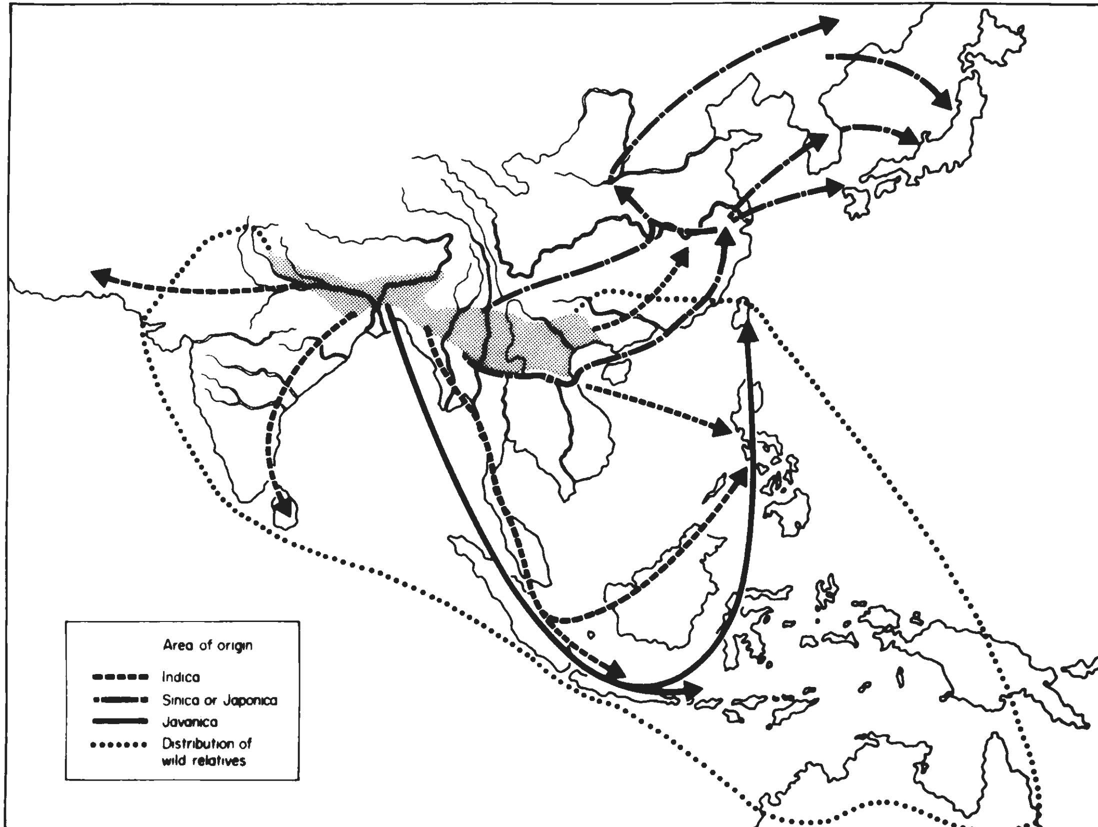

Figure 3. Extent of wild relatives and spread of ecogeographic races of *O. sativa* in Asia and Oceania (adapted from Chang, 1976c).

Guinean coast. The primary center was probably formed around 1500 BC, and the secondary centers developed 500 years later.

In West Africa, *O. glaberrima* is a dominant crop grown in the flooded areas of the Niger and Sokoto River basins and is broadcast on hoed fields. On shallowly flooded land, a rainfed wetland crop is either directly sown by broadcasting or dibbling, or transplanted. About seventy-five percent of the land planted to rice in Africa belongs to upland (dryland) culture, largely under the bush fallow or grass fallow system. *O. glaberrima* seeds are broadcast or dibbled after the ground has been hoed. Some African farmers still use axes, hoes, and bush knives in land preparation. In hydromorphic soils, the *glaberrima* behaves like a self-perpetuated weed (Chang, 1976b). In wetland fields planted to *O. sativa*, *glaberrima* has become a weed.

The African cultigen and its annual wild race (*O. barthii*) are less diverse than their Asian counterparts. While Porteres (1956) recognized two subspecies—*vulgaris* and *humilis*—in *O. glaberrima*, Oka and coworkers (Chu and Oka, 1972; Oka, 1974) believed that the *barthii-glaberrima* complex could be differentiated into two ecotypes: deepwater and upland. For areas where the water is deep, the African cultivars are inferior to the Asian cultivars in internode elongation (Chang et al., 1977).

Judging from the history of domestication and the extent of varietal diversity within the species, it appears plausible that the differentiation of *O. sativa* in Asia predated that of *O. glaberrima* in West Africa (Chang, 1976b). African cultivars show a high relative growth rate in thirty-day-old plants, a lower flag leaf photosynthesis, lower seed set and grain yield, and a lower harvest index than the Asian cultivars. This contrast is similar to that between *O. nivara* and the Asian cultivars (Cook and Evans, 1983).

CHANGES UNDER DOMESTICATION AND CULTIVATION

A number of important morphological and physiological changes took place during the cultivation and domestication of *O. sativa*. Larger leaves, longer and thicker culms, and longer panicles led to a larger plant size. Other increases were in the number of leaves and their rate of development, number of secondary panicle branches, grain weight, rate of seedling growth, tillering capacity, synchronization of tiller development and panicle formation, and panicle-to-tiller ratio. The net photosynthetic rate of individual leaves slightly increased, and the period of grain filling lengthened (Chang, 1976b). Photosynthetic duration of the flag leaf and harvest index both increased

(Cook and Evans, 1983). Concurrently, there were decreases in leaf interval, pigmentation (or its loss), rhizome formation, ability to float in deep water, awning, shattering, duration of grain dormancy, photoperiod response, and sensitivity to low temperatures (Chang, 1976b; Cook and Evans, 1983). The frequency of cross-pollination also declined, so that the crop became more inbred than the wild races (Oka and Morishima, 1967).

The rice plant underwent further changes when it was widely disseminated by cultivators from the humid tropics to subtropical zones and subsequently to the temperate zone. Some of the morphological and physiological changes, such as synchronous tillering, uniform ripening of whole plants, weakening of the ratooning ability, and loss of grain dormancy, were associated with advances in cultivation technique. As the crop moved farther north, the combined forces of natural and human selection, diverse climates, soils and seasons, and varied cultural practices led to the great ecologic diversity now found in the *O. sativa* cultivars of Asia. The crop became a true domesticate in the temperate areas (Chang, 1976c). The adaptive process associated with planting of harvested seed is nearly identical to those of the other cereals (Harlan et al., 1973).

Cultivators' preferences and socioreligious traditions have added much morphologic diversity to the cultivars: panicle size, panicle length, panicle density, grain size and shape, grain thickness, panicle rachis color, awn presence and length, sterile lemma color, hull color, seed coat color, amylose content, and gelatinization characteristics of the starchy endosperm (Chang, 1976b).

Evolution of New Cultural Types: Deepwater and Upland

The deepwater rices of Asia, which have a remarkable ability for internode elongation, may have acquired the floating habit from the wild perennial race (*O. rufipogon*) as rice cultivators moved into areas where the water was deep near the end of the monsoon season. These rices branched at the higher nodes and had rapid internode elongation during rises in water depth, adventitious roots at the upper nodes, and location- and maturity-specific photoperiod sensitivity (Chang, 1976b). The evolution of the deepwater rices has involved both differentiation-hybridization cycles (Harlan, 1970) and farmers' selection efforts (Chang, 1976b).

When rice was introduced into areas where the soil had poor moisture retention and the water table was rather low, the upland (dryland) type that evolved had early maturity, low tillering capacity, and deep and thick roots. In mainland Southeast Asia, this group is known as the hill rices. The upland rices have become markedly differentiated from the ancestral lowland type in that they grow better in aerobic soil (Chang et al., 1972b). The root length of some drought-resistant upland rices is comparable to that of wheat (IRRI, 1975).

Evolution of Seasonal and Hydro-Edaphic Types

In the Ganges River delta, crops for three seasons (winter, summer, and autumn) evolved to fit into varying water and temperature regimes. These are called boro, aus, and aman types by the farmers of Bangladesh and India. In most other parts of monsoonal Asia, two crop seasons are generally found: wet (main, kharif, maha) and dry (off, rabi, yala).

Deliberate human selection in a disruptive manner, along with contributions from the weed races, led to enormous diversity among rice cultivars in adaptability to climatic factors (mainly temperature and photoperiod), water regimes (deep, shallow, dryland, and various intermediaries), and edaphic conditions (saline, alkaline, acid, cold, etc.). The extent of variation in climatic and hydrologic adaptability among *O. sativa* cultivars (Fig. 4) is indeed remarkable for a tropically based and semiaquatic species (Chang and Oka, 1976; O'Toole and Chang, 1979).

As the tropics-based cultivars were brought northward and cultivated under more restricted growing seasons, the loss in photoperiod sensitivity and thermosensitivity was accompanied by reduced plant height, more determinate tillering habit, decreased competitiveness with weeds, more synchronous heading among tillers, longer grain-ripening period, and weaker ratooning ability. A more thrifty and productive plant type finally evolved and found its ecological niche in the temperate regions. This transformation is found in both the early-maturing indica rices of China and the high-yielding sinica race of East Asia (Chang, 1976b).

The Ecogeographic Races vs the Cultural Types

Rice workers were initially excited by the reports of Kato and his coworkers (1928, 1930) who found discontinuous morphological differences, F_1 hybrid sterility, and distinct serological reactions when rice varieties of Japan, China, Korea, India, Sri Lanka, and Indonesia were hybridized. The designation indica was used to label the tropical

Conventional classification of *O. sativa* cultivars.

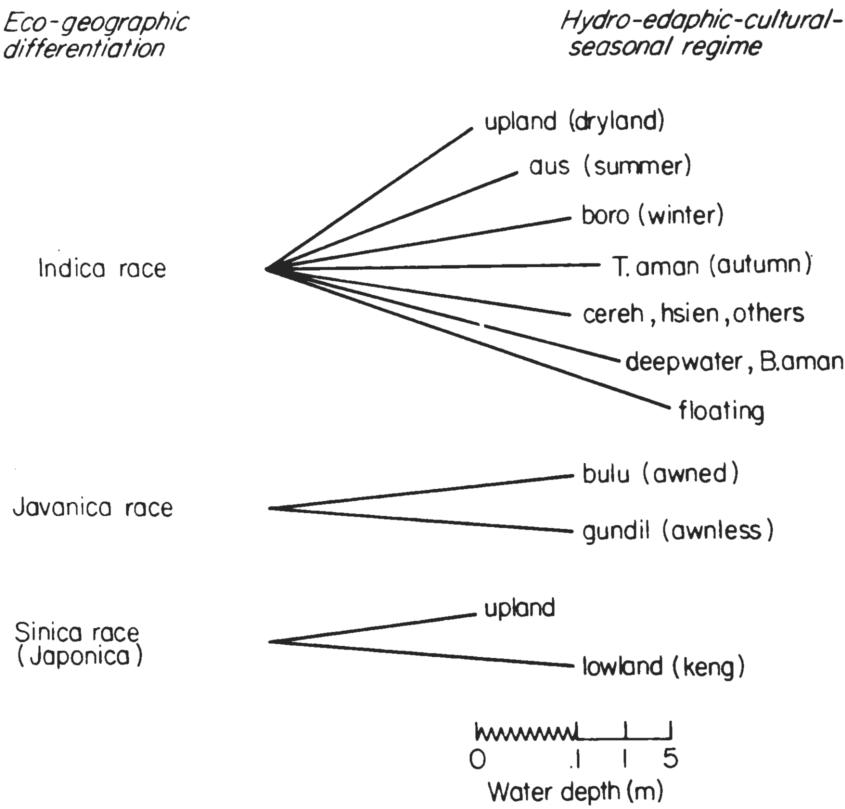

Figure 4. Grouping of Asian rice cultivars by ecogeographic race, hydrologic-edaphic-cultural regime and crop season. Cultivars grown in standing water belong to the lowland type.

rices and subtropical varieties of China, whereas japonica was proposed as a subspecies for the short- and roundish-grained varieties of Japan, China, and Korea. Indica and japonica correspondto the "hsien" and "keng" types of China. The terms "hsien" and "keng" have been used by the Chinese since the third century AD (Ting, 1949). Hence, the term sinica has been proposed to indicate the temperate zone race (Chang, 1976b, 1976c). Javanica was used to designate the Indonesian bulu (awned) and gundil (awnless) rices which have long panicles and peduncles as well as large and bold grains (Matsuo, 1952; Morinaga, 1954).

Studies by other Japanese workers soon revealed the existence of many varieties which did not fall under either subspecies (Terao and Mizushima, 1939). The aus varieties of Bengal region in India and Bangladesh, and the bulu rices of Indonesia showed high affinity with both the indica and japonica rices and were labeled as an intermediate type (Morinaga, 1968).

The major criterion in evaluating the genetic affinity among the three "subspecies" or ecogeographic races has been the fertility of the F_1 hybrid. The extent of sterility in the interracial hybrids varies from partial (fifteen to fifty percent) to high (more than fifty percent). Aberrant segregation and restricted recombination have been found in a number of crosses. Meiotic aberrations such as loose pairing, univalents, quadrivalents, inversions, and deletions characterize meiosis in some of the hybrids (see IRRI, 1964). Later studies at IRRI reveal that similar chromosomal aberrations can be found if varieties of the indica race coming from different areas are crossed, especially between the tall Indian varieties and the Chinese semidwarf indicas. Extensive investigations by Chinese, Indian, and Japanese workers revealed that both interracial and intraracial sterility exist and that temporal-geographic isolation has played a significant role in producing the genetic barriers. Moreover, the wide range of chromosomal aberrations found in the partially sterile hybrids cannot account for all of the F_1 incompatability, and genic imbalance may be a potent force in the expression of sterility (see Chang and Li, 1980). Indeed, some indica × indica crosses have been found to be more sterile than *O. sativa* × *O. nivara* crosses (Engle et al., 1969; Dolores et al., 1979).

Renewed interest in the ecogenetic differentiation has led to recent studies involving physiological and biochemical analyses. The findings emphasize the inadequacy of relying heavily on gross plant and grain morphology to characterize and classify the numerous rice cultivars. The grain size and shape of rices are now known to be subject to the rice growers' preferences and the predominant grain type of a region can be rapidly altered in a matter of several centuries (Watabe et al., 1970). Other criteria useful to a fuller understanding of the varietal complexes are amylose contents of the endosperm, temperature and photoperiod responses, edaphic-hydrological adaptation expressed in root characters, and grain ripening duration (Chang, 1976c; Lu and Chang, 1980).

