Toole, E. H., Toole, V. K., and Gorman, E. A. (1948). Vegetable seed storage as affected by temperature and relative humidity. *U.S. Dept. Agr. Tech. Bul. 972.*

Weibull, G. (1952). The cold storage of vegetable seed and its significance for plant breeding and the seed trade. *Agr. Hort. Genet. 10,* 97-104.

Weibull, G. (1955). The cold storage of vegetable seed--further studies. *Agr. Hort. Genet. 13,* 121-142.

White, J. (1909). The ferments and latent life of resting seeds. *Roy. Soc. London Proc. 81 (B550),* 417-442.

Zeleny, L. (1954). Chemical, physical, and nutritive changes during storage. *In* "Storage of Cereal Grains and Their Products" (J. A. Anderson and A. W. Alcock, eds.), 46-76. St. Paul, Minnesota.

6-6-19

THE PLANT SEED
Development, Preservation, and Germination

6-6-19
PN-AAQ-753
ISN=36090

GERMPLASM PRESERVATION: THE BASIS OF FUTURE FEAST OR FAMINE GENETIC RESOURCES OF MAIZE--AN EXAMPLE[1]

D. H. Timothy
M. M. Goodman

Departments of Crop Science and Statistics
North Carolina State University
Raleigh, North Carolina

In meeting the demands of increasing population and industrialization, society has reduced to an alarming degree the array of food production options. It has been estimated (Mangelsdorf, 1966) that man has used over 3000 species of plants for food and cultivated about 1500 species in sufficient quantity to have entered into commerce. Mangelsdorf states that about fifteen species actually feed the world. "These include five cereals: rice, wheat, corn, sorghum, and barley; two sugar plants: sugar cane and sugar beet; three 'root' crops: potato, sweet potato, and cassava; three legumes: the common bean, soybean, and peanut; and the two so-called tree crops: the coconut and banana."

More startling is our computation from world production figures (Food and Agriculture Organization of the United Nations, 1977) for wheat, rice, corn, barley, sorghum, oats, rye, the various millets, buckwheat, mixed grains, miscellaneous cereals, beans, peas, broad beans, lentils, chick peas, pigeon peas, cowpeas and all the other pulses, and the edible oilseeds such as soybeans, peanuts, sesame, rape, and sunflowers, which reveals that just three crops--wheat, rice, and corn--produce over 68% of the world's seed crop. Thus, the fate of millions hangs threadlike on the precarious balance of genetic systems of these three crops, their diseases and pests, and their interactions with environments.

[1]*Supported in part by NIH research grant number GM 11546 from the National Institute of General Medical Sciences, and by the Rockefeller Foundation grant in aid GA AGR 6905.*

Copyright © 1979 by Academic Press, Inc.
All rights of reproduction in any form reserved.
ISBN 0-12-602050-7

V

The so-called Green Revolution is identified with two of these crops, rice and wheat. The developmental concepts and research efforts of the Green Revolution, slightly modified, are being used with the third crop, corn. That these efforts have increased food production is undeniable, but they have compounded the problems of increased genetic uniformity and the obliteration of genetic variability. The success of the new cultivars associated with the technologies and thrust of the Green Revolution is destroying the genetic variability that makes success of such programs possible (Chang *et al.*, 1972; Galinat, 1974; Harlan, 1972; Wade, 1972; Wilkes and Wilkes, 1972). Genetic resources are also being lost by increased grazing pressure, abandonment of old farming systems, and various developmental processes of a burgeoning population. These pressures have destroyed, and will continue to destroy, sources of as yet unknown but potentially valuable genes necessary for future plant improvement. The gradual loss of germplasm is usually referred to as genetic erosion, but the term genetic wipe-out (Harlan, 1972) is currently more appropriate and less euphemistic. The wipe-out is occurring not only in wheat, rice, and corn, but in hundreds of species. If it continues unabated, we place man's future in serious jeopardy. The most feasible recourse to lessen that hazard seems to be to assemble the germplasm resources of our cultivated plants and their relatives, and to preserve those genetic resources in germplasm banks.

Plant breeders and other researchers involved in varietal or hybrid development are not usually concerned with overall genetic diversity, but with lesser amounts of genetic variability or homozygosity for problems at hand. Duvick (1975, 1977) has suggested that to some extent the liabilities of a narrow gene base of the varieties grown in a given year within a region are sometimes partially offset over time by rapid development of new varieties; offsetting insurance is provided by maintaining older and/or less popular varieties, and by the regional variation among varieties in different zones of adaption. To the limited extent that different breeding organizations use different source materials, a certain amount of involuntary germplasm conservation is often practiced. At present, however, much breeding work is concerned with repeated backcrosses of a few outstanding performers to sources of single-gene attributes for currently desired incorporation. Furthermore, new materials are usually derived from crosses among adapted types, although a modest trend toward the use of adapted by exotic crosses or the use of widely based synthetics (perhaps even including some exotic germplasm) may be beginning (Duvick, 1977).

Traditionally, the rationale for germplasm preservation is usually based on chromosomal genes (Smith, 1971); for example,

differences contained within the nucleus are due to additions, deletions, or substitutions of DNA segments in a chromosome, or differences are due to additions, deletions, or substitutions of multiple or partial chromosome sets. Unfortunately, the importance of cytoplasmic or extranuclear variation has been generally overlooked. However, the southern corn leaf blight epidemic of 1970 vividly illustrated the important differences among cytoplasms, as well as an agricultural vulnerability based on a single cytoplasm. Uniform cytoplasms are not only a potential hazard in plantings that utilize male sterility, but also in those widespread varieties derived from a common female background. The precise nature and location of cytoplasmic factors that control extranuclear inheritance of higher plants are not known, but differences in mitochondrial DNAs, and hence their genetic activity, have been correlated with disease reaction and male sterility/fertility in corn (Levings and Pring, 1976). Cytoplasmic inheritance is a useful phenomenon, and yet its occurrence in natural populations is poorly known and poorly understood. For years, phenotypic variation among cytoplasms has been amply demonstrated from genetic studies of male sterility and other manifestations of maternal inheritance. Only recently, however, has it been possible to attribute cytoplasmic variability to the DNAs of chloroplasts and mitochondria (Levings and Pring, 1976, 1977; Pring and Levings, 1978; Pring *et al.*, 1977).

GENE POOLS

The concept of a gene pool is a simple one. It is really nothing more than an assemblage of viable genetic variability. It is from such assemblages that man has been able to select genes that modify plants in a manner that man deems desirable. As with most simple concepts, the context in which it is used requires some definition, explanation, and restraint. In particular, the gene pool of the population biologist is often quite different from that of the plant breeder. The gene pool of the evolutionist or population biologist is usually the total genetic variation within a taxonomic unit, albeit a genus, species, or variety (Dobzhansky, 1951; Harlan and de Wet, 1971), whereas the gene pool of the plant breeder is usually much more limited in both scope and clarity of definition.

A gene pool, in most instances of current plant breeding and germplasm conservation usage, generally connotes the genetic variation of a specific population with at least a modicum of intermating, put together and maintained for some purpose other than maintaining the distinctive characteristics and genetic integrities of the indivdual components. Thus, gene

4

pools, to many a corn breeder, are his private stocks of intermating populations to which additional material is often added. A gene pool is his source of new variation. It may be composed of locally adapted commercial types; it may be composed of local and exotic material; or it may be all exotic. To breeders of self-pollinated crops, a gene pool might be a large, bulked population composed of many different kinds of material. It may be a population composed of segregating descendents from any sort of hybridization, or it may have a built-in system of intermating by using male sterility.

A gene pool is also commonly identified in terms of its proposed use. It can be many things: the Stiff Stalk Synthetic of Corn-Belt maize; the genetic marker stocks of maize endosperm mutants--perhaps for high lysine content; the short, stiff-strawed Mexican or Japanese wheats; the wheat, soybean, or alfalfa varieties grown in this country 40 years ago; the extant collection of indigenous maize varieties of the Americas; the wild and weedy populations of wheat in the Middle East; a wild species of lintless cotton from a Mexican arroyo; a sample of pine trees from the Caribbean; seed from a small grain field in Ethiopia; a grove of fruit trees on the Crimean hillside; the cytoplasms in a collection of a wild Mexican grass. Each of these is an example of a gene pool.