Thus the ecogenetic differentiation process was primarily based on natural and human selection in different environments after hybridization, segregation, or mutation during rice domestication and cultivation in the primary area of varietal diversity in the broad belt extending from the southern foothills of Himalaya to Vietnam and on the northern borders of the mountain ranges in southwest and south China (Chang, 1976c). Today one can find in the hills of Yunnan and Kweichow Provinces (China), where the sinica ("keng") rices were grown at elevations above 1,800 m, a mixture of sinica and indica rices growing at medium elevations, and exclusively indica ("hsien") rices at altitudes below 1,000 m (Ting, 1961).

The cultural types represent another dimension in grouping rice cultivars by their ecological adaptiveness. Both deepwater and upland types are found in the most diverse indica race. The temperate race (sinica) also has the dryland type but no deepwater type. The javanica race is grown exclusively in shallow wetland soils, but it is genetically close to the hill rices of mainland Southeast Asia and to the aus group of Bangladesh and India (IRRI, 1984a). Cold-tolerant varieties may be found in all three races, although they differ in growth stage-specific responses.

Scientific efforts in rice breeding which involve geographically divergent parents have added further complexity and confusion to the pattern of ecogeographic race formation. Biochemical analyses and numerical taxonomy may be helpful in clarifying some of the ambiguities.

ANTIQUITY AND DISPERSAL OF THE ASIAN CULTIGEN

Archaeological Findings

De Candolle (1882) postulated that rice cultivation in China preceded that of India. The oldest remains of cultivated rice, belonging to indica type and dating back to 5008 ± 117 BC[2] or 7,000 years BP[2],

[2]Dating abbreviations with capital letters—C^{14}-dated; with small letters—not C^{14}-dated; BP = before present.

were found in the excavations of the Ho-mu-tu site of east China (see Chang, 1983a). The remains of a slightly younger rice, dating back to about 4530 BC, comes from the Chalcolithic sample of northern India (Vishnu-Mittre, 1976). The oldest specimen of the sinica (keng) race found in East China is also dated at 7000 BP (Luo-jia-jiao Archaeological Team, 1981).

The much publicized rice remains excavated from Non Nok Tha in northern Thailand (Solheim, 1972) are no older than 4000 bc and probably of a wild type (Chang, 1976a). Thus, the cultivation of rice in China and India was not much behind that of the hexaploid common wheat in the Near East circa 5800 BC (Renfrew, 1969).

The Routes of Dispersal

The later dispersal of the Asian cultivars, mainly the indica race from India to the Middle East, North Africa, and then Europe, probably began as early as 1000 bc. Another route is from India to Madagascar and East Africa. Many javanica cultivars found their way from Indonesia into Madagascar. West Africa obtained rice varieties from Europe or directly from South Asia. European countries supplied most of the cultivars initially grown in South America. The United States obtained rice seed from Madagascar, South Asia, and East Asia. Rice cultivation in different countries presently covers a north-to-south spread from 53° north latitude along the Amur River on the Sino-Russian border to 40° south latitude in Argentina (Lu and Chang, 1980).

EVOLUTION OF THE RICE CULTURES

Rice grains were initially gathered and consumed by prehistoric people of the humid tropics who lived near the river estuaries along the wooded foothills where rice grew wild on poorly drained sites. These people also hunted, fished, and gathered other edible plant parts as food. At first, they ate the rice they gathered as a food supplement. Soon they developed a liking for the tasty cereal and searched for plants that bore larger panicles and heavier grains. This selection accelerated the evolution of the cultivated form. The gathering-and-selection process was more important to people who lived in areas of marked seasonal variations in rainfall or temperature, or both (Hawkes, 1970; Whyte, 1972), or where the water holes or pans dried up in the dry season.

Rice cultivation began when men or, more likely, women dropped seeds on the soil in low-lying spots near their homesteads, kept out the weeds and animals, and, probably, manipulated the water supply. The cultivation sites were moved nearer to the homesteads as people found that rice plants responded in yield to the enriched soil near their temporary settlements (Hawkes, 1969).

In more hilly areas of Southeast Asia or where the wet-dry alternation of seasons was less pronounced, rice was probably a secondary or a companion crop to root crops such as taro and yam. These situations existed in many parts of Southeast Asia until recent times. They have led to the postulate that man learned to plant vegetative parts before he learned to plant seeds, and that rice was a weed in taro gardens (Haudricourt and Hedin, 1943, quoted by Sauer, 1952). However, the recent (ca. 2000 bc) domestication of the yam (Alexander and Coursey, 1969) does not support this postulate. Moreover, the upland rices of Southeast Asia have more advanced features than the lowland varieties (Chang, 1976c).

As the early cultivators of rice migrated, they took the grains along and planted the seeds at their new homestead. The introduction of the tropically based race and strains into ecologically different habitats, followed by human selection, led to the rapid increase in ecologic diversity in subtropical areas (Chang, 1976b) and also created variants that matured early and escaped drought (Whyte, 1972).

In north China, the early rice fields of the Lungshanoid farmers (between 3200 and 2500 bc) were sparsely located on marshy but flood-free sites around river bends of the tributaries of the Yellow River in Honan and Shensi provinces, where millet was the predominant crop (Ho, 1969). The sites were generally between small rivers and wooded hills. The total area of rainfed rice was small. The climate in north China was more humid than at present (Chang, 1968).

The chronological sequence in planting rice in lowland (wetland) fields is from broadcasting to dibbling to transplanting. Land use is from shifting cultivation to unbunded permanent fields to bunded fields—first rainfed, later irrigated (Chang, 1983a). A fascinating account of retracing such a process in Bang Chan, Thailand, has been written by Hanks (1972) who also provided a useful integration among types of rice culture, energy requirement of each type, field size, human population density, and input/output ratio.

Ancient Chinese history and literature are surprisingly complete in recording developments in agricultural technology. The following developments and dates represent landmarks in the rice history of China, and some of the events have great impact on rice cultivation in neighboring countries: (a) water buffalo has been used as a draft animal since 1500-1100 bc; (b) rainfed wetland culture was well established by 1222 bc; (c) hoe has been used since 1122 bc; (d) flood control was practiced in 700 bc; (e) irrigation was implemented at 600-500 bc; (f) iron plow share, spade, and scythe have been used since 400 bc; (g) 'rice men' were appointed at 400 bc to supervise cultivation practices; (h) deep plowing and midseason cultivation were practiced before the Christian era; (i) transplanting was first mentioned at 146-167 ad; (j) foot-pedalled water pump was used at 618-906 ad; and (k) spike-tooth harrow and roller-compactor have been used since 960-1127 ad.

The transplanting process represents a dramatic advance in rice cultivation technique and led to enhanced productivity. Transplanting rice seedlings from nursery beds into the field gives the following advantages: (1) better weed control in nursery and field, (2) more efficient use of water during deficit in spring, (3) more intensive management of field, and (4) better utilization of land for rice and other crops. The spike-tooth harrow made puddled soils suitable for transplanting, and it has been widely adopted by rice farmers in Southeast Asia (Chang, 1976b).

CONSERVATION OF RICE GERMPLASM

Historical Developments

More than 100,000 cultivars of *O. sativa* probably existed before genetic erosion set in (Chang, 1984a). Since the early 1950s most Asian countries have made efforts to conserve their commerical varieties, both unimproved and improved. A number of foreign introductions of some fame were included in each national collection (IRRI-IBPGR, 1978, 1983; Chang et al., 1982a). However, coverage was generally poor on the land races of the remote areas. Few wild species have been conserved (Chang, 1972b).

Under the International Rice Commission (IRC) of the FAO, attempts were made during the 1950s to set up three regional collections for the three ecogeographic races: indicas at the Central Rice Research Institute (Cuttack, India), javanicas at the former Central Research Institute for Agriculture (Bogor, Indonesia), and japonicas at the National Institute of Agricultural Sciences (Hiratsuka, Japan). Another set of deepwater rices was maintained at the former

Agricultural Research Institute (now the Bangladesh Rice Research Institute) in Dacca, Bangladesh. The collections totalled 1,344 varieties, but in the absence of refrigerated storage facilities, the three centers in the tropics could not adequately maintain the seed viability (Parthasarathy, 1972).

After IRRI began its research operations in early 1962, it took on the role of a global depository and exchange center (Chang, 1972a). Through the cooperation of all national, regional, and international centers and assistance from anthropologists, missionaries, and service volunteers, IRRI obtained a duplicate set of the earlier collections from each center as well as recently collected samples of the two cultigens and wild taxa (Chang, 1980).

Since 1971, a coordinated program of field collection in fourteen Asian countries and several African countries has added 36,000 Asian cultivars and 7,684 African samples to the world's rice gene pools (Chang, 1983b; Ng et al., 1983).

IRRI's role in stimulating and coordinating the massive field operations is both catalytic and synergistic (Chang, 1984a). The extensive, massive collection efforts have not only saved the rice crop from a possible genetic wipeout (Anon., 1969; Frankel, 1970a; Browning, 1972; Harlan, 1972a; Wilkes and Wilkes, 1972) but also greatly enriched the germplasm available for the further improvement of the crop. In recent years, IRRI has returned thousands of accessions to donor countries where the cultivars or wild taxa are no longer grown or maintained in a viable state (Chang et al., 1982a; IRRI, 1982d).

The 6630-accession Assam Rice Collection (ARC) was assembled from northeast India during the late 1960s under a PL-480 project. It was found to contain a large number of disease- or insect-resistant accessions when the collection was grown and screened in India (Sharma et al., 1971) and at IRRI (see IRRI Annual Reports for 1976-1979, 1981). Teams of national workers and IRRI staff, canvassing in stress-prone environments of remote areas, identified more than 8,000 samples (Chang, 1980; IRRI, 1981), claimed by local workers or growers to have one or more pest-resistant or stress-tolerant traits. Most of these accessions, however, have poor agronomic characteristics and will require long breeding cycles before they become phenotypically acceptable.

Present Status of Major Rice Collections

The rice collection in the International Rice Germplasm Center (IRGC) at IRRI is a conglomerate of all other collections. At the end of

1983, the total holding contained 68,000 Asian cultivars and breeding lines, 2,600 *O. glaberrima*, 1,100 wild rices, and 690 genetic testers. The IRGC has short-, medium-, and long-term storerooms; the latter two rooms can hold 130,000 accessions each. A duplicate set is being stored at the U.S. National Seed Storage Laboratory, Fort Collins, Colorado. Meanwhile, IRRI, USDA, and the National Institute of Agrobiological Resources (NIAR) of Japan have agreed on a collaborative scheme to divide and share responsibilities in conserving different segments of the germplasm: indicas, javanicas, and wild species by IRRI; sinicas of East Asia by NIAR; and the U.S., South American, and Mediterranean cultivars by the USDA. The three agencies compare their collections to reduce redundancy and to ensure that every conserved stock is being stored at duplicate sites (Chang, 1983b).

The holdings of rice germplasm in the major national and regional centers are shown in Table 3. The storage conditions available at each center, and duplicate samples of each country or regional center being preserved by IRRI are also given. Among the institutions mentioned in the table, only IITA and IRAT included African rices and wild species of Africa in their collections.

The IITA has been designated by the IBPGR as a regional center for *O. glaberrima* and the African wild rices.

EVALUATION AND USE

A brief summary on the evaluation and use of the conserved rice germplasm follows. Detailed accounts may be found in Chang et al. (1975a, 1982a), Khush (1977a), and Chang (1982, 1984a).

Exchange and Evaluation

Among the major crops of the world, rice germplasm has seen the most dynamic and active state of being exchanged and cooperatively tested on a worldwide scale. International and interinstitutional activities were initiated in the early 1950s when the International Rice Commission of the FAO organized working group meetings on a regular basis. The coordinating role was shifted to IRRI in early 1962. Collaborative activities received a new impetus in 1975 when the International Rice Testing Program (IRTP) was established at IRRI with funding by the United Nations Development Programme (UNDP). The annual international rice research conference and the other symposia and workshops held at IRRI have provided the venue for rice

Table 3. Estimates on rice germplasm holdings in major centers and their storage conditions.[1]

Country/Center	Number of samples in national center		Duplicate samples in IRGC	Storage condition[2]
	Total	Indigenous		
Bangladesh	---	5,285	5,285	MT
Burma	---	2,080	1,724	MT
China (mainland)	40,000[3]	33,000	3,767	ST, MT, LT[4]
China (Taiwan)	6,520[3]	1,662	1,185	MT
India	35,000[5]	33,000	14,585	ST
Indonesia	7,500[0]	---	7,840	MT

[1]Sources: IRRI-IBPGR, 1978, 1983; Toll et al., 1980; RF, 1980; Kawakami and Fujii, 1981; primarily *O. sativa* accessions.

[2]ST = short-term, MT = medium-term, LT = long-term.

[3]Including many duplicates; collections scattered over more than 10 institutions.

[4]Under construction.

[5]Including many duplicates; collections scattered over 70 institutions; 15,000 accessions at CRRI; 3,464 accessions deposited at IRRI.

Table 3. (Cont.)

Country/Center	Number of samples in national center		Duplicate samples in IRGC	Storage condition
	Total	Indigenous		
Japan	42,455[6]	16,200+	978	MT, LT
Kampuchea	---	---	906	---
Korea (S.)	4,227	1,027	1,023	LT
Laos	---	---	1,431	---
Liberia	409	---	1,159	MT
Malasia	4,550	3,130	2,395	MT
Malagasy	2,000	2,000	218	ST
Nepal	780	---	1,247	ST
Pakistan	1,224	1,404	936	MT

[6]Including many duplicates; collections scattered over one national center (NIAR), more than 30 national and lesser experiment stations, 12 universities, and the Institute of Genetics; 18,000 accessions at NIAR.

Table 3. (Cont.)

Country/Center	Number of samples in national center		Duplicate samples in IRGC	Storage condition
	Total	Indigenous		
Philippines	---	1,187	3,954	ST
Sri Lanka	2,745	2,745	2,069	MT
Thailand	6,000	---	2,906	MT, LT
U.S.	18,065[7]	92	4,511	MT, LT
U.S.S.R.	3,514	---	372	LT, MT
Vietnam	---	---	1,634	---
IITA	7,633	n/a	1,024	MT
IRAT	3,842	n/a	1,577	MT

[7]Including deposits by IRRI; more than 5,000 accessions are held at BARC, Beltsville under MT storage as a working collection.

researchers to discuss and develop collaborative ventures in many areas of rice research (IRRI, 1980a).

In the early 1950s, the International Rice Commission promoted an international exchange of parents and their F_1seed under the Indica-Japonica Hybridization Project, which scored limited success (Parthasarathy, 1972). Soon after the IRRI germplasm bank provided its service to national and state centers in the mid-1960s, the bank became an active international exchange center, partly because it offered technical information related to the accessions and partly because it was able to circumvent political barriers between centers in seed exchange. Between 1962 and 1970, the bank dispatched 26,250 seed samples in response to 702 requests (Chang, 1972a). By 1983 the bank had provided more than 95,000 seed samples of the cultigens and wild species to thousands of rice scientists around the world. Responses to more than 3,000 requests may also indicate the magnitude of experiments for specific objectives being conducted by rice researchers in different countries. Moreover, the bank has supplied IRRI staff with about 350,000 seed samples, averaging about 30,000 samples a year during the last decade. Again, the statistics show the scope of IRRI's research activities under its Genetic Evaluation and Utilization (GEU) program which was formalized in 1974 (Brady, 1975).

No information is available on the scope of exchange by different national rice germplasm centers. Among the major rice-producing countries, Japan and the U.S. have the largest volumes of exchange.

Useful Genes from Evaluation Efforts

Under IRRI's GEU program, the IRTP nurseries, and the efforts of rice scientists in national programs, many useful sources of genes or cytoplasm have been identified and used (see Chang et al., 1982a).

The outstanding sources are mentioned below:

1. Semidwarfism: Deo-geo-woo-gen from Taiwan, China (cross made in 1949 in Taiwan led to the breeding of Taichung Native 1; both were used in 1962 by IRRI); Ai-jiao-nan-te and Ai-zai-zhen from Kwangtung, China (identified and crossed in 1956-58).
2. Early maturity: numerous sources from Bangladesh, China, India, and other countries.
3. Nitrogen response, partly expressed as lodging resistance: the Chinese semidwarfs, 'Ponlai' (keng) varieties of Taiwan, and U.S. varieties.

4. Resistance to tropical strains of bacterial blight: mainly from Bangladesh, India, and Indonesia.
5. Resistance to tungro virus: mainly from Bangladesh, India, and Thailand.
6. Resistance to grassy stunt virus: from one strain of *O. nivara* collected from Uttar Pradesh State, India.
7. Resistance to ragged stunt virus: from several diploid wild species of Asia.
8. Resistance to rice green leafhopper: from many tropical varieties of *O. sativa* and several *O. glaberrima* strains.
9. Resistance to brown planthopper: mainly from south India and Sri Lanka.
10. Resistance to stem borers: from India, Taiwan, and Bangladesh.
11. Resistance to gall midge: from India and Thailand.
12. Tolerance to low night temperatures: from Indonesia, Nepal, China, and Japan; also from upland varieties of Southeast Asia and South America.
13. Tolerance for salinity: from Sri Lanka and India.
14. Flood tolerance and submergence tolerance: from Bangladesh and India.
15. Cytoplasmic male-sterility: from a Chinese wild rice (Wild Abortive).

Use in Rice Improvement

The successful uses of the exotic germplasm sources have been documented by Chang (1967, 1979a, 1980, 1982, 1983b, 1984b), Chandler (1968), IRRI (1972, 1982b), Huang et al. (1972), Beachell et al. (1972), Khush (1977a, 1977b, 1980), Dalrymple (1978), Chang et al. (1982a), and Herdt and Capule (1983). The term Green Revolution has been used to designate the high-input agricultural technology associated with the semidwarf wheats and rices (see Chang, 1979a).

The enormous contributions of the useful genes in rice germplasm to increased rice production may be summarized as follows:

1. More than 90% of the rice area in China is either double-cropped by high yielding varieties (with at least one crop by the semidwarfs) or planted to the hybrid rices (Shen, 1980).
2. About 40% of the rice area in eleven Asian countries (Bangladesh, Burma, India, Indonesia, Korea, Malaysia, Nepal, Pakistan, Philippines, Sri Lanka, and Thailand) are planted to the

semidwarfs, amounting to 32.9 million ha (Herdt and Capule, 1983). Most of the high-yielding semidwarfs (HYVs), which were developed by IRRI, also have multiple resistance to diseases and insects (Khush, 1980).

3. Between 1965 and 1980, rice production in eight Asian countries (Bangladesh, Burma, China, India, Indonesia, Philippines, Sri Lanka, and Thailand) increased by 65%, estimated at 117.4 million metric tons of paddy worth about $19.4 billion. The contribution of the improved varieties to the increase amounted to 27.4 million tons or $4.5 billion. These estimates exclude data from Korea, Nepal, Pakistan, and Vietnam where the impact of the HYVs has been impressive but variable (Herdt and Capule, 1983).

It may be concluded that these returns based on worldwide annual expenditures of about $1.25 million on rice germplasm conservation represent a most profitable scientific investment (Chang, 1984a).

Other Potential Uses

In addition to contributions to yield increases, the rich variability in the rice germplasm has furnished rice scientists with unique and unprecedented opportunities to expand the scope of their research activities through interdisciplinary collaboration. The returns from a number of pioneering studies on the rice plant and several components associated with its diverse ecosystem, both physical or biotic, are beyond measures by monetary returns.

Revealing and useful findings and applications have been obtained from the "exotic germplasm" in the following fields of study:

1. Environmental effect on plant type, nitrogen nutrition, growth and yield (Tanaka et al., 1964, 1966; Tsunoda, 1965; Beachell and Jennings, 1965; Yoshida et al., 1972).
2. The ecogenetics of plant type and varietal adaptation (Chang, 1967; Chang et al., 1969; Chang and Tagumpay, 1970; Chang and Vergara, 1972; Chang and Oka, 1976; Chang and Li, 1980).
3. Varietal reactions to different mineral disorders and other adverse soil factors (Tanaka and Yoshida, 1970; Ponnamperuma, 1977b).
4. Varietal responses to biotypes of major insects (Pathak, 1977).
5. Elucidations of the insect and vector relationship in virus diseases (Ling, 1972).

6. Gene-for-gene relationship between the blast fungus and rice varieties (Kiyosawa, 1976).
7. Transfer of brown planthopper resistance from tropical varieties into Japanese varieties (Kaneda and Ikeda, 1983).
8. Tolerance for cold temperatures at various growth stages (Nishiyama, 1976; Vergara et al., 1976; Satake and Toriyama, 1979).
9. Drought resistance (O'Toole and Chang, 1979; IRRI, 1982c) and genetic studies on rice roots (Armenta-Soto et al., 1983).
10. Stresses of excess water (Vergara and Dikshit, 1982).
11. Biological nitrogen fixation (Roger and Kulasooriya, 1980; Watanabe and Brotonegoro, 1981; Venkataraman and Watanabe, 1982).

The economic potentials of applying the useful information to production technology have been partly realized in several instances related to varietal development and soil fertilization, while others largely related to ecosystem management will be realized in the coming decades to meet the impending food needs (IRRI, 1982a; Swaminathan, 1983a).

LESSONS FROM CROP EVOLUTION, GEOGRAPHY, AND HISTORY TO AID IN GENETIC CONSERVATION

What are the lessons learned from this summary of the origin of the rice plant and the processes of ecogenetic diversification? The following seem pertinent:

1. An in-depth multidisciplinary study and analysis have yielded a more balanced picture than a single discipline-oriented approach. Recent findings in the earth sciences, archaeology, anthropology, and biogeography have greatly broadened our sights and led to a new understanding of the complex subject.
2. Vavilov's center of variability is not necessarily the hearth of domestication, as pointed out by Isaac (1970) and Harlan (1971). Similarly, the area where the maximum diversity of wild relatives is found may not coincide with the magnitude of varietal diversity in that geographic region of agricultural origin (Zohary, 1970; Whyte, 1972).
3. It would be fallacious to predict events of the past basing solely on plant samples of recent origin, because the occurrence of plant dispersal, human migration, and introgression in nature are beyond our limited knowledge.

4. The movement of a genetically plastic plant such as rice into entirely new environments has led to a broad spectrum of ecodiversifications which exceeded the scope of the wild progenitors. Upland rice is a unique example. The presence of coadapted complexes appears strong in upland, deepwater, and cold-tolerant rices.
5. The evolution of a new ecogeographic race may only take a few millenia (Chang, 1976b). Human preference can also drastically alter the principal cultivars grown in an area within five to eight centuries (Watabe et al., 1970).
6. Human contacts in prehistoric times are undoubtedly earlier and more numerous than the dates and events given by historians (Chang, 1983a).
7. Land races with high tolerance for climatic, hydrologic, or edaphic stresses are likely to be found in those ecological niches where such stresses exist. Similarly, high resistance levels to diseases and insects are often found in areas where multiple cropping is practiced and little pesticides are applied.
8. Wild species may be found in those areas where historical documents recorded their presence in earlier periods (Chang, 1983a). Re-canvassing may turn out to be fruitful.
9. The remarkably rich genetic diversity in rice has been essentially conserved because: (a) plant breeding began late in rice, (b) conservation efforts started before the Green Revolution, and (c) many ecological niches require the planting of specialized land races (Vaughan and Chang, 1980; Chang et al., 1982a). The massive collection efforts since 1971 have averted the widely publicized fears of a genetic wipeout of rice germplasm (Anon., 1969; Frankel, 1970a; Browning, 1972; Harlan, 1972a; Wilkes and Wilkes, 1972).
10. Genetic conservation can be implemented with limited resources as long as the workers are interested and willing to strive (Chang, 1984a). Returns from the utilization of useful germplasm are enormous and unprecedented (see Herdt and Capule, 1983).
11. Geographic areas that remain rich in genetic diversity, such as northeast India, northern Burma, and southwest China, coincide with those where maximum climatic-physiographic-hydrologic-edaphic variations existed and diversification began early. These areas lie within the belt of early differentiation of the cultigen (Chang, 1976c).

12. Detailed characterization of the ecosystem of different germplasm-rich areas would help genetic conservation.

How can the conservationists make use of such information? Glimpses into the past can be helpful in planning explorations or re-collections, designing and accelerating evaluation experiments, and providing a continuous evolutionary potential of the conserved materials during the maintenance and utilization phases.

LIST OF ACRONYMS

AVRDC—Asian Vegetable Research and Development Center, Shanhua, Taiwan, China.

CATIE—Centro Agronomico Tropical de Investigacion y Enseñanza, Turrialba, Costa Rica.

CGIAR—Consultative Group on International Agricultural Research, Washington, D.C.

CIAT—Centro Internacional de Agricultura Tropical, Cali, Colombia.

CIMMYT—Centro Internacional de Mejoramiento de Maiz y Trigo, El Batan, Mexico.

CIP—Centro International de la Papa (International Potato Center), Lima, Peru.

EUCARPIA—European Association for Research on Plant Breeding.

FAO—Food and Agriculture Organization of the United Nations, Rome, Italy.

GEU—Genetic Evaluation and Utilization Program of IRRI.

IBP—International Biological Program.

IBPGR—International Board for Plant Genetic Resources, Rome, Italy.

ICARDA—International Center for Agricultural Research in the Dry Areas, Aleppo, Syria.

ICRISAT—International Crops Research Institute for the Semi-Arid Tropics, Patancheru (A.P.), India.

IITA—International Institute of Tropical Agriculture, Ibadan, Nigeria.

IRAT—Institut de Recherches Agronomiques Tropicales et des Cultures Vivrieres, Paris, France.

IRGC—International Rice Germplasm Center at IRRI, Los Baños, Philippines

IRRI—International Rice Research Institute, Los Baños, Philippines.

IRRN—International Rice Research Newsletter published by IRRI.

IRTP—International Rice Testing Program coordinated by IRRI, Los Baños, Philippines.

IUCN—International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

NAS—National Academy of Sciences, Washington, D.C.

NIAR—National Institute of Agrobiological Resources, Tsukuba, Japan.

NIAS—former National Institute of Agricultural Sciences, Tsukuba, Japan (now NIAR).

NPGRB—National Plant Genetic Resources Board of the U.S.

NPGS—National Plant Germplasm System of the U.S.

NSSL—National Seed Storage Laboratory, Ft. Collins, Colorado.

ORSTOM—Office de la Recherche Scientifique et Technique d'Outre-Mer, Paris, France.

PCARR—former Philippine Council for Agricultural Resources and Research (now Philippine Council for Agricultural Resources, Research and Development), Los Baños, Philippines.

RF—Rockefeller Foundation, New York.

TAC—Technical Advisory Committee of the Consultative Group on International Agricultural Research (CGIAR), Rome, Italy.

UNDP—United Nations Development Programme, New York.

UNEP—United Nations Environment Program, Nairobi, Kenya.

USAID—United States Agency for International Development, Washington, D.C.

USDA—United States Department of Agriculture, Washington, D.C.

WWF—World Wildlife Fund, Gland, Switzerland.

Appendix II. Common and scientific names of crop plants cited in the text.

Crop plant	Scientific name
Alfalfa	*Medicago sativa* L.
Banana	*Musa* spp.
Barley	*Hordeum vulgare* L.
Beans	*Phaseolus* spp.
Broadbean	*Vicia faba* L.
Cabbage, Chinese	*Brassica chinensis* L.
Cabbage, head	*Brassica oleracea* L.
Cacao	*Theobroma cacao* L.
Cassava	*Manihot esculenta* Crantz
Chickpea	*Cicer arietinum* L.
Coconut	*Cocos nucifera* L.
Coffee	*Coffea arabica* L. and *C. canephora* Pierre ex Froehner
Corn (maize)	*Zea mays* L.
Cotton	*Gossypium* spp.
Cowpea	*Vigna unguiculata* (L.) Walpers
Gram, black	*Vigna mungo* L. (*Phaseolus mungo* L.)
Jute	*Corchorus capsularis* L. and *C. olitorius* L.
Lentil	*Lens culinaris* Medikus (*Lens esculenta* Moench)
Lupine	*Lupinus* spp.
Millet, finger	*Eleusine coracana* (L.) Gaertn.
Millet, foxtail	*Setaria italica* (L.) Beauv.
Millet, pearl	*Pennisetum typhoides* (Burm. f. Stapf et Hubbard

Appendix II. (Cont.)