Each gene pool contains a gene or group of genes that may or may not exist elsewhere. Perhaps of more importance are the arrangements of certain genes in individual chromosomes, their balance with those in other chromosomes, the stability of that whole chromosome structure, and the function of that structure in gene-cytoplasm interactions. The population structure of primitive cultivars or landraces and their related wild and weedy species is a highly integrated system of genetic and environmental balance. It is to these gene pools that man has continually turned in the search for genetic material to improve his foodstuffs. It is to these gene pools that he must turn for present and future plant breeding needs. For millennia, these populations, subjected to natural and artificial selection, have served as conservatories of the heredities of our plant resources.

CROPS, WILD SPECIES, AND WEEDS

Somewhere in the haze of antiquity man began to select and domesticate plants, apparently as a series of independent happenings in widely separated areas (Baker, 1971; Harlan, 1975a). Archeological and botanical evidence indicates great amounts of initial variability during the first stages of domestication followed by increasing phenotypic uniformity as

5

the crop became increasingly domesticated (Mangelsdorf, *et al.*, 1967; Oka and Morishima, 1971). Periodic infusions of new germplasm from wild or related species and cultivars released new genetic combinations, sometimes in an explosive display of diversity. Selection among the myriad offspring of this array often resulted in enormous jumps of productivity and, within any given locale, a gradual return to visual uniformity.

Man in his travels and migrations carried his foods from one region to another. Throughout this process the plant was continually subjected to the rigors of each environment into which it had been thrust. On top of such "natural" selection, man also imposed his own selection criteria for certain characteristics. The interaction of man, the plant, and the environment went on for hundreds and hundreds of years. Thus, for any one species, certain varieties developed in one region, while other similar but distinct varieties developed in other regions (Hussaini *et al.*, 1977). These varieties are called primitive cultivars, indigenous varieties, races, farmer varieties, or landraces. The characteristics of these were and are as varied as their uses, the people who grew them, and the environments in which they were grown. The enormous stores of genetic variability contained in the landraces are now being lost at a continually increasing rate.

Wild species closely related to cultivated plants are important as occasional and natural genetic contributors to our crops, and also as possible progenitors of the economic species. Our understanding of how and from what our food plants originated is vague in most instances, but is becoming more clearly understood in others. Interest in the origin of crops is more than academic. In some cases, the immediate predecessor from which the cultivated species evolved is extinct, but a primeval source may still be extant. Some crops may have evolved as polyploid derivatives of one or more species, others may be simple diploids, and some may have arisen from weeds of a different crop.

Origins are sometimes complex, but once understood, illustrate an evolutionary road map. By following those same pathways, artificial hybridization with an ancestral wild species can often be used more easily to bring a desired gene into the cultivated relative than would be the case using a more distant relative. The substituted chromosome carrying the gene from the wild relative will have additional genes that are undesirable in an economic plant. Breaking that linkage and recombining the alien gene into the appropriate chromosome of the economic species is easier if the chromosomes are reasonably homologous. Other things being equal, a putative parental species would be used for gene transfer rather than a more distantly related relative. However, the use of wild relatives is not restricted to those of closest relationship. Closely

6

and distantly related species have been used in a number of ways to transfer desirable characters to wheat, cotton, tobacco, and rice (Beasley, 1942; Chang *et al.*, 1972; Gerstel, 1945; Sears, 1956).

The weedy relatives associated with landraces are at various stages of intermediacy between the cultivar and its wild relative. They may accommodate gene exchange in either direction. The variation of a weedy population can be enormous. One segment of the population may mimic the landrace at a particular growth stage, another segment may flower at the same time as the cultivar, yet another may be easily spotted as closely resembling the wild plant (Wilkes, 1972a). Continued association, gene exchange, and selection of cultivars and their weedy relatives have resulted in weedy populations that assume racial properties (Chang, 1976; Wilkes, 1977). They are highly integrated genetically and buffered cytologically. The blocks of genes from wild and cultivated parents have been broken down through long periods of time by various recombinations of the wild and cultivated genes.

Sterility of hybrids between weedy and cultivated forms is not as severe as that often encountered in crossing wild and cultivated species (Harlan *et al.*, 1973). The value of weedy relatives has often been grossly overlooked and their directed exploitation for improving cultivated plants is practically nonexistent. Most often collectors tend to bypass them for cultivated varieties and wild species. Even worse, most plans for the collection and preservation of germplasm do not include the weedy forms.

The populations of landraces and their wild and weedy relatives are genetically balanced with the environment. This allows the frequencies of various portions of the populations to ebb and flow in response to natural selection pressures. The greater the diversity of the population, the more plastic its response may be.

The basic population structure is determined principally by the mode of reproduction (Stebbins, 1950). Individuals in the cross-pollinators are generally in a highly heterozygous state, and each plant of the population is essentially distinct from all others. The self-pollinators are composed of great numbers of homozygous individuals. However, the self-pollinators have appreciably more diversity, and especially more heterozygosity, than is often realized (Allard, 1965; Allard *et al.*, 1968; Marshall and Allard, 1970). There is usually a small percentage of out-crossing, and although the return to homozygosity is rapid, occasional out-crossing permits a continuous source of new recombinations, first as segregating heterozygotes and then as a series of stabilized homozygotes.

1

Some species--cotton and sorghum, for example--are intermediate in their mode of reproduction, and have characteristics common to both selfing and out-crossing species.

Asexual species are of a special nature, but they may contain tremendous stores of variability. Their variability is released by occasional out-crossing to nearby related and sexual species, or by a rare breakdown of asexual control and the subsequent completion of fertilization (de Wet and Harlan, 1970; Harlan *et al.*, 1964). In addition to its relationship to population structure, the mode of reproduction affects collecting or sampling techniques and maintenance of germplasm (Frankel and Bennett, 1970; Frankel and Hawkes, 1975).

PREVIOUS COLLECTIONS: GOOD AND BAD

With a few exceptions, our past efforts at plant collection have been extremely pragmatic. The collections were sporadic, unsystematic, poorly funded, and usually the effort of a few men racing against time. Too often, we responded as a reaction to a specific need, frequently a disease- or pest-related problem. An expedition would be organized, collections made and distributed to researchers who would, it was hoped, isolate the resistant gene to be incorporated into breeding material, and then the collection would be discarded. When the next crisis occurred, we went through the same orchestrations. The wild and landrace populations were considered as everlasting founts. The concept was, of course, erroneous. The complete disappearance of wild populations and landraces from areas of thousands of square miles is being documented repeatedly (Frankel and Bennett, 1970; Committee on Genetic Vulnerability of Major Crops, 1972). Much of the variability from those areas has been lost. In some cases it all would have been lost had it not been for all-too-few farsighted efforts to collect some of that germplasm. An excellent, unfortunately rare example is the case of the corn varieties that preceded the famous Corn Belt hybrids.

Fortunately, we do have many thousands of individual collections of our major crops. For example, the world collections may contain 26,000-30,000 wheats (Harlan, 1972), 22,000 sorghums (Webster, 1976), 12,000-14,000 rices (Chang *et al.*, 1975), and 1000 or so finger millets. The USDA wheat collection contains over 19,000 accessions, mostly assembled since 1948 because the original collections were lost (Committee on Genetic Vulnerability of Major Crops, 1972). The U. S. peanut collection contains approximately 6000 entries (Hammons, 1976), whereas cotton and soybeans number around 3000 (J. A. Lee, personal communica-

tion) and 7000 (C. A. Brim, personal communication), respectively. Maize accessions in Latin American germplasm banks approximate 24,000 (Brown, 1975).