Crop plant	Scientific name
Mungbean (green gram)	*Vigna radiata* L. (*Phaseolus aureus* Roxb., *Vigna aureus* (Roxb.) Heppe)
Oat, common	*Avena sativa* L.
Oat, red	*Avena byzantina* Koch
Peanut (groundnut)	*Arachis hypogaea* L.
Potato, common	*Solanum tuberosum* L.
Quinine	*Cinchona* spp.
Rape, oilseed	*Brassica napus* L.
Rice, Asian (common)	*Oryza sativa* L.
Rice, African	*Oryza glaberrima* Steud.
Rye	*Secale cereale* L.
Ryegrass	*Lolium* spp.
Safflower	*Carthamus tinctorius* L.
Sorghum	*Sorghum bicolor* (L.) Moench
Strawberry	*Fragaria* spp.
Sugarcane	*Saccaharum officinarum* L.
Sweet potato	*Ipomoea batatas* (L.) Lam.
Tea	*Camellia sinensis* (L.) Kuntze
Tomato	*Lycopersicon esculentum* Mill.
Triticale	*Triticosecale* spp.
Wheat, emmer	*Triticum turgidum* L. var. *dicoccum* (*T. dicoccum* Schrank.)
Wheat, durum	*Triticum turgidum* L. var. *durum* (*T. durum* Desf.)
Wheat, timopheevii	*Triticum timopheevii* Zhukowski
Wheat, bread	*Triticum aestivum* var. *aestivum*, var. *compactum* and var. *sphaerococcum*
Yam	*Dioscorea* spp.

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IOWA STATE JOURNAL OF RESEARCH MAY, 1985 497-527
Vol. 59, No. 4

EXOTIC MAIZE GERMPLASM: STATUS, PROSPECTS, AND REMEDIES[1]

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ABSTRACT. In the United States and Canada, exotic maize germplasm can be domestic unadapted germplasm, temperate foreign germplasm, or tropical or semitropical germplasm. U.S. and Canadian plant breeders have made extensive use of elite but unadapted domestic germplasm. This paper documents the extent of usage of temperate, semitropical, and tropical sources of exotic maize germplasm currently in use in the U.S. It also describes a successful attempt to adapt specific elite sources of tropical germplasm to U.S. growing conditions and a systematic way to choose promising sources of exotic germplasm from the broad array of tropical and semitropical maize germplasm represented by the various Latin American collections. While attempts to use exotic maize germplasm have thus far been limited, ineffective, and rather static, an example presented demonstrates that barriers to use of elite tropical maize germplasm can largely be broken within six years if breeding materials are chosen appropriately. Choice of breeding materials, indeed, is critical to the success of an exotic maize breeding program, yet it is an area that receives very little attention in current programs.

Index Descriptors: exotic maize germplasm, maize germplasm, races of maize, tropical maize hybrids, maize heterotic patterns, U.S. maize hybrids.

Exotic germplasm is usually considered to include all sources of unadapted germplasm: domestic, temperate, and tropical. In this overall sense there has been considerable use of exotic maize germplasm, both in experimental work and in farmers' fields. This paper will provide evidence of the current use of temperate, semi-tropical and tropical exotic germplasm in United States hybrids and will suggest methods which might be used to integrate exotic maize germplasm into domestic breeding programs. Current use of exotic maize germplasm was determined by a survey reported at the 1983 Crop Science Society meetings (Goodman, 1983b).

The exotic germplasm that has entered into most widely sold hybrids is familiar to those who have been associated with Mid-western corn breeding. For example, the Stiff Stalk Synthetic inbreds,

[1]Paper No. 9580 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695-7601. This investigation was supported in part by NIH Research Grant No. GM11546 from the National Institute of General Medical Sciences of the U.S.A. and by a grant from Pioneer Hi-Bred International.

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especially B14A, B37, and B73, the Lancaster inbreds, C103, Mo17, and Oh43, and many derivatives of both sets have to be regarded as exotic in the Southern U. S. or in Canada, yet they have been widely used in both places. As recently as the late 1950s, southern hybrids were largely tall, late maturing and more suited for forage than for grain production. In North Carolina, shorter, earlier, midwestern-type hybrids, introduced during the 1950s virtually established corn as a viable cash crop in the state. These short, early hybrids were clearly distinct from those grown in the South only fifteen years earlier. In Canada, corn production was limited in acreage as little as twenty years ago, when maize was largely restricted to the Great Lakes area and was mostly of the Northern Flint type. Thus, in both the southern and northern regions of the corn growing areas encompassed by the U. S. and Canada, exotic, but domestic, germplasm now actually predominates.

Both in the South and in Canada, exotic germplasm from Australia (Table 1), Europe (Table 2), and South Africa (Table 3) has also been used. Hybrids with Australian germplasm include Pioneer brand 309B, the first Midwestern-type hybrid widely grown in North Carolina, Pioneer brand 3147, and DeKalb brand 1214. Examples of hybrids containing European germplasm include Funks brand G-4141 and G-4040, Pioneer brand 3993 and 3994, and Northup King brand PX9288. DeKalb brand XL74B and XL394 include South African germplasm. All of the exotic materials represented in Tables 1 to 3 represent sources of temperate germplasm that may well trace back originally to U. S. sources.

The tremendous diversity within the tropical and semitropical collections of maize has been recognized for decades as offering an opportunity to broaden the genetic base of maize hybrids in the U. S. Most of such exotic maize germplasm is not well adapted to major production areas of the U. S., and using it in breeding programs presents formidable problems. When germplasm is introduced from areas differing significantly in day length and climatic conditions from those of U. S. maize production areas, lack of adaptation presents severe problems for breeders to overcome.

In the Central Corn Belt, relatively little exotic germplasm has proceeded from breeders' plot to commercial seed production, although the germplasm base is still probably wider than is readily apparent (Duvick, 1975). Excluding the contributions of temperate accessions from Australia, Europe, and South Africa, very little exotic germplasm has actually been integrated into commercial hybrids (Table 4). Such hybrids are largely attributable to the breeding staffs of several major

Table 1. Hybrids sold in the U. S. during 1983 with exotic germplasm of Australian origin.

Company	Hybrid	Type[a]	% Exotic	Units Sold[b]	Region of Adaptation
Pioneer	3147	MSX	25	220,000	South
DeKalb	XL25A	SX	12	170,000	Corn Belt
DeKalb	XL30A	MSX	12	25,000	Corn Belt
Pioneer	3179	MSX	25	20,000	South
DeKalb	1214	DX	25	7,000	South
			TOTAL	442,000	
				(1.9% of U. S. requirements)[c]	

[a] MSX = modified single cross; SX = single cross; DX = double cross.

[b] A unit consists of 80,000 kernels.

[c] Based upon approximately 80 million acres planted at an average rate of 23,000 kernels per acre (see Zuber, 1975; Zuber and Darrah, 1980).

companies (Table 5 and 6). Examples of hybrids containing Caribbean germplasm include Funks brand G-4734 and G-4949A and Pioneer brand 3160 (described by Brown, 1982, with additional detail provided by Duvick, 1984) and 3328. DeKalb hybrids XL73 and XL309 are the only examples which include Mexican germplasm, while several companies (Cargill, DeKalb, Migro, and Hoegemeyer) market hybrids with small amounts of Argentine germplasm.

To date, public breeding and training programs have not released either inbred lines or breeding materials appropriate for direct, successful inbred line development from tropical exotic materials. The publicly available lines with exotic germplasm that are currently being used are B64 and B68 (Argentine), F2 and CO255 (European), and T232 (South African), all of temperate origin. A total of at least thirty privately developed inbred lines, based in part upon exotic germplasm, are being used (Table 5), and half of those include tropical germplasm. I know of only one inbred line based upon any teosinte

Table 2. Hybrids sold in the U. S. during 1983 with exotic germplasm of European origin.

Company	Hybrid	Type[a]	% Exotic	Units Sold	Region of Adaptation
Funks	G-4141A	MSX	37	140,000	North
Funks	G-4224	MSX	37		
Funks	G-4342	MSX	37		
Funks	G-4438	MSX	37		
Northrup King	PX9288	SX	20	40,000	North
Pioneer	3994	3X	25	30,000	North
Funks	G-4141	SX	50	25,000	North
Jacques[b]		3X	12	20,000	North
Pioneer	3993	3X	25	12,000	North
Funks	G-4040	SX	50	10,000	North
Cargill[b]		3X	8	5,000	North
Jacques[b]		3X	12	5,000	North
Jacques[b]		MSX	12	2,000	North
Funks	G-4084	3X	25	1,000	North
			TOTAL	290,00	
			(1.3% of U. S. requirements)		

[a] MSX = modified single cross; SX = single cross; 3X = three-way cross.

[b] Hybrid number unavailable.

Table 3. Hybrids sold in the U. S. during 1983 with exotic germplasm of South African origin.

Company	Hybrid	Type[a]	% Exotic	Units Sold	Region of Adaptation
DeKalb	XL74B	MSX	12	36,000	South
Pioneer	3328[b]	MSX	12	17,000	South
DeKalb	XL394	MSX	25	15,000	South
DeKalb	XL74A	SX	12	13,000	Corn Belt
DeKalb	XL74	SX	12	5,200	Corn Belt
			TOTAL	86,200	
			(0.4% of U. S. requirements)		

[a] MSX = modified single cross; SX = single cross.

[b] This hybrid also has 12% Cuban ancestry.

germplasm that has ever been used commercially in corn grown for grain production. Jim Mock (personal communication) reports that a Northrup King line was derived from ($B14^3 \times$ teosinte) and used in four former Northrup King hybrids, PX59, PX69, PX69A, and PX664. He estimates the teosinte contribution to be about 8% in the line. He also suggests that several experimental hybrids currently undergoing tests contain a line tracing to the same pedigree.

At present, only about 4% of the total U. S. maize acreage is being planted with hybrids containing any non-U. S. germplasm (Table 7), and those hybrids generally have only 10 to 25% exotic germplasm. Thus, foreign exotic germplasm currently accounts for less than 1% of the U. S. maize germplasm base, and tropical exotic germplasm accounts for only a fraction of that.

The general trend toward use of exotic germplasm seems to be static, although Duvick (1981, 1984) reported a gradual increase of the germplasm base of corn in the U. S. over the past decade. In order to prepare a report (Goodman, 1983b) on the use of exotic germplasm in maize for the 1983 American Society of Agronomy meetings, a comprehensive survey on the use of exotic germplasm in corn was mailed to fifty-five seed companies. Usable responses were obtained

Table 4. Exotic germplasm known not to trace back to U. S. sources.

Company	Hybrid	Type[a]	% Exotic	Origin	Units Sold	Region of Adaptation
Funks	G-4611	MSX	3	Caribbean	56,000	South
Funks	G-4733	MSX	6			
Funks	G-4734	MSX	12			
Funks	G-4776	MSX	25	Caribbean	38,000	South
Funks	G-4949A	MSX	31			
Funks	G-4740	MSX	31			
Funks	G-5820	DX	31			
DeKalb	XL73	SX	12	Mexican	24,000	Corn Belt
Pioneer	3160	SX	12	Cuban	18,000	South
Pioneer	3328[b]	MSX	12	Cuban	17,000	South
Cargill[c]		MSX	6	Argentine[d]	15,000	Corn Belt
DeKalb	XL309	3X	12	Mexican	12,000	North
Hoegemeyer	SX2649	SX	6	Argentine[d]	8,000	Corn Belt
Pioneer	3187	MSX	12	Cuban	8,000	South
Cargill[c]		MSX	3	Argentine[d]	5,000	Corn Belt
Migro	SPX36	SX	12	Argentine[d]	3,000	Corn Belt
Pioneer	3009	DX	12	Cuban	2,500	South
Hoegemeyer	EX60568	SX	35	Caribbean	100	Corn Belt
DeKalb	2929	SX	6	Argentine[d]	100	North
				TOTAL	206,700	
				(0.9% of U. S. requirements)		

[a] MSX = modified single cross; DX = double cross; SX = single cross; 3X = three way cross.

[b] This hybrid also has 12% South African ancestry.

[c] Hybrid number unavailable.

[d] At least a remote possibility exists that some Argentine germplasm traces back, in part, to U. S. sources.

Table 5. Numbers of lines containing exotic germplasm by company and by type of germplasm, and as a percentage of total lines used by each company.

Company	No. With Tropical Germplasm	No. With Temperate Germplasm	% of Lines Used
Funks	11	1	17
Pioneer	4	3 (incl. 1*)[a]	5
DeKalb-Pfizer	2	6 (incl. 1*)	8
Cargill[b]	1	2	3
Hoegemeyer	1	1*	7
Jacques	0	4 (incl. 2*)	17
Northrup King	0	2	3
NAPB	0	1*	3
Sturdy Grow	0	1	6
Anonymous	0	1*	6
Others[c]	0	0	0

[a] Numbers of publicly available lines indicated with an asterisk.

[b] Including ACCO and PAG.

[c] Including O's Gold, Golden Harvest, Asgrow, Ring Around, Pride, Ferry Morse, Sokota, Voris, Gutwein, Coker, Custom Farm, Taylor Evans, and several smaller companies.

from thirty-five. Since several anonymous replies were received, it is impossible to say exactly which major companies were missed, but signed replies were not received from Garst, McCurdy, NC+, or Pfister (El Paso). (Tables 1 through 5 were condensed from that survey.) Most companies reported that 90-100% of their lines undergoing development lack exotic germplasm. The companies surveyed represent at least 75% of the hybrid seed corn market in the U. S., a market increasingly dominated by Pioneer (Table 6).

Table 6. Share of U. S. corn acreage by company.[a]

Company	1975-76 % Acreage	1977-78 % Acreage	1979-80 % Acreage	1981-82 % Acreage[b]
Pioneer	26	29	35	39
DeKalb-Pfizer[c]	25	21	16	13
Funks	9	7	6	6
Northrup King	4	4	4	5
Cargill[d]	5	5	5	5
O's Gold[e]	1	1	3	3
Golden Harvest	2	3	2	3
Jacques	2	2	2	3
Asgrow[e]	1	1	2	1
Others	25	27	25	22

[a] Adapted from unpublished exhibit at the National Agricultural Marketing Association Short Course, January 24-26, 1983, Des Moines, Iowa; Claffey (1981); Miller Agrivertical (1980, 1981, 1982); Butler and Marion (1983); and Mooney (1983).

[b] Data partially adapted from Mooney (1983); caution should be exercised, as most of Mooney's information on corn is inaccurate.

[c] Combined total for DeKalb and Pfizer (Trojan).

[d] Includes ACCO and PAG.

[e] O's Gold was recently acquired by Upjohn, the parental corporation of Asgrow.

Predictions by most companies suggest that, within the next fifty years, the percentage of Corn Belt hybrids containing exotic germplasm will increase from about 3% to about 5 to 10%. Several companies, however, suggested values ranging from 15 to 30% partially exotic hybrids. One, suggesting 100%, is neither marketing nor developing exotic-based materials. Funks, with substantial experience with exotic germplasm, feels that all its southern hybrids will contain some exotic germplasm within fifty years.

In the New World, some 250 to 300 races of maize have been identified (Brown and Goodman, 1977). They are represented by

Table 7. Summary (from Tables 1 to 5) of 1983 U. S. corn hybrids incorporating exotic germplasm.

Source	No. of Hybrids	No. of Companies	Units Sold	Areas of Adaptation
Australia	5	2	442,000	South; Corn Belt
Europe	14	5	290,000	North
South Africa[a]	5	2	86,200	South; Corn Belt
Caribbean	8	2	94,100	Corn Belt
Cuba[a]	4	1	45,500	South
Mexico	2	1	36,000	Corn Belt; North
Argentina	5	4	31,100	Corn Belt; North
		TOTAL	1,007,900	(4.4% of U. S. requirements)

[a] One hybrid (17,000 units) includes both Cuban and South African parentage.

Table 8. Heterotic responses known and used by corn breeders.[a]

DOMESTIC HETEROTIC PATTERNS	
Reid × Lancaster	Stiff Stalk × Lancaster
TROPICAL HETEROTIC PATTERNS	
Cuban Flint × Tuxpeño	Tuxpeño × C.T.F.[b]
Cuban Flint × Tusón	Tusón × Chandelle
Tusón × Tuxpeño	Tuxpeño × ETO
C.T.F.[b] × Chandelle	Chandelle × Haitian Yellow
Cuban Flint × C.T.F.[b]	Cuban Flint × Perla
TROPICAL × DOMESTIC HETEROTIC PATTERN	
Tusón × U. S. Southern Dents	

[a] Adapted from Brown (1975), Hallauer (1978), Wellhausen (1978) and Gerrish (1983).

[b] C.T.F. = Coastal Tropical Flint (Carribean Flint).

perhaps 25,000 individual accessions. However, as indicated in Table 7, virtually all hybrid corn sold in the U. S. is derived from only one race, Corn Belt Dent. Throughout the temperate zones of the world, commerical corns have been derived from races representing about 2% of the available germplasm. These materials include the Corn Belt Dents, the Northern Flints, and the Cateto (Argentine) Flints. On a worldwide basis, most commercial maize is derived from only six major racial groups (less than 5% of the available sources) including the groups mentioned above, plus the Mexican Dents, the Caribbean Flints, and the Tusons. If currently used (but unmarketed) breeding materials are considered, temperate corn breeders are probably sampling about 5% of the available races of maize, whereas, worldwide, breeders are experimenting with 10% of the races available (Goodman, 1983). The majority of the experimental materials, however, will never reach farmers' fields. Despite a relatively limited germplasm base, United States corn breeders are continuing to make consistent and relatively constant yield improvements at the rate of about one bushel per acre per year (Sundquist et al., 1982).

Occasionally exaggerated claims have been made about the importance of specific sources of germplasm. None with which I am familiar has been as erroneous as the presentation of Mooney (1983), who suggests that Mayorbella maize and *diploperennis* teosinte have both had major impacts on disease resistance in U. S. maize. While such sources of germplasm may eventually contribute to U. S. maize hybrids, neither presently are used in anything other than occasional experimental hybrids of no immediate consequence to U. S. maize production.

A number of known heterotic responses (Table 8) are being widely exploited by breeders. For example, virtually all Midwestern hybrids make use of either Reid × Lancaster or Stiff-Stalk × Lancaster hybrids (Baker, 1984). There is a definite need to determine how various elite, exotic germplasms combine with various elite domestic materials, but little current information is available other than work now being summarized by Stuber (1978; also unpublished data) and limited data published recently by Gerrish (1983). The U. S. National Germplasm System has thus far been ineffective in the introduction of exotic germplasm into active breeding programs for corn (and many other crops; see GAO, 1981; Goodman, 1984).

Several reasons can be advanced to explain the limited use of exotic germplasm in the U.S.

1. Adverse photoperiod response masks desirable characters.

2. Improvement of landrace materials is forty years behind currently used breeding materials.
3. Linkages between favorable and unfavorable genes in exotic × adapted populations cannot readily be broken.
4. No current basis exists for choosing the best exotics for use in breeding. Randomly chosen materials (foreign or domestic) no longer have much future in today's plant breeding.

The major weaknesses of most exotics include:

1. Poor roots,
2. Weak stalks,
3. High ears and tall plants,
4. Tendency toward barrenness, especially when crowded,
5. Susceptibility to smut,
6. Low yields of those very early exotics that flower during usual U. S. pollinating seasons,
7. High moisture and slow dry down of kernels.

In addition, exotic performance, *per se*, in U. S. summer nurseries is virtually useless as a guide towards choosing materials for breeding use, mostly as a result of adverse photoperiod sensitivity.

The above notwithstanding, numerous attempts have been made to incorporate exotic germplasm into U. S. breeding programs (see reviews by Duvick, 1977; Brown, 1979, 1982, 1983). I will note following only examples of recent efforts to develop breeding materials of exclusively or almost exclusively exotic germplasm. Gerrish (1980, 1983) used a backcross technique to develop essentially daylength neutral populations of several different tropical and subtropical races of corn. Typically these conversions contained about 5 to 12% temperate germplasm. D. L. Thompson (unpublished), Department of Crop Science, North Carolina State University, successfully followed a similar procedure with some tropical synthetics. Hallauer (1981) adapted the tropical synthetic ETO to midwestern growing conditions by direct selection operating solely with the synthetic. The synthetics with which Hallauer and Thompson worked were breeding populations and are probably of more immediate use to plant breeders than are the conversions developed by Gerrish (1980). However, if we are ultimately to identify useful heterotic patterns among the tropical and semitropical races of maize, we will need many more conversions of known racial origin such as those made by Gerrish (1980).

Several years ago, I became convinced that use of exotic germplasm in the U. S. would soon be both necessary and desirable. Furthermore, I was convinced that most breeders who had once tried using exotic germplasm seriously would not try it again unless sufficient genetic enhancement of exotic materials were accomplished so that immediate progress, equivalent to that available from current elite, adapted materials, would be possible. In addition, to avoid the interpretation that the temperate portion of a tropical-temperate admixture had been rescued through selection, I wanted to work with 100% exotic materials, with no adapted germplasm included in their pedigrees. In order to establish that use of 100% exotic materials was feasible and to do this reasonably quickly, I decided to work with elite tropical hybrids. The rationale was that these materials : (1) represented elite germplasm; (2) being hybrids, might have complementary loci for daylength adaptation; and (3) had been through the inbreeding process, thus presumably eliminating many deleterious alleles.

The hybrids chosen represented a range of geographic adaptation and a range of public and private breeding organizations. Most hybrids had performed well in worldwide trials conducted by CIMMYT (1972, 1974). Nine hybrids (Table 9) were crossed in a diallel fashion. The thirty-six populations from these crosses and the nine hybrids themselves were then maintained by sib mating within single, nominally thirty-plant, plots for five and six generations for the populations and hybrids respectively. These forty-five sets were grown in Raleigh, North Carolina, from 1976-1981. At no time did the *total* population size of all the sets combined exceed 1,500 plants; a typical population size would be 700 plants. Three or four sibbed ears from each plot were usually saved to provide seed for the next year (larger population sizes would have been desirable and would have resulted in a much slower rate of inbreeding). Early, short, erect plants with good silk-tassel nick and, whenever possible, some evidence of prolificacy were selected for sibbing each generation. Healthy plants were chosen for these sib matings, and all plants were punctured at the base during late May or early June and again in late July or early August to attempt to induce lodging via stalk rot. Those populations which responded to selection were maintained; those which did not were discarded. In the summer of 1982, a sufficient number of the materials were flowering simultaneously with B73 so that topcrosses could be made with B73. Thirty-six experimental topcrosses were planted in a test with five replications in the summer of 1983 conducted at a single location at Raleigh, North Carolina. Plot size was fifteen feet by thirty-eight inches with nominally thirty plants per plot; the date of planing was April 30. Date of harvest was August 25. The purpose of the experiment was to compare maturity, plant height, and lodging of these testcross hybrids with a range of acceptable commercial materials. Yield was a secondary consideration. Three widely different commerical hybrids were used as checks: (1) Pioneer 3369A (early, widely used); (2) Pioneer 3165 (mid-season, new hybrid); and (3) Northrup King 508 (late-season, southern hybrid).

From Table 10, where the entries are ranked by an index which penalizes exotics for high moisture and lodging, several points are immediately apparent. First, three hybrids, Agroceres 155, H-5, and Pioneer X105A predominate in the materials judged to be sufficiently adapted for testing. Second, two hybrids (H503 and H508) were completely eliminated from these tests. Third, the tested materials do approach available commercial materials in maturity, stature, and perhaps, even in yield. We are planning to test some of these materials further by using both B73- and Mo17-type testers during the coming year.

Many of the materials listed in Table 10 are clearly too tall, and the grain is too wet, but several are no later or wetter than Pioneer brand 3165, and many outyielded Pioneer brand 3369A, both good hybrids. Few are as late or as wet as Northrup King brand 508. The low yields of Northrup King 508 should not be considered typical; we had a very hot, dry summer, and very late materials suffered more than most others.

To examine the response of the lines over generations of sibbing, the various generations were planted in a randomized complete block design with families acting as (confounded with) blocks. The material was planted on May 5, 1983, about three weeks later than usual, and despite irrigation, plants did not grow vigorously. Thus, the coefficients obtained for plant height, ear height, silk date, tassel date, and lodging, when regressed upon number of generations of sibbing (Table 11) are probably minimal estimates. After five generations of selection for earliness, most of the lines were still slow in maturing. However, an average decrease in silk and tassel dates of one to two days per generation was evident despite the effects of increasing inbreeding. After two additional generations of selection, several lines now flower almost simultaneously with B73. These include 82-88-1, 82-88-17, and 82-89-1. Only seven (including 82-92-7 and 82-104-3) of thirty-six lines tested were much later than B73, and only one of those (82-93-13) was more than ten days later than B73. The differences between

Table 9. Tropical and subtropical maize hybrids used as exotic material for breeding for adaptation to U. S. Growing conditions at Raleigh, N.C.

		Original				
Hybrid	Source	Silk Date (Mo/day)	Tassel Date (Mo/day)	Plant Height (Ft)	Ear Height (Ft)	Lodging Score[a]
Agroceres 155	Agroceres (Brazil)	7/30	7/23	11	7	1
Agroceres 504	Agroceres (Brazil)	8/03	7/31	12	7	1
H-5	CNTA (Guatemala)	7/19	7/15	9	6	1
H-101	CNTA (Guatemala)	7/27	7/19	11	7	1
H-503	INIA (Mexico)	8/15	8/11	12	8	1
H-507	INIA (Mexico)	8/17	8/17	12	8	2

(Cont. on following page.)

Table 9. (Cont.)

		Original				
Hybrid	Source	Silk Date (Mo/day)	Tassel Date (Mo/day)	Plant Height (Ft)	Ear Height (Ft)	Lodging Score[a]
Pioneer X105A	Pioneer (Jamaica)	7/16	7/12	11	7	1
Pioneer X304A	Pioneer (Jamaica)	7/19	7/15	11	7	1
Pioneer X306B	Pioneer (Jamaica)	7/27	7/21	10	6	1
Checks						
Pioneer 3369A		6/29	6/29	9	5	1
McNair 508		7/11	7/11	10	6	1
Pioneer 3160		7/01	7/01	9	5	1

[a] 1 = excellent to 5 = poor.

Table 10. Performance in the summer of 1983 at Raleigh, N. C. of crosses of 100% exotic lines with B73.

Cross	Yield[a] (bu/a)	% H_2O	Lodging Score[b]	Pl Ht (ft)	Ear Ht (ft)	Silk Date (mo/day)	Tasl Date (mo/day)	Index[c]	Origin[d]
Pioneer 3165	119	37	1.0	7.4	4.0	7/14	7/13	94	-----
B73 × 82-89-8	103	36	1.0	7.8	4.0	7/13	7/10	81	P.105 × H5
B73 × 82-88-17	110	37	1.2	8.0	4.0	7/12	7/11	77	P.105 × H5
B73 × 82-89-1	97	35	1.0	7.8	4.0	7/13	7/10	77	P.105 × H5
B73 x 82-101-12	97	36	1.0	7.6	4.0	7/14	7/13	74	P.105 × Ag.155
B73 × 82-102-12	93	36	1.0	8.0	4.0	7/14	7/12	72	P.304 × Ag.504
B73 × 82-88-1	104	37	1.2	7.8	4.0	7/12	7/10	71	P.105 × H5
Pioneer 3369A	90	31	1.2	7.8	4.0	7/10	7/9	67	-----
B73 × 82-91-8	87	36	1.0	8.4	4.4	7/13	7/12	66	Ag. 155
B73 × 82-101-7	98	36	1.2	7.8	4.0	7/14	7/12	66	P.105 × Ag.155
B73 × 82-106-12	86	36	1.0	8.6	4.4	7/14	7/12	64	P.304 × H101

(Cont. on following page.)

Table 10. (Cont.)

Cross	Yield[a] (bu/a)	% H_2O	Lodging Score[b]	Pl Ht (ft)	Ear Ht (ft)	Silk Date (mo/day)	Tasl Date (mo/day)	Index[c]	Origin[d]
B73 × 82-103-6	86	36	1.0	7.2	4.0	7/14	7/10	63	P.105 × H5
B73 × 82-103-1	88	38	1.0	7.8	4.0	7/15	7/11	62	P.105 × H5
B73 × 82-90-6	89	39	1.0	8.0	4.2	7/14	7/12	62	P.105 × P.306
B73 × 82-94-7	88	38	1.0	8.2	4.2	7/12	7/11	62	P.105
B73 × 82-87-18	103	37	1.4	8.0	4.0	7/12	7/12	60	P.105
B73 × 82-104-3	89	40	1.0	8.0	4.2	7/15	7/12	60	P.306 × H5
B73 × 82-92-7	88	40	1.0	7.8	4.0	7/14	7/12	58	H5
B73 × 82-88-19	86	39	1.0	8.2	4.2	7/13	7/12	57	P.105 × H5
B73 × 82-99-2	84	35	1.2	7.8	4.0	7/13	7/11	55	H5 × Ag.155
B73 × 82-106-4	75	35	1.0	8.4	4.4	7/14	7/13	54	P.304 × H101
B73 × 82-94-4	82	39	1.0	8.0	4.2	7/13	7/11	54	P.105

(Cont. on following page.)