Individual researchers are the principal agents in maintaining significant portions of these collections. Most of the wild and related species are maintained, as are the cytoplasmic, chromosomal, and genetic marker stocks, at the individual discretion, effort, and initiative of a handful of persons. None of the states has a suitable arrangement for the maintenance of germplasm on a broad scale. The National Seed Storage Laboratory at Fort Collins is not expected to fill the need for some time to come, if ever (Current Policy Statement, National Seed Storage Laboratory, U. S. Department of Agriculture, mimeographed, undated). Recent reorganization of the USDA, aside from its benefits, has demolished national leadership pertaining to specific crop plants. The recently organized National Plant Germplasm System was designed to meet the highly variable needs of the U.S. plant scientists and will provide a state-federal forum for considering matters of mutual importance, apparently with appreciable consideration given to both U.S. regional and national needs (Agricultural Research Service, 1977). It remains to be seen if the new organization will permit the high level of performance needed. Although those associated with the former Plant Introduction Service and the New Crops Research Branch have done their utmost (Burgess, 1971), they have been severely limited by several inadequacies. Most of the forage collections, for example, were and are maintained at various USDA Plant Introduction stations. Many of these collections are cross-pollinated. Yet the Plant Introduction Service was forced to plant these collections in short rows, one collection beside another, and allow fertilization to occur without pollination control. A collection originating from Turkey may then be fertilized by others from Greece, Spain, Algeria, or France. The researcher who subsequently tries to use seed increased or rejuvenated from that Turkish collection will have no idea of what kind of material he is really working with. If he is trying to locate geographical sources of certain genetic characters, he is defeated or severely handicapped, before he starts. This is not a condemnation of the Plant Introduction personnel; they are dedicated people. They do the best they can with inadequate funding, inadequate facilities, and inadequate numbers of professional and subprofessional personnel. It is the same story in most areas of the world.

Appreciable portions of these collections are redundant. Individual accessions within them may have gone around the world several times with intervening stops at various experimental stations. Each time they reenter this country they are given a new accession number. Many were collected over periods

9

of years from the same area, sometimes at the same site. The collection areas were limited to those politically accessible, and oftentimes along roads that were the shortest distance between cities. Now, there is nothing wrong with this, but it does create a false sense of security when collections are considered in terms of numbers only. As a consequence of the collecting and accessioning procedures, our samples of germplasm are genetically much narrower than their numbers would indicate at first glance. Even at second and third glances, the documentation and peregrinations of many of the collections preclude tracing them to their geographical origin. In addition to the redundancies of the collections, there are geographical and evolutionary voids.

Systematic collections are needed. The variation of each crop species and its relatives must be sampled in areas of differing ecology and culture, especially in zones of great variation. It matters little if these areas are referred to as Vavilovian centers of origin, areas of diffuse origin, centers of diversity, microcenters, or whatever. What matters is that the variability within those areas be maintained. However, there are problems in doing that. An illustration of the situation with corn might be helpful. Under ordinary circumstances the details presented would only be of interest to specialists. These details, however, are often unavailable even in the reports of the various germplasm committees, and the maintenance of germplasm is critically dependent upon such details. The maize collections have probably been studied, documented, described, and maintained more thoroughly than those for any other crop. Thus germplasm resources for other crops are likely to be even less well preserved than those for maize.

MAIZE AND ITS RELATIVES

There is good evidence that at least one kind of cultivated corn originated in the Tehuacan Valley of Mexico (Galinat, 1971, 1977; Mangelsdorf *et al.*, 1964, 1967; Mangelsdorf, 1974). To date, there is no other archeobotanical evidence indicating a different site of origin. For several thousand years, the small cobs of this primitive plant, now extinct, sustained its cultivators. Then the primitive corn began to accumulate new characteristics, presumably from the incorporation of germplasm from a related wild grass, teosinte, and to assume the proportions of present day landraces.

Today in the Valley of Mexico, teosinte, the same species that contributed to maize evolution thousands of years ago, is found as a weed in maize fields. Its reproductive isolation

from maize is not complete, and so a small percentage of hybrids and backcrosses are generated each season. These fields are microcenters of evolutionary activity between a crop and its weedy relative. Other forms of teosinte are found in different regions as a wild plant not intimately associated with the cultivated crop (Galinat, 1972; Wilkes, 1967). Teosinte has distinct races, and its distribution is limited to Mesoamerica. All described races are annual. The tetraploid perennial species is extinct, except for individual plants grown in greenhouses and experimental gardens.

Tripsacum, the other relative of maize, is perennial and can be crossed experimentally with maize but not with teosinte. Its role in the evolution of maize is not clear, although it may be associated with certain characteristics of South American maize. The 11 described species of tripsacum form a polyploid series found in certain habitats from Connecticut to Paraguay (Cutler and Anderson, 1941; de Wet *et al.*, 1976; Hernandez and Randolph, 1950; Randolph, 1970).

Only in the last 15 years has a reasonable collection of the maize relatives been attempted. A fairly systematic collection of teosinte is now in hand (Wilkes, 1972b), but the tripsacum collection is probably less than a thousand plants. These collections were made by students of maize with sporadic funds from philanthropic or granting agencies and have been maintained under all manner of cooperative word-of-mouth agreements among the interested scientists. Only during the last 5 years has an institutional interest with suitable facilities and long-range probabilities been indicated.

MAIZE COLLECTIONS, RACES, AND MAINTENANCE

When Wellhausen and his colleagues initiated the cooperative corn program of the Mexican government and the Rockefeller Foundation, they began by collecting the local varieties of corn. These indigenous strains were to be the basis of the breeding program. The collections soon became a hodgepodge of incomprehensible variability. To bring order out of chaos, the indigenous strains were classified into races and the study was published as the "Races of Maize in Mexico" (Wellhausen *et al.*, 1952). This classical example was followed by a series describing the races of maize in South America, the Caribbean, and Central America (Brieger *et al.*, 1958; Brown, 1960; Grant *et al.*, 1963; Grobman *et al.*, 1961; Hatheway, 1957; Ramírez *et al.*, 1960; Roberts *et al.*, 1957; Timothy *et al.*, 1961, 1963; Wellhausen *et al.*, 1957). From some 11,000 collections of indigenous varieties in the Western Hemisphere, over 280 races of maize were described. Morphological, physio-

logical, genetical, and geographical characteristics were included, and in some cases cytological and ethnobotanical information as well. It was intended that the racial descriptions be preliminary and that they serve as a logical starting point for additional studies of maize, its evolution, and its utilization. Studies of this nature have been limited (Bird and Goodman, 1977; Goodman and Bird, 1977; Hernandez and Alanis, 1970); a general survey of the races of maize by Brown and Goodman (1977) provides an overall view of the races of the Americas; the present-day races of maize are postulated by Mangelsdorf (1974) to have descended in six lineages from wild races.

The maize collections were initiated at three primary germplasm banks: Chapingo, Mexico; Medellín, Colombia; and Piracicaba, Brazil. While procedures and results differed somewhat among these centers, all were faced with common problems. A brief description of some of the procedures, goals, and achievements of the Andean center at Medellín suggests the scope of the project.

The Andean collections were usually made by obtaining 10 to 15 ears of each sample from farmers' fields and houses, granaries, and marketplaces. The ears were sent to Medellín, Colombia, where they were cataloged, documented, and measured for numerous characteristics. The ears were shelled, except that three ears of each sample were retained as museum specimens; only two rows of grain were removed from the specimen ears. These large samples of seed were put into storage for maintanance. As precaution against loss, smaller duplicate seed samples were put in cold storage at Medellín and also sent to the seed storage center at Glenn Dale, Maryland, maintained by the Division of Foreign Plant Introduction of the USDA.

The inadequacies of the Medellín storage facilities were alleviated over a 10 year period. In the interim, it was necessary to rejuvenate seed stocks periodically to maintain germination. Corn is cross-pollinated and heterozygous; the integrity of the collection could be lost very quickly by natural selection, a too small number of plants involved in the increase, or improper pollinating procedures. Attempts to prevent genetic loss were made by using careful pollinating techniques in populations as large as possible, using open pollination in large blocks spatially isolated from other maize, planting single collections on three separate dates to allow for differences in flowering, planting at appropriate altitudes, or sending the long-day responsive stocks to Mexico or Iowa. There were some genetic shifts and losses of complete samples, but by and large the effort was successful, although extremely costly in terms of manpower, money, and the use of experiment station facilities. It was apparent that the operation of the

17

cooperative Colombian Government-Rockefeller Foundation corn improvement program and the maintenance of the individual samples of the Andean Maize Germplasm Bank could not continue indefinitely at the same level of operation.