Table 10. (Cont.)

Cross	Yield[a] (bu/a)	% H_2O	Lodg-ing Score[b]	Pl Ht (ft)	Ear Ht (ft)	Silk Date (mo/day)	Tasl Date (mo/day)	Index[c]	Origin[d]
B73 × 82-88-20	79	38	1.0	7.4	4.0	7/14	7/11	53	P.105 × H5
B73 × 82-90-11	81	40	1.0	7.6	4.0	7/15	7/13	51	P.105 × P.306
B73 × 82-93-13	76	38	1.0	8.6	4.6	7/17	7/13	50	H101
B73 × 82-102-6	77	40	1.0	7.6	4.0	7/14	7/13	46	P.304 × Ag.504
B73 × 82-88-2	89	37	1.4	7.4	3.8	7/13	7/11	46	P.105 × H5
B73 × 82-98-23	73	39	1.0	8.2	4.0	7/17	7/14	45	Ag.155 × Ag.504
B73 × 82-92-5	81	38	1.2	7.4	4.0	7/13	7/10	44	H5
B73 × 82-105-7	86	36	1.4	8.0	4.0	7/13	7/12	44	P.105 × H101
B73 × 82-93-1	77	37	1.2	8.2	4.2	7/14	7/12	44	H101
B73 × 82-98-18	75	39	1.2	8.4	4.6	7/15	7/13	38	Ag.155 × Ag.504
B73 × 82-107-7	81	37	1.4	7.6	4.0	7/15	7/13	36	P.105 × P.306

(Cont. on following page.)

Table 10. (Cont.)

Cross	Yield[a] (bu/a)	% H_2O	Lodg-ing Score[b]	Pl Ht (ft)	Ear Ht (ft)	Silk Date (mo/day)	Tasl Date (mo/day)	Index[c]	Origin[d]
B73 × 82-87-15	87	39	1.6	7.8	4.0	7/14	7/12	33	P.105
Northrup King 508	63	46	1.0	8.2	4.2	7/21	7/20	22	-----
B73 × 82-91-29	77	38	1.6	8.0	4.4	7/15	7/13	21	Ag.155
B73 × 82-104-5	63	43	1.2	7.8	4.2	7/15	7/12	18	P.306 × H5
B73 × 82-99-13	90	38	2.0	8.6	4.4	7/14	7/11	15	H5 × Ag.155
B73 × 82-105-19	75	36	1.8	8.0	4.2	7/15	7/12	12	P.105 × H101
MEANS	86	38	1.2	7.9	4.1	7/14	7/12	53	
LSD (.05)	19	2.5	0.5	0.7	0.4	1.83	1.28	27	

[a] Yield measured as bushels per acre on a plot (15 ft) plus alley (3 ft) basis.

[b] Excellent = 1; poor = 5.

[c] Index = 100 + Yield - 2(Moisture) - 50(Lodging).

[d] Origin of tropical portion of pedigree is given in Table 9.

Table 11. Means of plant height, ear height, silk date, tassel date, and lodging score and their respective regression coefficients upon generations for the tropical maize derivatives studied at Raleigh, N.C.

	Generation						Standard error	Check Values (Pioneer 3369A)	Regression on generations	r^2
	0	1	2	3	4	5				
Plant height (Ft)	7.2	6.4	6.7	6.1	5.5	5.3	0.69	7.2	-0.31	0.69
Ear height (Ft)	4.1	3.6	3.4	3.1	2.9	2.6	0.57	3.5	-0.28	0.62
Silk date (Mo/day)	8/7	8/8	7/29	8/1	8/2	7/28	7.8	7/13	-1.67	0.50
Tassel date (Mo/day)	7/30	8/2	7/25	7/28	7/27	7/27	6.0	7/13	-0.99	0.52
Lodging (1=good; 5=bad)	1.2	1.0	1.0	1.0	1.0	1.0	0.20	1.0	-0.03	0.35

B73 and the tropical lines almost doubled, however, in our cool, wet spring of 1984.

We plan to continue to work with these lines by continuing selection for earliness, but we also are intercrossing unrelated (by original pedigree) lines and carrying out another cycle of selection for good, earlier materials. Virtually all the interline hybrids flowered between Pioneer brand 3369A and Funks brand G-5820 in our fall 1983 Florida nursery. I have no doubt that lines earlier than B73 and Mo17 will be derived from these materials; I do, however, suspect that high moisture levels may still be a problem with such lines.

As a result of this work—in winter nurseries in Florida and in summer nurseries in North Carolina—it has become apparent that choices of exotic germplasm must be made under short-day conditions. Figure 1 presents an approximate distribution of the yield of a set of tropical maize accessions when grown under short-day conditions. Figure 2 divides that distribution into parts attributable to early-, medium-, and late-maturing accessions (under short-day conditions). The area of interest to most centrally located corn breeders is cross-hatched in each case. A Canadian breeder perhaps would be most interested in elite early accessions. When the complete set of accessions is grown under the long days typical of U. S. summers, the yield distribution changes dramatically (Figure 3). Yields of the latest maturing accessions (under short days) are reduced almost to zero, and the bulk of the medium maturity accessions (under short days) also yield very little when grown under long days. Many accessions from these two maturity groups will fail to flower before frost in the central Corn Belt. Only some of the earliest (under short days) tropical maize accessions reliably flower before the end of the normal pollinating season in that part of the U. S., as indicated in Figure 4. These accessions usually mature very rapidly in the tropics, and, like many northern U. S. and Canadian hybrids, they escape insects, diseases, and drought, which may accompany the later maturing, maincrop corn in their regions of adaptation. These accessions are unlikely candidates for yield improvement because of their adaptation to extreme earliness in their native environments. They also have proved to be less promising materials for disease, insect, root, or stalk improvement work; Zapalote Chico is a good example. At the same time, many highly touted exotics, such as most Tuxpeños, some Caribbean Flints, and some Tusons, are inherently much later than such commercial hybrids as Pioneer brand 3369A, Funks brand G-5820, or even Northrup King brand 508, when grown under short days. Prospects for using such inherently late materials are limited

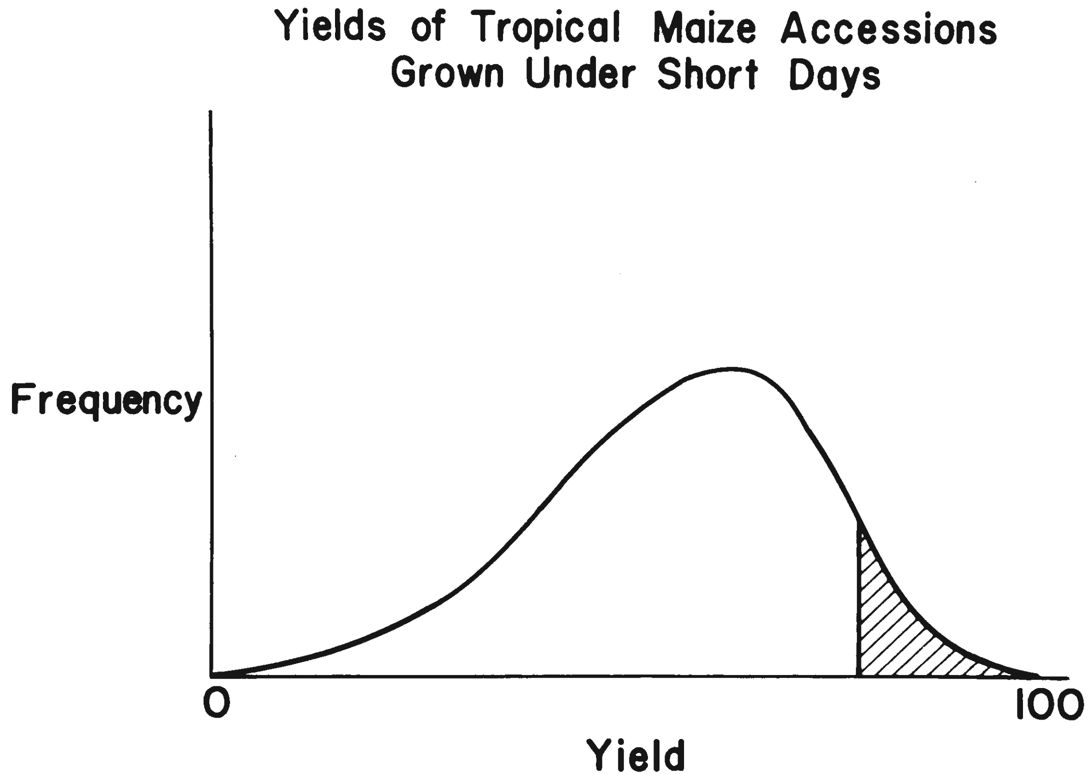

Figure 1. Approximate yield distribution of tropical maize accessions grown in a short day environment. Best yielding accessions highlighted by cross hatching.

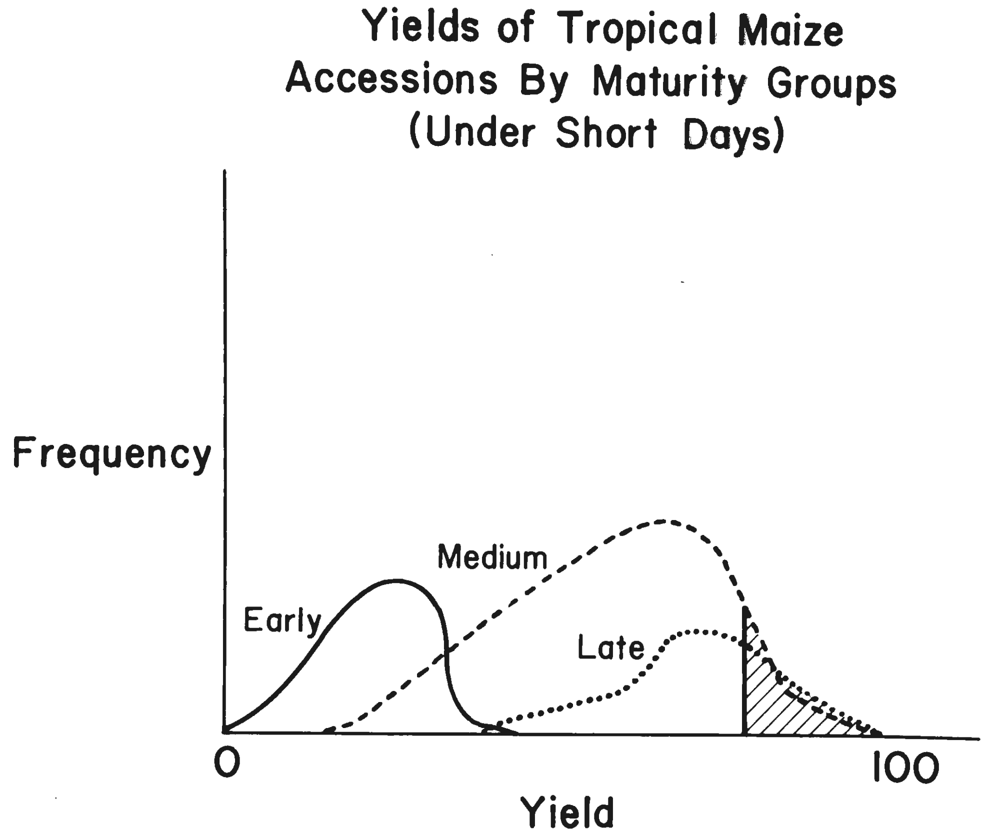

Figure 2. The yield distribution of Figure 1 divided into components attributable to early-, medium-, and late-maturing (under short days) accessions. Best yielding accessions highlighted by cross-hatching.

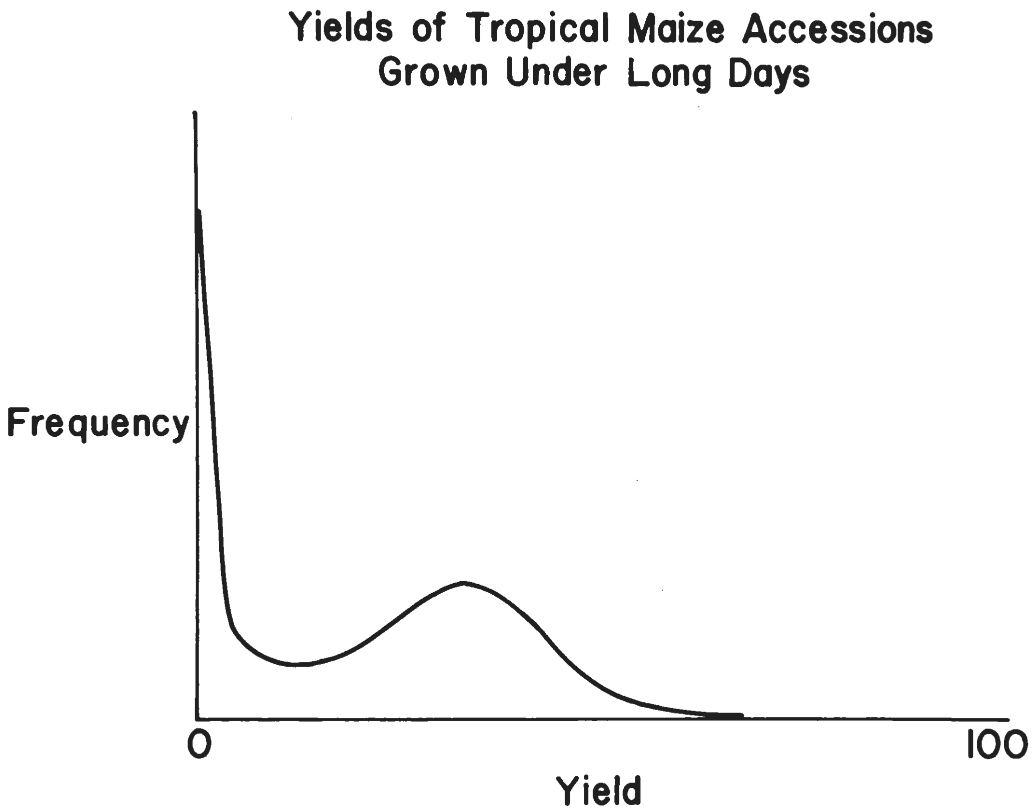

Figure 3. Approximate yield distribution of the accessions illustrated in Figure 1 when grown under the long-day conditions typical of U. S. summers.

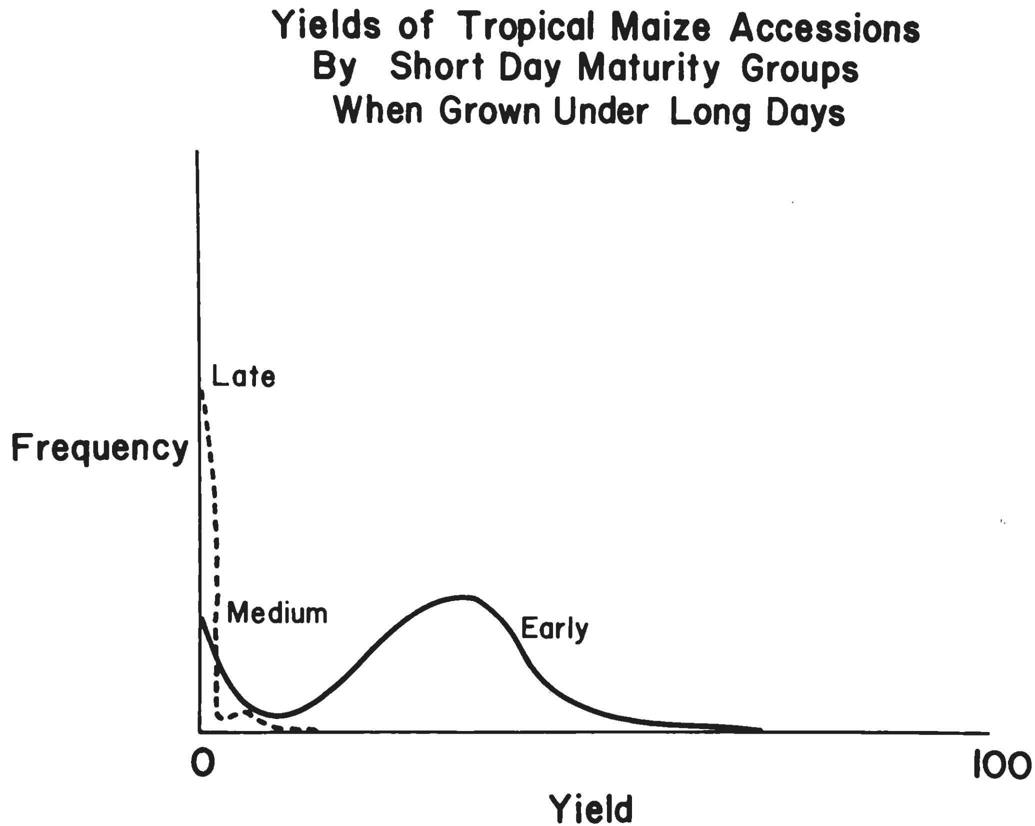

Figure 4. The yield distribution of Figure 3 divided into components attributable to early-, medium-, and late-maturing (under short days) accessions.

Table 12. Agronomic characteristics of desirable typical maize collections with early maturity (grown under short days October, 1983 to February, 1984; Homestead, Florida).

Race or Entry	Collection	Yield/ plant (Gm/pl)	Lodg- ing Score[a]	Flower date (Mo/da)	% H_20	Ears/ plant	Ear qual. Score[a]
B73 × Mo17		95	9.0	11-28	29	0.96	8.5
Cateto Sulino	ARG III	69	6.0	11-27	34	1.09	8.0
Cateto Sulino	URG IV	62	5.5	11-26	29	0.96	7.5
Cateto Culino	URG II	54	6.0	11-27	33	0.90	8.5
Nal-tel A T B	GUA 220	53	7.0	11-24	19	1.07	9.0
Nal-tel B T B	GUA 280	52	7.5	11-24	21	1.00	9.0
Cateto Sulino	ARG V	49	6.0	11-30	30	0.89	8.0
Zapalote Chico	OAX 50	47	7.0	11-24	20	0.95	8.5
Conico Norteño	GTO 23	46	5.5	11-22	25	1.04	7.0
Nal-tel B T B	GUA 145	46	6.5	11-26	23	1.01	9.0

(Cont. on following page.)

Table 12. (Cont.)

Race or Entry	Collection	Yield/ plant (Gm/pl)	Lodg-ing Score[a]	Flower date (Mo/da)	% H_2O	Ears/ plant	Ear qual. Score[a]
Zapalote Chico	OAX 48	45	5.0	11-22	23	1.01	9.0
Nal-tel B T B	GUA 765	44	6.5	11-24	21	1.01	9.0
Nal-tel A T B	GUA 111	44	7.5	11-25	22	0.94	9.0
N de T Caliente	GUA 146	44	7.0	11-30	23	1.02	8.5
Pojoso Chico	BOV 713	40	7.5	11-30	26	0.99	8.0
H. de O. Occidentales	NAY 29	40	6.5	11-30	28	0.93	7.0
Araguito	VEN 568	37	8.0	11-20	19	1.64	9.0
Araguito	VEN 628	36	8.0	11-19	18	1.49	9.0
MEANS		43	5.9	11-27	28	0.92	7.4
LSD(.05)		11	1.7	2.3	6	0.23	1.2

[a] 9 = excellent to 1 = very poor.

since both day length response and late maturity have to be modified in the progeny of any successful cross between such materials and an inbred or hybrid of normal maturity. A logical conclusion is that choice of exotic sources should be based upon performance of the sources themselves, or their performance as hybrids with adapted materials, under short day conditions in direct comparison with adapted, commercial hybrids.

Early fall planting (preferably September) in southern Florida is one appropriate test environment. Evaluation of exotics *per se* is quite feasible under such conditions that are those used for thousands of acres of emergency hybrid and foundation seed production this (1983-84) year. The major problem encountered, other than logistics, is that many accessions (exotic *and* adapted) have considerable inbreeding depression. Thus, accessions meeting minimum culling levels for lodging, disease and insect resistance, plant and ear height, and maturity may merit further evaluation even if yield is not truly outstanding. However, simple screening for maturity, lodging, and minimum yield eliminates well over 50% of most sets of exotic accessions (Goodman, 1983a). Many exotics are susceptible to barrenness under high plant densities and also are subject to poor silk/tassel nick; these are characters that can be easily studied under such conditions.

We grew one such trial which was planted on October 3, 1983, and harvested February 6, 1984. In this trial we re-tested all but one of the fifty typical collections having short day maturities equivalent to adaptation to the northern Corn Belt and having previously met minimum culling levels for agronomic performance (Goodman, 1983). This test was our first experience with machine, rather than hand, planting in Florida, and our stands were not very uniform. Nevertheless, entry differences were large, so we again used culling levels to identify a set of collections for re-testing next year (Table 12).[3] The culling levels were a yield of 35 g/plant or 20 bu/acre, a lodging score of 5.0, an ear number of 0.85/plant, and an ear quality score of 7.0. The entries were grown in nominally fifty plant, 19 ft, two row plots, with row spacing of 3 ft and alleys of 5 ft. All plants were hand

[3]All of the collections listed in Table 12 should be available from CIMMYT (address: CIMMYT Maize Germplasm Bank, Londres 40, Apartado Postal 6-641, Mexico 6, D. F., Mexico), except for Ven 568 and 628 (Araguito) and Bov 713 (Pojoso Chico), which are available from ICA (address: Maize Germplasm Bank, ICA, Apartado Aereo 7984, Bogota, Columbia), and Gto 23 (Conico Norteño), which is available from INIA (address: Maize Germplasm Bank, INIA—Chapingo, Apartado Postal 10, Chapingo, Mexico 56230, Mexico).

harvested. No collections approached the yield or lodging score of the check hybrid, B73 × Mo17, but there is much variation within many of these collections, especially those having Roman numerals rather than Arabic numerals in the collection numbers in Table 12. Such collections are composites of a few to many collections (Paterniani and Goodman, 1977). Note that not all of these collections were as slow in drying as the check, a rare occurrence among exotics. Gua 220 (Nal-tel ATB) and Gua 146 (Negro de Tierra Caliente) were notably fast dryers, especially significant considering Florida's relatively high humidity and cool winter temperatures. These materials are most likely more suitable for use in Minnesota than for Iowa or North Carolina. The purpose of these studies is to acquire the basic agronomic data on the typical collections, maturity group by maturity group, in a uniform, systematic fashion, so that breeders, geneticists, and pathologists will have a basis for selection among these (and among other racially classified but untested) collections. These seventeen collections represent nine races, and there are probably several hundred additional, untested collections of these particular races. Many of the untested collections would likely be superior to the typical collections tested. However, these particular races are far more likely to be useful agronomically than the remaining fifty or so races of equivalent maturity that have been eliminated on the basis of earlier data. Having conducted this small experiment with only fifty entries and two replications, we plan next year to try testing a wider range of maturities including most of the remaining collections listed in Goodman (1983a).

Perhaps the limited success in using exotic germplasm in the past can be attributed more to poor choices of populations than to the choices of the breeding schemes employed. However, most plant breeding courses with which I am familiar devote far more time to choices among breeding methods than to choices of breeding materials. Of the four factors in a breeding program (choice of breeder, choice of material, choice of breeding methods, availability of testing facilities), choice of materials is one of the most readily and cheaply changed and perhaps the one most critical to the success of the program.

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IOWA STATE JOURNAL OF RESEARCH / MAY, 1985 529-539
Vol. 59, No. 4

FOREST GENETICS AND FOREIGN POLICY

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ABSTRACT. The number of U. S. supported foreign forestry activities is increasing, especially in the developing world. Many of these projects deal with reforestation. In contrast to foreign agricultural projects, there is relatively little forest genetics research that supports the new forestry development projects. However, in the last 25 years the USDA through its Special Foreign Currency Research Program, bilateral agreements, and science and technology exchanges has supported cooperative forest genetics research in 22 countries. These modest research programs have provided a sound basis for forest germplasm exchanges and testing, for initiating tree improvement activities, and for the rapid exchange of research data and technical literature. These projects have encouraged, strengthened, and directly supported both basic and applied forest genetic research projects in a number of countries. Although modest compared to current agricultural activities, the international role of forest genetics and tree improvement is expanding. These research efforts in forest genetics are in direct support of U. S. foreign policy goals as well as meeting domestic national needs.

Index Descriptors: forest genetics, tree improvement, germplasm exchanges, international forestry programs, Special Foreign Currency Research Program, PL-480.

The importance of agricultural germplasm in international trade and policy is generally well understood. Of 26 major agricultural crops cultivated in the United States, only one is native to the United States. It is clearly in the United States' self interest to encourage and to support the conservation and wise management of important exotic agricultural germplasm. In fact, from the time that our nation was established, the government has supported the systematic collection of agricultural plants. In more recent years it has supported international cooperation in the conservation and maintenance of agricultural germplasm in their centers of origin (Burgess, 1971). In most cases, however, these genetic programs have been directed to safeguarding of agricultural crops of major importance to the developed nations. This was perfectly natural at the time the programs were initiated. Presently, however, the emerging developing nations are seriously challenging the established agricultural germplasm management systems insisting that they play a greater role, that their agricultural

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needs be considered, and that they receive a greater portion of the benefits from the use of their germplasm (FAO Conference, unpublished resolution).

Genetic issues associated with the forestry sector are far different from those for agriculture. We need to be aware of these differences in order to understand the development of forest genetic activities in the U. S. and internationally.

Unlike modern agriculture, forestry in the United States is not dependent on exotic germplasm. To be sure, some exotic germplasm is used in forestry programs in the United States, but such germplasm represents only a very small percentage of our planting program. Among the hundreds of native species, only approximately 50-100 non-native tree species are grown in any quantity in the United States (Wright, 1976).

In contrast with agricultural crops, forest germplasm in the United States has an extremely broad natural genetic base, i.e., forest tree improvement programs are relatively young, and we still have much of the original natural genetic diversity to manage. Most forest geneticists are still dealing with essentially wild populations. Forest genetics as a serious discipline is only approximately 60 years old. The first forest genetics institute in the world was only established in 1927 in California (Stone, 1968). The real growth in forest genetics did not take place until after World War II, and most of the major forest genetics and tree improvement programs have only been established in the last 15 to 30 years. Forest genetics clearly is a young science.

Because of the richness in number of tree species, their broad genetic base and adaptability, U. S. tree germplasm is doing well in over 80 countries. U. S. tree germplasm has found a home from central Sweden to the plains of New Zealand. Some native U. S. species such as Monterey pine (*Pinus radiata* D. Don.) have become the mainstay of foreign, commercial forestry enterprises as in New Zealand, Chile, Republic of South Africa, and Australia. The second most planted tree species in the People's Republic of China are the southern pines, loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) (Kellison et al., 1982). Even our lowly, native black locust (*Robinia pseudoacacia* L.) is one of the most widely planted tree species in the world.

Biologically, U. S. woody species have the broad genetic base to fit many different environmental niches around the world. It is thus not surprising that eventually forest genetics would have a role to play in foreign policy. Yet even today the role that forest genetics can play internationally is little understood or even recognized.

There are four main objectives to our foreign forestry germplasm activities:

1. Forest genetics can play a critical role in support of U. S. foreign policy by providing a sound technical base for forest development projects.
2. Certain forest management problems in the U. S. can be solved by the use of exotic forest germplasm.
3. There are commercial and trade opportunities that can be developed and exploited that involve the selling and exchanging of forest germplasm.
4. Forest germplasm exchanges provides a viable means for obtaining current and often unpublished foreign research information and data.

Unlike modern agriculture, international information centers for given tree crops do not yet exist. Thus information exchanges are still essentially between individual scientists, selected institutions, or a relatively few international organizations.

IN SUPPORT OF FOREIGN POLICY

Immediately following World War II, the U. S. supported a number of forestry and natural resource projects as an integral part of restoring badly damaged economies mainly in Europe. Our government supported both research and development projects and encouraged tree planting for erosion control, watershed stability, fuelwood needs, and traditional forest products. In many cases because of the destruction of native forests, there was considerable interest in introducing U. S. species. In some cases initial introductions had taken place on a small scale prior to the war.