After the indigenous strains of maize from each of the Andean countries had been classified into races, the decision was made to begin forming racial composites of the individual strains according to that biological classification. It was also decided that certain of the individual collections of each race should be maintained individually. The procedure was initiated with the collections comprising the races of maize in Colombia. From among all the collections from that country designated as representative of a race, usually three to five strains were chosen as "type" or "typical" examples of that race, and these were individually maintained and increased. Taxonomically, these would be analogous to syntypes. The other equally representative collections of that race were designated as "others"--taxonomically analogous to paratypes. Subsequent monographs that described the Andean races listed the collections as "types" (Bolivia, Chile, Ecuador) or "typical" (Venezuela, Peru) and "others." The compositing system consisted of mixing together equal numbers of viable seeds (as determined by germination tests) from each collection. Race "A" composite therefore included the "type" or "typical" collections as well as "others," that is, the composite was made from syntypes and paratypes. Additional composites from each race were sometimes made, for example, of only the "type" collections. "Some races contained subgroups differing, for example, in grain color or kernel characteristics. Therefore, if race 'C' had both yellow and white grain [subgroups], and also flour and flint starch texture [subgroups], there may have been five different composites made for this race [within each of the collection groupings of "type" and "type" plus "others"]: White flint, yellow flint, white flour, yellow flour, segregating for starch and color. Likewise, the collections intermediate between races 'A' and 'B' were [often] composited to form one population of 'A-B' germplasm (Timothy, 1972, p. 649). In this paper, the individually maintained "type" or "typical" collections will be referred to as "type" collections, and composites of syntypes and/or paratypes will be referred to as typical composites.

This system of germplasm preservation is a compromise, but it maintains a few "type" individual collections of each race and still permits maintenance of large seed supplies of each of the typical racial composites. "Numerous requests from all parts of the world are more easily filled. It also allows more thorough study and evaluation of native races to determine the sources of genes for yield, insect resistance, and other economic characteristics" (Timothy, 1972, p. 649). A request was

13

made for approximately 5 kg of each typical racial composite and each "type" collection from this increase to be sent to the United States for long-term storage at the National Seed Laboratory at Fort Collins, Colorado. Compliance with that request was begun. Large quantities of additional seed of that same material were stored at the Colombian Germplasm Bank.

By 1963, descriptions of all the known races of maize in Latin America had been published. Much of the North American corn was preserved and described. Workers in Africa, Asia, and Europe were collecting, preserving, and cataloging the races there. For the first time, the variation of an important world crop would be categorized in units of workable size representing easily recognized groups. Moreover, the variability of that crop would be preserved as a legacy for the future. At least that was the thought.

CURRENT STATUS: THE LATIN AMERICAN MAIZE COLLECTIONS

Once germplasm is collected, cataloged, described, and stored away in a freezer it tends to be forgotten. The attitude seems to be that it was job well done and now we must get on with other things. Also, over relatively short periods of time there are changes in personnel and institutional attidudes and policies. Additionally, there is usually little funding and little or no program for maintaining and studying germplasm collections. In 1963, however, the general impression was that the corn germplasm collection was in pretty good shape.

By 1968, it was apparent that despite the extensive preparations that had been made to preserve maize germplasm, problems had begun to arise. (Many of the details and arrangements in this and subsequent paragraphs are based on personal knowledge and experience). The germplasm banks in Brazil, Colombia, Mexico, and Peru, which maintained all American collections except those from the United States and Canada, were all faced with maintenance problems similar to those referred to above. There were other problems as well: numerous breakdowns of refrigeration equipment, power failures, various strikes or civil disorders which prevented personnel from entering the facilities, and drought or flooding during the growing seasons when seed increases were made.

Duplication of material and effort was no guarantee of preservation. For example, the Chilean collections were sent to Mexico and Iowa for seed increase and for recording of plant data to be used in describing the Chilean races. The data and seed from Mexico were sent back to Colombia by air shipment. Both were lost. The duplicate data books and seed samples retained in Mexico for such an eventuality were also lost in

14

a flood (the agronomist responsible for them died in the disaster). In short order, rejuvenated seed of the collections from the Chilean highlands and the data from those collections were wiped out, although the lowland Chilean increases and data recording by Pioneer Hi-Bred International in Iowa were successful.

Most all of the standby collections--duplicate samples of about 4 ounces or 200 seeds of each of the original collections had been shipped to Glenn Dale, the USDA's Maryland Plant Introduction Station. These numbered about 11,000 entries (Committee on Preservation of Indigenous Strains of Maize, 1954, 1955). From there they were sent in the mid-1960s to the National Seed Storage Laboratory, USDA-ARS, Fort Collins, Colorado, but they were not officially accepted because of variable germination, small seed lots, lack of an agreement for rejuvenation of viability, and perhaps other reasons. After negotiation with the International Maize and Wheat Improvement Center (CIMMYT), Mexico City, the Cuban, Guatemalan, and South American collections were shipped from Fort Collins to CIMMYT (about 7000 entries), and the remainder were discarded by Fort Collins. Most (about 600) of the Bolivian collections were grown out in the winter of 1969 at Tepalcingo by CIMMYT. Only a few produced seed; the remainder were lost. Thus, 7 years after the last of the race bulletins appeared, the standby collections were reduced from about 11,000 entries to 7000 entries, and the germplasm collections of two countries (Mexico and Bolivia) and one region (the West Indies) were essentially eliminated from the group.

The status of the individual collections at the various germplasm banks varies greatly. Some collections are classified by race, some are not. Some of those classified are listed in the race bulletins or elsewhere as being "type" collections; most are not. Only the status of the "type" collections is reasonably known at present, although a cataloging process of many of these collections is under way (Information Sciences/Genetic Resources Program, 1977). It is suspected that the status of the other collections is poorer, but this may not always be so. CIMMYT until recently had only relatively few individual "type" collections from Mexico, Central America, and the Caribbean, despite a rather large number of accessions. Many of CIMMYT's individual collections have been assembled in recent years by E. Hernandez X., A. Blumenschein,, José Jiménez, and Pablo E. Daza B. as the bank was started only in 1960, after the original collections had been completed. Many others were deposited at CIMMYT by the Brazilian bank at Piracicaba, which now maintains only racial composites (personal communication, M. Gutiérrez., CIMMYT; Kashiwakura and Paterniani, 1972). Consequently, seed requests for collections that were used and documented in describing "The Races of Maize in Mexico"

15

(Wellhausen *et al.*, 1952) have often been filled with seed supplies from other collections.

The Instituto Nacional de Investigaciones Agricolas (INIA) has the most complete set of Mexican, Guatemalan, and Caribbean individual collections. INIA inherited the germplasm bank of the cooperative program of the Rockefeller Foundation and the Mexican government. (Some Guatemalan collections have been salvaged by CIMMYT from the standby collections formerly at Fort Collins, but many Guatemalan collections are quite difficult to maintain at CIMMYT). Many of INIA's Guatemalan collections are original (nonincreased) seed. Neither CIMMYT nor INIA has a frost-free high altitude experiment station that would enable them to maintain late maturing, high altitude collections.

Most of the individual collections from eastern South America (the Guianas, Brazil, lowland Bolivia, Paraguay, Uruguay, and Argentina) made by the Institute of Genetics, Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo, at Piracicaba in Brazil, are no longer maintained there. That bank did not utilize modern cold storage equipment and has been essentially phased out (Kashiwakura and Paterniani, 1972). It is to be replaced by a new bank under the auspices of EMBRAPA (Empresa Brasilera de Pesquisa Agropecuaria). Most of those individual collections formerly stored at Piracicaba have been increased by CIMMYT either from the standby collections from Fort Collins or other sources, however, and are still available.

Many of the Peruvian collections are maintained by the Programa Cooperativa de Investigaciones en Maíz, Universidad Agraria--La Molina, Lima, Peru, which assumed responsibility for them, leaving the Colombian bank with responsibility for the other Andean collections. Many of the Peruvian collections adapted to altitudes of about 2000 to 2800 m were lost due to lack of facilities to increase collections at those altitudes. Efforts are under way in Peru to recollect and replace the representative materials which have been lost. In addition, the Peruvian portion of those standby collections from Fort Collins that are no longer available elsewhere is being increased in Peru under an agreement with CIMMYT.