Once the foreign economies were rebuilt, U. S. supported forestry projects essentially ended until the environmental concerns of the 1960s and the fuelwood crises of the 1970s. It was during the mid 1970s that the Agency for International Development (AID), which is the major U. S. agency for foreign development, recognized the need to place more emphasis on forestry programs (McPherson, 1983). A major activity was directed at the establishment of plantations to supply fuelwood for rural as well as urban populations. Other AID programs dealt with erosion control, agroforestry, and commercial forestry efforts (Zerbe et al., 1980). It soon became apparent that a major constraint to such programs is the lack of appropriate seeds and an adequate knowledge of, or species suitable for, local conditions.

We in forestry unlike modern agriculture prefer to use local tree species when possible. Unfortunately, it is becoming more apparent that the local human pressure on native forests has destroyed or narrowed the genetic base to such a degree that local species cannot be used in the short-term. We are becoming more dependent on the use of exotic species. There remains a major lack of scientific information to support large scale tree planting programs in many regions of the world. To address this information gap in the international forestry area, the U. S. has responded with a series of forestry research and development programs. They can be characterized as a series of cooperative efforts including national bilateral agreements, U. S. Government direct assistance programs, direct or indirect support of existing international organizations as FAO and USDA sponsored forestry research programs.

The following discussion concerns primarily those programs in which I have had some direct participation. It should provide a useful overview of the type and extent of foreign research involvement in forest genetics.

FOOD FOR PEACE PROGRAM

The first substantial foreign forest genetics activity was supported by the Food for Peace Program also known as The Special Foreign Currency Research Program (SFCRP) (Fowells, 1970). Following World War II, the U. S. Government began a program to reduce worldwide hunger and malnutrition. Countries repaid the U. S. in their own currencies, and most of the repayments remained in the host countries. These funds were then used to improve their quality of life; i.e., to build schools, roads, and hospitals and to support research. As part of this research effort, forest geneticists and associated researchers initiated joint research in over 30 countries. Studies included flowering physiology, hybridization, population studies, tissue culture, seed source tests, and biochemical studies. Most of these studies were completed by the late 1960s as the funds were no longer available or were devoted to other uses.

For example, completed studies in Columbia, Chile, Brazil, and Uruguay were involved with the evaluation of genetics and physiology of slash (*Pinus elliottii*, Engelm.) and loblolly pine (*Pinus taeda* L.). These studies included seed source studies in the individual countries as well as flowering physiology and tissue culture investigations. Studies in Columbia explored grafting using different root stock and scion combinations. Flowering was also carefully studied since flowering

Table 1. Countries in which major forest genetics and related projects were supported by Special Foreign Currency.

Country	Number of Projects	Country	Number of Projects
Brazil	1	Pakistan	16
Chile	3	Peru	1
Columbia	2	Poland	15
Egypt	3	Spain	3
Finland	12	Sri Lanka	2
Greece	3	Taiwan	1
India	17	Tunisia	1
Israel	3	Uruguay	1
Italy	3	Yugoslavia	10
Korea	1		

of these species became erratic in the tropics. Results have been published in both internal reports and scientific publications. In Columbia, one investigation was directed to the tissue culture of forest trees (Borchert, 1968). These early investigations served as a basis for future forestry development programs in these countries.

In Finland, SFCRP supported basic research in population genetics, flowering biology and seed orchard establishment (Koski, 1967). Some of these most basic research studies in forest genetics have directly supported parallel programs in the United States.

Table 1 summarizes the countries and the number of major genetic or related studies that were conducted (International Research Division, 1980).

Currently, forestry research is only funded in India and Pakistan. The major active studies in Pakistan include superior tree selection studies of poplar clones, provenance trials with Himalayan blue pine (*Pinus wallichiana* A. B. Jacks) and screening trees and woody shrubs for the arid zones (Sheikh et al., 1984). We are also supporting a number of related programs including management of improved poplar selections and a modest program of selecting species for windbreaks. In India, the current major genetic studies deal with the tree improvement in forest red gum (*Eucalyptus tereticornis* Sm.). New studies are underway in tissue culture and genetic selection of fuelwood trees.

In many of the developing countries, research is underway in forest genetics, but results are rarely published. We have used Special Currency Funds to a limited extent to get these data organized and published. Such is the case in Pakistan, where Special Currency Funds were used to prepare and publish a monograph on river redgum (*Eucalyptus camaldulensis* Dehn.), coolabah (*E. microtheca* F.v.M.) and forest red gum (*E. tereticornis* Sm.) (Quadri, 1982).

Because of the frequency of requests for information on arid land species and because there is relatively little research in the U. S. in this area, we have encouraged considerable arid land research. For example, in Pakistan we are screening 62 species from 22 genera under semi-arid conditions at nine sites (Sheikh et al., 1984). The designs are simple, but the results have been most promising. Such research most likely would not have been done by the more traditional methods of funding by the host countries. As the situation permits, similar studies are being established in other countries in an effort to screen the same germplasm in as many environments as possible.

In Egypt, the main aim of the investigation was the identification and screening of tree species for windbreaks and shelterbelts. This has led to the development of a number of linear plantations and the establishment of a small private particle-board plant. We have collected across North Africa and the Middle East one of the finest collections of *Eucalyptus camaldulensis*, (El-Lakany et al., 1980) and recently completed a collection of *Casuarina* (Badran and El-Lakany, 1977). In Egypt, we are also screening for tolerance to an array of soil conditions and already have detected several promising seed sources of *Eucalyptus camaldulensis* for salt conditions. This modest project has demonstrated the feasibility of planting trees for an array of uses in the Egyptian western desert in conjunction with their agricultural projects. In fact, these windbreaks are making the agricultural projects in the western desert feasible.

AID RELATED PROJECTS

In support of AID activities, modest research and development programs have been initiated in forest genetics or tree improvement in 35 countries. For the most part, these projects have included germplasm collections, species tests, and seed production. In a few cases, the projects have involved training geneticists. Currently, we are screening approximately 210 species from 50 genera. In addition, we are assisting in the development of forest tree germplasm conservation programs in at least 15 countries. These efforts are currently requested and supported by various Science and Technology agreements between the U. S. and the other nations.

BILATERAL AGREEMENTS

With the passing of the Food for Peace program, the U. S. has initiated bilateral research agreements with several countries. With Israel, we are currently conducting *Eucalyptus* propagation studies. With Yugoslavia, we are continuing a joint investigation on the incompatibility systems between European Black Pine (*Pinus nigra* Arnold) and Scots pine (*Pinus sylvestris* L.) and the means for mass production of a hybrid between these species (Vidakovic, 1983). In Poland, we have an excellent joint study on the genetic basis for forest tree resistance to toxic gases (Mejnartowicz, 1983). In fact, related studies on the impact of toxic gases on the genetics, physiology, and growth of forest trees have been underway in Poland since the 1960s. Furthermore, growth and flowering physiology investigations have been conducted in Poland for over 15 years, and one of these is still being supported, providing much needed basic information (Zelawski et al., 1972). Like the SFCRP funding, funds for these projects are limited, and we can expect fewer new projects. Yet such research efforts have many direct benefits to U. S. programs as well as the host countries. Some of the more basic studies were initiated in foreign institutions before they were done in our own laboratories.

SCIENCE AND TECHNOLOGY EXCHANGES

In addition to the above projects, USDA, through its Office of International Cooperation and Development (OICD), supports several scientific exchanges in forest genetics. Recently a six-year research project with Spain was completed under this program. In the course of the Spanish project, 15 forest tree species and 192 seed sources were planted in 32 locations in northern Spain. Although the project has officially ended, cooperation will continue since these test plantings have yet to be evaluated. A list of the species now being tested in Spain is provided in Table 2. The results of this type of investigation will have application outside of Spain. In fact, many of the same seed sources have also been supplied to France, Great Britain, and West Germany.

Table 2. Major tree species introduced into Spain under the OICD program.

Species	Number of Seed Sources	Locations
Abies concolor (Gord. & Glend.) Lindl.	1	1
Juglans nigra L.	12	3
Libocedrus decurrens Torr.	1	1
Pinus contorta Engelm.	23	5
Pinus jeffreyi Grev. & Bulf.	4	2
Pinus ponderosa Laws	2	1
Pinus sabiniana Dougl.	10	2
Prunus serotina Ehrh.	22	5
Pseudotsuga menziesii (Murb.) Franco	87	18
Quercus rubra L.	35	6
Sequoia sempervirens (D. Don) Endl.	5	3
Sequoiadendron giganteum (Lindl.) Bucholz	5	2

Other Science and Technology genetic research projects have been initiated with several Eastern Bloc countries. Although the program with the USSR is officially over, we are still conducting annual exchanges of germplasm. From the USSR, we have obtained excellent collections of Scots pine (*Pinus sylvestris* L.) and white elm (*Ulnus pumila* L.) as well as Siberian larch (*Larix sibirica* Ledeb.), Siberian stone pine (*Pinus sibirica* Du Tour), Korean pine (*Pinus koraienis* Siebold & Zucc.), and new collections of cold hardy material from eastern USSR. Exchanges of germplasm are still taking place providing also an opportunity for the science community to communicate in these difficult political times.

During the last five years, we have also initiated a series of studies with the People's Republic of China. Our first major effort is loblolly and slash pine seed source studies in eastern China. Within the next two years, we are planning an empress-tree (*Paulownia tomentosa* (Thunb.) Sieb. & Zucc) test of at least four species in the southern United States. Our first study with these species was established in Hawaii during 1981, and we expect more cooperative studies to follow which are of direct benefit to both countries (Krugman et al., 1983).

We have received quantities of seed of 210 species representing 81 genera from China for distribution in the U. S. as well as to other countries; and this material has been provided to over 70 cooperators in the U. S. New cooperative programs are in the planning stages with Chile, France, West Germany, and Australia. With both Chile and Australia, we hope to develop better mechanisms for germplasm collections and exchanges. We have also exchanged scientists and plant material with France and have initiated several hardwood genetic studies with red oak (*Quercus rubra* L.), walnut (*Juglans nigra* L.), and black cherry (*Prunus serotina* Ehrh.). We have used these exchanges to develop a workable international network for germplasm collecting and exchanges, the lack of which has formerly been a major constraint to such exchanges.

Like agronomists, foresters are concerned with the conservation of forest germplasm. Forest tree species are also subjected to forces that threaten their genetic base. Unlike the agricultural community, there does not appear to be the same sense of concern or urgency in the forestry community. Through FAO we have attempted to surface the many issues of genetic resource management and have attempted to convince governments that it is in their best interest to maintain as broad a genetic base as possible. Currently we have number of cooperative efforts underway identifying strategies for the forestry sector. For AID forestry and natural resources programs, the Peel Act requires AID funded projects to address the issue of the maintenance of genetic diversity. How AID will respond to this issue will be interesting. A strategy paper is being developed for their global programs which is their first such effort in the forestry sector.

CONCLUSION

U. S. forest genetics and tree improvement activities will play a larger role in the international arena as our foreign aid program expands. In far too many countries, the main natural resource problems are associated with a limited forest resource and major needs for large scale reforestation programs for an array of purposes. Unlike agriculture, the scientific base to support a number of the proposed forestry projects is lacking. Although further research certainly can fill many of the information gaps, these forestry development projects must be initiated as quickly as possible. Forest geneticists need to use their experience and knowledge in making a contribution to the success of these projects. Forest geneticists, especially those from the U. S., however, have not been adequately employed in project design or establishment. U. S. forest geneticists have not played a major international role. The projects described in this paper clearly indicate that there are areas in which forest geneticists can make a useful contribution to foreign policy by the use of our expertise in international natural resource efforts. It is apparent that we can no longer overlook the forestry sector if our nation's foreign policy is to raise the quality of life in other countries. I see forest genetics playing a more fundamental role in natural resource development.

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IOWA STATE JOURNAL OF RESEARCH / MAY, 1985 541-542
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BOOK REVIEW

Heath, Maurice E., Robert F. Barnes, Darrel S. Metcalfe. 1985. *Forages, The Science of Grassland Agriculture.* Fourth Edition. Iowa State University Press. Ames, IA. Cloth (ISBN-0-8138-0680-1) $34.90.

The fourth edition of *Forages*, edited by Heath, Barnes, and Metcalfe, employs the same approach as with earlier editions. Well over one hundred authors and coauthors write the individual chapters in their specialty areas. Over sixty new authors have been added in this edition, so the fourth edition is not only updated, but there are also new areas and some different approaches to the subject matter. In many cases the chapters are more extensively referenced than those in earlier editions.

The book is divided into five parts. There is an introductory section with five chapters devoted to the place forages have in agriculture, the environment, and society. The second section opens with chapters on botany, nitrogen fixation, seed production, and breeding. It has twenty-two chapters on the major forage plants used in the United States. The third section deals with forage production practices and the principles behind them. This section also includes physiological considerations and forage recommendations as they are relevant to specific areas of the U. S. The fourth section addresses forage utilization as pasture, hay, and silage as well as their interactions with livestock. The book concludes with a series of chapters on forages for particular livestock types. A useful appendix is included with common and botanical names and silo capacities. A glossary is provided as well.

Forages contains even more information than earlier editions in its compact concise chapters. It covers, as best one can, all aspects of forage production in the United States. The book does not give localized views of the various subjects, but for the most part emphasizes principles with examples. The subjects are generally covered with sufficient depth as to provide an undergraduate student with a good background in the subject matter.

The book contains much more information than most undergraduate teachers can use in a course, so assignments need to be carefully made so that the student knows what information is most pertinent in a given situation. In some instances information may be in several places in the book; e.g., seeding information will appear in the chapters that deal with forage seedings in various areas, as well as in the chapter on seeding. Questions at the end of the chapters focus students on the important points. *Forages* is illustrated well with photographs and tables but might benefit from even greater use of figures and diagrams. The book covers the humid area of the United States better than the semi-arid areas; nevertheless there is a fair amount of material on the drier areas. The information is quite accurate, which is to be expected when specialists write the chapters.

The book fits well in an undergraduate course in forage crops, because the instructor can depend upon it to supply background information. When supplemented with local material in the form of handouts or lecture, the book can be an integral part of a forages course. *Forages* also has value because it shows undergraduates the complexity of the forage industry in the United States. Even parts of the book that are unused in a certain area have value, because students realize that there are other situations much different than theirs and can avoid becoming too localized or restricted in their thinking. *Forages* continues to be an excellent reference book for anyone who needs information on forages—so many students elect to keep it. Although it will not give local precise recommendations necessarily, it does provide the background and principles in forage species, management, and utilization.

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