The collections from Venezuela, Colombia, Ecuador, Peru, Bolivia, and Chile were originally to be stored in Colombia at what is now the Instituto Colombiano Agropecuario (ICA) with standby samples at Fort Collins. Almost all the standby samples made it to Fort Collins (and then to CIMMYT), but the Chilean and Peruvian samples are not currently available from Colombia.

A portion of the story of the Chilean collections has already been presented. Fortunately, the low altitude Chilean "type" collections were increased in the United States by

16

W. L. Brown, of Pioneer Hi-Bred International, and placed in Fort Collins. They are still there and appear to have good germination. Those collections remained at Fort Collins even though the standby collections were sent to CIMMYT. In addition, it has been possible to salvage a number of the high altitude Chilean "type" collections from the well-traveled standby collections (now at CIMMYT).

The Peruvian collections unfortunately were given two sets of collection numbers. One set was used in Peru and published (Grobman *et al.*, 1961), while another set was used in Colombia, Fort Collins, and in the reports by the Committee on Preservation of Indigenous Strains of Maize (1954, 1955). Thus, use of the Peruvian seeds from the standby collections from Fort Collins to replace lost collections in Peru has been hindered by the lack of a complete cross-listing of the two sets of collections numbers. No cross-listing of the two sets has apparently ever been published. Adequate safeguards for the Peruvian collection were further hampered because the complete set of Peruvian collections was never received in Colombia; hence no complete set of standby collections was ever assembled.

The Bolivian "type" collections stored in Colombia were neglected for several years but are now being increased for tentative transfer to CIMMYT (Brown, 1975). It appears that a number of them (mostly high altitude materials) have been lost, but until the increases have been completed, their exact status must remain in doubt. Duplicate samples of many of the low altitude Bolivian "type" collections had been saved by W. L. Brown of Pioneer Hi-Bred International. These have been increased in Florida and sent to CIMMYT as a precaution against still further erosion of the Bolivian collections. Unfortunately, Mario Gutiérrez, who rescued CIMMYT's maize germplasm bank from chaos in the mid-1960s, and who was responsible for salvaging not only many of the well-traveled standby collections but also most of the collections from the former bank at Piracicaba, Brazil, is no longer at CIMMYT. As a result, many of the plans (such as those for the transfer of the Bolivian collections to CIMMYT) for the preservation of maize germplasm at CIMMYT seem unlikely to be achieved.

The Colombian bank will remain in charge of the collections from Venezuela, Colombia, and Ecuador. The "type" collections from Venezuela and Colombia are generally viable and available from ICA. In the recent past, at least, this has been much less so for Ecuador, especially highland Ecuador, but the standby collections (now at CIMMYT) have filled the gap reasonably well. Many of the Colombian "type" collections were increased and placed in Fort Collins (the only country for which this seems to be true). These increases remained in Fort Collins when the standby collections were removed.

17

In addition to individual collections, there are several kinds of composites, most of which remain poorly described, if at all. The typical composites of most Colombian races are still at Fort Collins. The typical Colombian composites, as well as the typical composites of most races from Venezuela and Ecuador, are available from ICA. A smaller proportion of typical composites from Bolivia is available from the same source. The latter three sets (Venezuela, Ecuador, and Bolivia) apparently were not deposited in Fort Collins. Composites were never made for the Chilean races, but composites for most of the Peruvian races were made at La Molina, Peru, where they are still generally available. The composites developed at the Brazilian germplasm bank were not deposited in Fort Collins but were sent to Mexico and, for the most part, are available from CIMMYT (Paterniani and Goodman, 1978). (No "type" collections were ever designated for most of the races of eastern South America). Mexican racial composites of uncertain origin are still at Fort Collins. Outside the Andean region, and perhaps within that region in recent years, some collections may have been assigned to a race even though they were not typically representative of that race. Perhaps they possessed more characteristics of that race than of any other, but admixtures from other sources should have precluded their inclusion in representative racial composites or as representative specimens of a particular race.

Apparently there was some indiscriminate compositing of the individual collections in certain maintenance programs, without proper assurance that even the individual "type" collections were also being maintained. From the plant breeding viewpoint, this can be an acceptable and very logical procedure. In fact, the formation of complex composites of *unrelated* materials is often indicated, insofar as the immediate needs of feeding people by modern agricultural production is concerned. Broad-base composites are often thought of as gene pools, and a breeding program frequently has several of them. But as a procedure for preserving genetic resources they are completely unacceptable as they result in the loss of the biosystematic identity and the genetic integrity of their individual components.

In Brazil and during certain periods at CIMMYT, but not at INIA, in Mexico, the development of racial or subracial composites apparently took precedence over the maintenance of many "type" or other individual collections. In fact, until recently, relatively few "type" collections from Mexico and Guatemala were stored at CIMMYT. Before CIMMYT was organized most of these collections had been stored at INIA; relatively few of them, usually collections of special interest, were utilized in the corn breeding programs at CIMMYT. As a result of the emphasis on composites, some of the individual and "type" collections were lost. In the case of the Brazilian individual collections,

18

the duplicate or standby samples (now at CIMMYT) were available to replace many of the lost collections. However, the Mexican samples among the Fort Collins standbys were discarded before it was realized that many of them were not available in Mexico.

Tables I and II summarize the general status of the "type" collections of Latin American maize, when such collections have been designated, and the status of the racially classified collections when "type" collections were not designated. A number of the high altitude collections from Ecuador are in the process of being salvaged from the standby Fort Collins collections, so their availability is limited. The status of collections from Bolivia and Chile is critical, and much of the maize of Central America (except Guatemala) remains undescribed.

TABLE I. Status of the Number of Individual "Type" Collections of the Latin American Races of Maize as of April 1978

Country or region	*Typical collections listed*	*Typical collections still available*
Mexico[a]	*154*	*132*
Guatamala	*180*	*115*
Honduras[b]	*1*	*0*
El Salvador[b]	*2*	*2*
Nicaragua[b]	*1*	*0*
Costa Rica[b]	*3*	*2*
Cuba[c] *and the West Indies*	*49*	*39*
Venezuela	*86*	*86*
Colombia	*129*	*127*
Ecuador	*154*	*150*
Peru	*183*	*154*
Bolivia[d]	*141*	*106*
Chile[e]	*80*	*56*
Argentina[c,d]	*26*	*23*
Paraguay[c,d]	*13*	*9*
Totals	*1202*	*1001*

[a]*Includes the collections of Hernandez and Alanis (1970).*
[b]*Essentially unstudied.*
[c]*Fairly well collected and studied, but few if any "type" collections have been documented.*
[d]*See Table II also.*
[e]*Many of these in immediate danger of complete loss.*

19

TABLE II. Current Status of Racially Classified Individual Original Collections from the Brazilian Germplasm Bank[a]

Country or region	Collections classified	Collections still available
Argentina	57	50
Uruguay	81	20
Paraguay[b]	48	36
Brazil[b]	984	577
Guianas[b]	21	12
Bolivia	19	18
Totals	1210	713

[a]*No "type" collections have been identitied for most of the races described at that bank (does not include any post 1965 collections, which have yet to be described and documented).*

[b]*The western part of Paraguay, much of Amazonas, and the less accessible parts of the Guianas are still largely uncollected.*

Several described races have apparently been completely lost (Polulo and Negrito from Chile, several subraces of Quicheño from Guatemala, Amarillo de Ocho and several subraces of Capia from Argentina, Harinoso Dentado from Colombia). All the "type" collections have been lost for the races Rienda and Jora from Peru, Paru from Bolivia, and Coastal Tropical Flint from Dominica. In addition, W. H. Hatheway's collections from Cuba apparently were not deposited in any of the germplasm banks.

Finally, the North Central Plant Introduction Station of the USDA at Ames, Iowa, has a large collection of U. S. Indian corns assembled principally by W. L. Brown, A. E. Longley, and H. C. Cutler (many of these were salvaged by Longley, later increased by Brown, and redeposited with the USDA after the USDA had discarded them), as well as an abundance of poorly documented open-pollinated varieties and miscellaneous undocumented plant introductions (from various catalogs and seed lists of the North Central Regional Plant Introduction Station, Ames, Iowa). These have never been studied in the same detail as have the Latin American races. The USDA itself has never

20

had a comprehensive collection of Latin American maize, but the materials at Ames are generally believed to be well maintained.

That, in brief, is the status of the collections of American maize. What is going on now is a last-ditch stand (Brown, 1975) to prevent further loss of something which many people had assumed was well preserved. The situation with other crops is probably not any better. Indeed, it appears uniformly worse.

CONCLUSIONS

Germplasm resources are fast disappearing, and there is urgent need to collect and preserve those resources. In the past there have been mistakes of omission and commission, inadequate support in maintaining the integrity of germplasms, unfavorable weather conditions, and so forth. But perhaps most damaging to the maintenance of germplasm and the integrity of its individual components is the concept of manipulating the formation of gene pools. If the concept of a gene pool, insofar as germplasm maintenance is concerned, could be likened to a military motor pool composed of separately usable units, rather than a beachcomber's stew pot into which everything was dumped and blended, we would be much better off.

To use genetic variability most intelligently, we must know where, and preferably how, it originated, not only for disease or insect resistance but also for yield and quality features of the market. As we search for these genes, it is increasingly clear that if we understand the evolutionary relationships of the crops and their relatives, modification of the crops to suit our needs becomes easier. To do all this requires that the essential integrity of the germplasm be preserved. Only when all individual collections cannot be maintained should composites be initiated. Compositing should be done only on a biologically systematic basis with as many categorical units as possible. (An excellent example of where it is much better to be a splitter rather than a lumper). We do not deny that progress, even occasionally spectacular progress, can be made on a hit-or-miss basis where the breeder knows virtually nothing about the sources of his material. However, long-term progress depends upon accumulated knowledge of source materials and guaranteed access to them.

Methods of conserving genetic resources vary according to the crop. Each nation cannot maintain a complete germplasm collection for each crop. The scope and cost of the program would be too large and much material would be unadapted.

Various national, philanthropic, and multinational entities have increased their interest in germplasm resources (Harlan, 1975b), but much of the activity has been of a survey-discussion nature and often reiterative, with one group repeating the work of another albeit at different levels of planning and/or organization. A few action programs have been initiated within the past ten years, but private opinions differ from official positions in regard to success. However, awareness of the germplasm problem is reaching higher levels of institutional management, and it is hoped that well-founded programs will emerge from the scores of committee reports, working papers, and organizational charts. The ponderous natures of governments and multinational organizations do not seem to offer much immediate hope for solving the problem. Several of the philanthropic foundations and some of the international research centers that they support (CIMMYT, the International Rice Research Institute, and the like) are hampered less by the demands of protocol and seem to offer the best possibility for immediate and interim germplasm maintenance facilities until additional organizations are properly established and operational. Current efforts of the IBPGR (International Board for Plant Genetic Resources, 1975, 1976) to collect germplasm from critical areas are bearing fruit, although the ultimate success of those efforts in germplasm preservation remains to be seen.

"The maintenance of a living collection is usually regarded as a routine and time-consuming, yet essential, task. Much of the material maintained there seems to be of little current interest--occasionally, of course, a threatened epidemic or new insight into a disease problem will generate a sporadic interest in screening everything available. A great deal of the material that leaves the bank is discarded; it is regarded as a gift, not as a loan. Surely a more suitable arrangement could be devised. One possibility is the development of germplasm maintenance centers in which maintenance is regarded as the primary goal, not as a by-product of breeding activities. In this connection it is worth noting that the plant breeder, entomologist, or plant pathologist tends to regard a germplasm collection as an inexhaustible source from which he can extract only such experimental material as is of interest for his specific purposes. On the contrary, the experimental taxonomist, crop plant evolutionist, and ethnobotanist consider the entire collection to be necessary experimental material--quite apart from its potential economic value. They need to preserve and study as wide a variety of material as they can manage and to use it continuously. Because all classifications have to be revised as new material is collected and new analytical procedures developed, the experimental taxonomist's work is never done. A germplasm center could effectively serve a dual purpose as experimental material for several disciplines and as a

22

reliable and continuing source of germplasm for the plant breeder. Coupling these two objectives could relieve the plant breeder of a routine chore and provide the taxonomist and others with facilities and experimental material not now available to them" (Committee on Genetic Vulnerability of Major Crops, 1972, p. 301-302). It is clear from the example with maize that germplasm banks have not functioned satisfactorily, either as germplasm banks per se, or as by-products of breeding programs. Loss of material has been excessive, even with close monitoring by interested, dedicated philanthropic organizations. Virtually no systematic studies of the vast collections have been made since the collections were assembled and described, and even fewer results of such studies have been published. The conversion of germplasm banks from last-resort sources of material for plant breeding projects into functional and continuing centers for systematic studies of these vast collections appears to be long overdue.

The other alternatives appear to be loss of the material, which we can hardly afford, or the preservation intact of current sites harboring the various centers of variability of our current and future major crops (Iltis, 1972; Committee on Germplasm Resources, 1978). We do not deny the appeal of the latter alternative, which clearly merits more attention than it has received, but it would need to be accompanied in any case by centers for the study of such materials and germplasm banks for standby storage. An eminent colleague, W. C. Gregory, has vividly delineated the problem in a personal communication: "In his efforts to solve the problem [of germplasm erosion] and to stem the loss, man may be holding a straw against the sea. It appears that the richness and variety of the genetic resources of man's cultivated crops reflect the multiplicity and variety of man's own civilizations both in space and in time. His crops appear to be as wild as he is wild, diverse as he is diverse, opportunistic as he is opportunistic, stable as he is stable, and as uniform as he is uniform. In this view, the forces with which the plant breeder must deal in stemming the loss of genetic resources are the forces of Americanization, Westernization, Europeanization, industrialization, and modernization of the Andean Indian, the denizen of the Amazon, the unique amd multiple peoples of the Caucasus, the Himalayan valleys, and western China, the human interfaces of Nepal, Assam, Abyssinia, and Ethiopia. Thus the voice, 'crying among the weeds,' is being and will be swept away by the winds of the human assault on poverty, starvation, and ignorance--the very things the plant breeder has dedicated his life to alleviate....

"The collection from gene pools and maintenance of germplasm banks in the centers of western-type plant breeding establishments, in tropical gardens, and other contrived facilities may be at best a temporary or stop gap measure, at worst a waste of

23

time and money. The problem will require measures commensurate with the social upheaval working against the survival of genetic resources. My own personal view is that present trends indicate that modern world production technology will expedite the annihilation of such genetic resources as we now have...."

Regardless of the outcome of the discussions concerning the internationally oriented germplasm maintenance centers, the United States needs a frost-free maintenance facility in the tropics or subtropics (Ad hoc Subcommittee of the Agricultural Research Policy Advisory Committee, 1973). The existing facilities at Miami, Florida and Mayaguez, Puerto Rico are inadequate for the above purposes. Many of the U.S. crops are subtropical. Many of their relatives are also perennial and flower only under a short day regime. A living collection of such plants suitable for the dual objectives previously mentioned can be established only in a subtropical, frost-free environment.

The prodigious agricultural production of the United States is based on introduced plants. Some of these plants were from Latin America in Precolumbian times, but the fact remains that none of the important food crops originated in this country. Throughout the world, the major crops are being introduced and promoted on an intensifying scale. It should not be necessary or otherwise desirable to depend so completely on so few crops. There are scores of minor crops which have never been subjected to modern agricultural research. Fifty years ago, it would have been difficult to imagine the present-day importance of sorghum or soybeans. Many of the minor crops would probably respond, just as have soybeans and sorghum, to intensive research efforts. They, too, should be collected and preserved.

Neolithic man began the Agricultural Revolution by domestication, selection, and transportation of plants. He was able to do this because of variability. We, in the midst of sporadic surpluses or of impending shortages and cyclical famines, must maintain what we can of the remaining variation. That variability, maintained in natural gene pools, is valuable stuff. Our legacy to future generations should be adequate germplasm resources from those gene pools, properly maintained, studied, distributed, and replenished.

SUMMARY

A biosystematic rationale is given for the preservation of plant germplasm. The disappearance of genetic resources from natural or agricultural ecosystems, from previous collections of plant material, and from germplasm maintenance operations is noted. A brief history of the collections of indigenous strains of maize and the races of maize in the Americas illustrates the

24

aims, successes, problems, pitfalls, and failures of germplasm maintenance programs. We concluded that the maintenance of existing plant germplasm is imperative; that accessions be maintained individually rather than composited; that germplasm maintenance centers not be considered strictly as service units but be involved in, or allied with, biosystematic research; that adequate tropical or subtropical germplasm maintenance and research facilities are needed for major and minor crops of the United States. Because the backbone of U.S. agriculture is introduced germplasm, it is essential that we collect, maintain, and replenish those genetic resources for our future.

NOTE ADDED IN PROOF

Since this paper was written, two events particularly relevant to the second paragraph of the section MAIZE AND ITS RELATIVES have been published. Tetraploid perennial teosinte has been rediscovered (Guzmán Mejia, R., [1978]. Redescubrimiento de *Zea perennis* [Gramineae]. Phytologia 38, 177). A diploid perennial teosinte, morphologically primitive but infertile with maize, has also been found (Iltis, H. H., Doebley, J. F., Guzmán M., R., and Pazy, B. [1979]. *Zea diploperennis* [Gramineae]. A new teosinte from Mexico. Science 203, 186-188).

ACKNOWLEDGMENTS

Some of the details and arrangements pertaining to the maize collections have been obtained at various times by personal communication with: Hermilio Angeles A., Mexico; A. Blumenschein, Brazil; Louis N. Bass, United States; W. L. Brown, United States, Clímaco Cassalett D., Colombia; Mario Gutiérrez G., Mexico and Brazil; E. Hernandez X., Mexico; Howard L. Hyland, United States; Edwin James, United States; Ernesto Paterniani, Brazil; Ricardo Sevilla, Peru; Howard Sprague, United States; E. J. Wellhausen, Mexico. The cooperation and advice of these specialists is gratefully acknowledged. We are also grateful for various committee reports, minutes, and other documents made available to us by the Rockefeller Foundation, U.S. Department of Agriculture, and the Agency for International Development.

Paper no. 5641 of the Journal Series of the N. C. Agricultural Experiment Station.

25

REFERENCES

Ad hoc Subcommittee of the Agricultural Research Policy Advisory Committee (1973). "Recommended Actions and Policies for Minimizing the Genetic Vulnerability of our Major Crops." A Special Report, Agricultural Research Policy Advisory Committee, The USDA and the Nat. Assoc. State Univs. and Land Grant Colleges Cooperating, Washington, D. C.

Agricultural Research Service (1977). "The National Plant Germplasm System." Program Aid Number 1188, USDA, Washington, D. C.

Allard, R. W. (1965). Genetic systems associated with colonizing ability in predominantly self-pollinating species. *In* "The Genetics of Colonizing Species" (H. G. Baker and G. L. Stebbins, eds.), pp. 49-75. Academic Press, New York.

Allard, R. W., Jain, S. K., and Workman, P. L. (1968). The genetics of inbreeding species. *Advan. Genet. 14,* 55-131.

Baker, H. G. (1971). Commentary. *In* "Man Across the Sea" L. C. Riley, J. C. Kelley, C. W. Pennington, and R. L. Rand, eds.), pp. 428-444. Univ. of Texas Press, Austin.

Beasley, J. O. (1942). Meiotic chromosome behavior in species, species hybrids, haploids, and induced polyploids of *Gossypium. Genetics 27,* 25-54.

Bird, R. McK., and Goodman, M. M. (1977). The races of maize V: grouping maize races on the basis of ear morphology. *Econ. Bot. 34,* 471-481.

Brieger, F. G., Gurgel, J. T. A., Paterniani, E., Blumenschein, A., and Alleoni, M. R. (1958). "Races of Maize in Brazil and other Eastern South American Countries." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 593, Washington, D. C.

Brown, W. L. (1960). "Races of Maize in the West Indies." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 792, Washington, D. C.

Brown, W. L. (1975). Maize germplasm banks in the Western Hemisphere. *In* "Crop Genetic Resources for Today and Tomorrow." (O. H. Frankel, and J. G. Hawkes, eds.), pp. 467-472. Cambridge Univ. Press, Cambridge.

Brown, W. L., and Goodman, M. M. (1977). Races of corn. *In* "Corn and Corn Improvement" (G. F. Sprague, ed.), pp. 49-88. Amer. Soc. Agron., Madison.

Burgess, S. (1971). "The National Program for Conservation of Crop Germ Plasm (A Progress Report on Federal/State Cooperation)." Univ. Printing Dept., Univ. of Georgia, Athens.

Chang, T. T. (1976). The origin, evolution, cultivation and diversification of Asian and African rices. *Euphytica 25,* 425-441.

Chang, T. T., Sharma, S. D., Adair, C. R., and Perez, A. T. (1972). "Manual for Field Collectors of Rice." Internat. Rice Res. Inst., Los Baños.

Chang, T. T., Villareal, R. L., Loresto, G., and Pèrez, A. T. (1975). IRRI's role as a genetic resource center. *In* "Crop Genetic Resources for Today and Tomorrow" (O. H. Frankel and J. G. Hawkes, eds.), pp. 457-465. Cambridge Univ. Press, Cambridge.

Committee on Genetic Vulnerability of Major Crops. (1972). "Genetic Vulnerability of Major Crops." Nat. Acad. Sci., Washington, D. C.

Committee on Germplasm Resources. (1978). "Conservation of Germplasm Resources: An Imperative." Nat. Acad. Sci., Washington, D. C.

Committee on Preservation of Indigenous Strains of Maize. (1954). "Collections of Original Strains of Maize," Vol. 1 Nat. Acad. Sci.-Nat. Res. Council, Washington, D. C.

Committee on Preservation of Indigenous Strains of Maize. (1955). "Collections of Original Strains of Maize," Vol. 2, Nat. Acad. Sci.-Nat. Res. Council, Washington, D. C.

Cutler, H. C., and Anderson, E. (1941). A preliminary survey of the genus *Tripsacum. Ann. Missouri Bot. Garden 28,* 249-269.

de Wet, J. M. J., Gray, J. R., and Harlan, J. R. (1976). Systematics of *Tripsacum* (Gramineae). *Phytologia 33,* 203-227.

de Wet, J. M. J., and Harlan, J. R. (1970). Apomixis, polyploidy, and speciation in *Dichanthium. Evolution 24,* 270-277.

Dobzhansky, T. (1951). Mendelian populations and their evolution. *In* "Genetics in the 20th Century" (L. C. Dunn, ed.), pp. 573-589. MacMillan, New York.

Duvick, D. N. (1975). Using host resistance to manage pathogen populations: A corn breeder's commentary. *Iowa State J. Res. 49,* 505-512.

Duvick, D. N. (1977). Major United States crops in 1976. *Ann. N. Y. Acad. Sci. 287,* 86-96.

Food and Agriculture Organization of the United Nations. (1977). *1976 FAO Productions Yearbook, Vol. 30,* Food and Agriculture Organization of the United Nations (FAO), Rome.

Frankel, O. H., and Bennett, E., eds. (1970). "Genetic Resources in Plants--their Exploration and Conservation." Blackwell, Oxford.

Frankel, O. H., and Hawkes, J. G., eds. (1975). "Crop Genetic Resources for Today and Tomorrow." Cambridge Univ. Press, Cambridge.

21

Galinat, W. C. (1971). The origin of maize. *Ann. Rev. Genetics 5,* 447-478.

Galinat, W. C. (1972). Preserve Guatemalan teosinte, a relict link in corn's evolution. *Science 180,* 323.

Galinat, W. C. (1974). The domestication and genetic erosion of maize. *Econ. Bot. 28,* 31-37.

Galinat, W. C. (1977). The origin of corn. *In* "Corn and Corn Improvement" (G. F. Sprague, ed.), pp. 1-47. Amer. Soc. Agron., Madison.

Gerstel, D. U. (1945). Inheritance in *Nicotiana tabacum* XX. The addition of *Nicotiana glutinosa* chromosomes to tobacco. *J. Hered. 36,* 197-206.

Goodman, M. M., and Bird, R. McK. (1977). The races of maize IV: Tentative grouping of 219 Latin American races. *Econ. Bot. 31,* 204-221.

Grant, U. J., Hatheway, W. H., Timothy, D. H., Cassalett D., C., and Roberts, L. M. (1963). "Races of Maize in Venezuela." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 1136, Washington, D. C.

Grobman, A., Salhuana, W., and Sevilla, R., in collaboration with Mangelsdorf, P. C. (1961). "Races of Maize in Peru." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 915, Washington, D. C.

Hammons, R. O. (1976). Peanuts: genetic vulnerability and breeding strategy. *Crop Sci. 16,* 527-530.

Harlan, J. R. (1972). Genetics of disaster. *J. Environ. Quality 1,* 212-215.

Harlan, J. R. (1975a). "Crops and Man." Amer. Soc. Agron., Madison.

Harlan, J. R. (1975b). Our vanishing genetic resources. *Science 188,* 618-621.

Harlan, J. R., and de Wet, J. M. J. (1971). Toward a rational classification of cultivated plants. *Taxon 20,* 509-517.

Harlan, J. R., Brooks, M. H., Borgaonkar, D. S., and de Wet, J. M. J. (1964). Nature and inheritance of apomixis in *Bothriochloa* and *Dichanthium*. *Botan. Gazette 125,* 41-46.

Harlan, J. R., de Wet, J. M. J., and Price, E. G. (1973). Comparative evolution of cereals. *Evolution 27,* 311-325.

Hatheway, W. H. (1957). "Races of Maize in Cuba." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 453, Washington, D. C.

Hernandez X., E., and Alanis F., G. (1970). Estudio morfologico de cinco nuevas razas de maíz de la Sierra Madre Occidental de Mexico: Implicaciones filogenéticas y fitogeográficas. *Agrociencia 5,* 3-30.

Hernandez X., E., and Randolph, L. F. (1950). "Descripción de los Tripsacum diploides de Mexico: Tripsacum maizar y Tripsacum zopilotense spp. nov." Fol. Tec. No. 4. Ofic. Estud. Esp. Sec. Agr. y Ganad. Mexico, D. F.

28

Hussaini, S. H., Goodman, M. M., and Timothy, D. H. (1977). Multivariate analysis and the geographical distribution of the world collection of finger millet. *Crop Sci. 17,* 257-263.

Iltis, H. H. (1972). The extinction of species and the destruction of ecosystems. *Amer. Biol. Teacher 34,* 201-205.

Information Sciences/Genetic Resources Program. (1977). "Maize Directory--1977." IS/GR, Univ. Colorado, Boulder.

International Board for Plant Genetic Resources (1975). "The Conservation of Crop Genetic Resources." Whitefriars Press, London.

International Board for Plant Genetic Resources (1976). "Priorities Among Crops and Regions." Food and Agriculture Organization of the United Nations (FAO), Rome.

Kashiwakura, Y., and Paterniani, E. (1972). O armazenamento de sementes de milho em dessecador com silica gel e em câmera seca, e o seu efeito na preserva ção da viabilidade de sementes de milho. Universidade de São Paulo Escola Superior de Agricultura "Luiz de Queiroz," Instituto de Genetica. *Relatorio Cientifico 6,* 38-48.

Levings, C. S. III, and Pring, D. R. (1976). Restriction endonuclease analysis of mitochondrial DNA from normal and Texas cytoplasmic male sterile maize. *Science 193,* 158-160.

Levings, C. S. III, and Pring, D. R. (1977). Diversity of mitochondrial genomes among normal cytoplasms of maize. *J. Hered. 68,* 350-354.

Mangelsdorf, P. C. (1966). Genetic potentials for increasing yields of food crops and animals. *Proc. Nat. Acad. Sci. (U.S.) 56,* 370-375.

Mangelsdorf, P. C. (1974). "Corn: Its Origin, Evolution and Improvement." Harvard Univ. Press, Cambridge.

Mangelsdorf, P. C., MacNeish, R. S., and Galinat, W. C. (1964). Domestication of cron. *Science 143,* 538-545.

Mangelsdorf, P. C., MacNeish, R. S., and Galinat, W. C. (1967). Prehistoric wild and cultivated maize. *In* "The Prehistory of the Tehuacan Valley, Volume One. Environment and Subsistence." (D. S. Byers, ed.), pp. 178-200. Univ. of Texas Press, Austin.

Marshall, D. R., and Allard, R. W. (1970). Maintenance of isozyme polymorphisms in natural populations of *Avena barbata*. *Genetics 66,* 393-399.

Oka, H., and Morishima, H. (1971). The dynamics of plant domestication: Cultivation experiments with *Oryza perennis* and its hybrid with *O. sativa*. *Evolution 25,* 356-364.

Paterniani, E., and Goodman, M. M. (1978). "Races of Maize in Brazil and Adjacent Areas." International Maize and Wheat Improvement Center (CIMMYT), Mexico City.

29

Pring, D. R., and Levings, C. S. III. (1978). Heterogeneity of maize cytoplasmic genomes among male-sterile cytoplasms. *Genetics 89,* 121-136.

Pring, D. R., Levings, C. S. III., Hu, W. W. L., and Timothy, D. H. (1977). Unique DNA associated with mitochondria in the "S" type cytoplasm of male sterile maize. *Proc. Nat. Acad. Sci. (U.S.) 74,* 2904-2908.

Ramírez E., R., Timothy, D. H., Díaz B., E., and Grant, U. J., in collaboration with Nicholson C., G. E., Anderson, E., and Brown, W. L. (1960). "Races of Maize in Bolivia." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 747, Washington, D. C.

Randolph, L. F. (1970). Variation among *Tripsacum* populations of Mexico and Guatemala. *Brittonia 22,* 305-307.

Roberts, L. M., Grant, U. J., Ramírez E., R., Hatheway, W. H., and Smith, D. L., in collaboration with Mangelsdorf, P. C. (1957). "Races of Maize in Colombia." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 510, Washington, D. C.

Sears, E. R. (1956). The transfer of leaf-rust resistance from *Aegilops umbellulata* to wheat. *In* "Genetics in Plant Breeding." Brookhaven Symposia in Biology *9,* 1-22.

Smith, H. H. (1971). Broadening the base of genetic variability in plants. *J. Hered. 62,* 265-276.

Stebbins, G. L. (1950). "Variation and Evolution in Plants." Columbia Univ. Press, New York.

Timothy, D. H. (1972). Plant germplasm resources and utilization. *In* "The Careless Technology: Ecology and International Development." (M. T. Farvar, and J. P. Milton, eds.), pp. 631-656. Natural History Press, Garden City, N. J.

Timothy, D. H., Pẽna V., B., and Ramírez E., R., in collaboration with Brown, W. L., and Anderson, E. (1961). "Races of Maize in Chile." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 847, Washington, D. C.

Timothy, D. H., Hatheway, W. H., Grant, U. J., Torregroza C., M., Sarria V., D., and Varela A., D. (1963). "Races of Maize in Ecuador." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 975, Washington, D. C.

Wade, N. (1972). A message from corn blight: The dangers of uniformity. *Science 177,* 678-679.

Webster, O. J. (1976). Sorghum vulnerability and germplasm resources. *Crop Sci. 16,* 553-556.

Wellhausen, E. J., Roberts, L. M., and E. Hernandez X., in collaboration with P. C. Mangelsdorf. (1952). "Races of Maize in Mexico." Bussey Institution, Harvard Univ., Cambridge.

Wellhausen, E. J., Fuentes O., A., and Hernández Corzo, A., in collaboration with Mangelsdorf, P. C. (1957). "Races of Maize in Central America." Nat. Acad. Sci.-Nat. Res. Counc. Publ. 511, Washington, D. C.

Wilkes, H. G. (1967). "Teosinte: The Closest Relative of Maize." Bussey Institution, Harvard Univ., Cambridge.

Wilkes, H. G. (1972a). Maize and its wild relatives. *Science 177*, 1071-1077.

Wilkes, H. G. (1972b). Genetic erosion in teosinte. *Plant Genet. Resources News. 28*, 3-10.

Wilkes, H. G. (1977). Hybridization of maize and teosinte, in Mexico and Guatemala and the improvement of maize. *Econ. Bot. 31*, 254-293.

Wilkes, H. G., and Wilkes, S. (1972). The green revolution. *Environment 14*, 32-39.