

FOR CONFERENCE USE ONLY
Not For Quotation

PLANT GERMPLASM RESOURCES AND
UTILIZATION IN INTERNATIONAL
DEVELOPMENT

D. H. Timothy

0554
CONFERENCE ON THE
ECOLOGICAL ASPECTS OF
INTERNATIONAL DEVELOPMENT
AIRLIE HOUSE, WARRENTON, VA. DEC. 9-11, 1968

"International development" is a nebulous term, and its meaning seems to reflect the opinion, interest and profession of the beholder. The literature is of such prodigious nature that an "authority" can be found to substantiate almost any viewpoint. This being the case, I call forth the brothers Paddock (29), Theodore W. Schultz (37) and W. David Hopper (18). If a synthesis of these writings can be formulated, it is this: Agricultural potential is a source and as such must be transformed from a traditional way of life into a dynamic conglomerate of agribusiness, beginning now with quick payoff items of improved seeds and cultural practices which are based on research. Other things can come later. This seems to be realistic. The infrastructure in other sectors can come later, since their usefulness and economic return are incongruous in the midst of prolonged and widespread famines. The President's Science Advisory Committee Report on "The World Food Problem" (35), probably the most comprehensive study made, concluded:

"1. The scale, severity, and duration of the world food problem are so great that a massive, long-range, innovative effort unprecedented in human history will be required to master it.

"2. The solution of the problem that will exist after about 1985 demands that programs of population control be initiated now. For the immediate future, the food supply is critical.

Paper number _____ of the Journal Series of the North Carolina State University
Agricultural Experiment Station, Raleigh, North Carolina.

Professor of Crop Science, North Carolina State University, Raleigh, North Carolina.

"3. Food supply is directly related to agricultural development and, in turn, agricultural development and overall economic development are critically interdependent in the hungry countries.

"4. A strategy for attacking the world food problem will, of necessity, encompass the entire foreign economic assistance effort of the United States in concert with other developed countries, voluntary institutions, and international organizations."

The changing currents of emphasis in development programs over the past 20 years have illustrated many errors of policy, judgment, and execution. From these, and a host of other ills, we hopefully have learned that success is difficult, perhaps unattainable, under the tenets of any one particular profession, and probably doomed with a policy of one to two-year personnel and funding in any or all sectors. However, there has been, over this same 20-year period, an outstanding example of continuous and concentrated effort - that of the cooperative agricultural programs of the Rockefeller Foundation. Many of the examples and data from these programs will be used in this presentation.

Substantial increases in food supply are possible in the near future and over the long term. In discussing germplasm resources and utilization, some distinction will be made between germplasm utilization in international development in the broadest sense; i. e., the policy of a government for total development which might require several generations, or that which must stave off the impending famines and chaos of the shorter term during the last quarter of this century. Procedures for either course of action would be different, but both would be based upon demonstrated biological principles. In the end, progress will depend upon a thorough knowledge of the species, its variability and evolution, environmental conditions under which the plant

will or will not grow, and then being able to change or manipulate any or all of those factors.

It has been estimated that man has used 3,000 or more plant species for food, and has cultivated at least 150 species to the extent that they have entered into commerce (24). This same authority states that of these, about 15 species of plants actually feed the world. "These include five cereals: rice, wheat, corn, sorghum, and barley; two sugar plants: sugar cane and sugar beets; 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."

These crops and others have long been associated with man. The earliest records, about 9,000 years ago at Jarmo in the Iraqi Kurdistan, indicate the reaping and grinding of two-row barley and two forms of wheat by the villagers (6). Plant domestication was advanced, although plant selection had not been carried far. The paleoethnobotanical studies of Helbaek (17) have shown the effect of man's early migrations on distribution of useful plants and animals. While field peas, lentils and vetch types were found at Jarmo, it is not certain that they were domesticated at that early date. However, by 5000 BC, flax was grown in the foothills of the Kurdish mountains and the plains of Mesopotamia and Egypt. Between the third and fourth millenium BC, lentils were in Egypt and Hungary, and Swiss deposits have yielded pea and blue betchling remains. The horse bean was in the Mediterranean area between 3000 and 2000 BC and had arrived in Britain by the first millenium BC. Thus, with the domestication, selection, and transport of plants and animals, stone age man began the Agricultural Revolution. By continuing this process, moving to more fertile areas, increasing productivity, and accumulating surpluses, the people of southern Mesopotamia had begun to support an urban

civilization. We still return to this fertile crescent for collecting germ-plasm. Many of the wheats and their wild relatives are endemic there. The remarkable accomplishments of late stone age man in domesticating plants may never be equalled. Oddly, their agriculture built a civilization. Now, our civilization must build an agriculture. With the possible exceptions of the bread wheats and some of the leguminous pulses, the plants listed in Table 1 were domesticated by Neolithic man (14). Furthermore, with the probable exception of the pumpkin, none of these crops is indigenous to the United States. The agriculture of the United States, the most productive in the world, is based on introduced plants. Not one of the commercially important crops is native to this country. Peanuts and soybeans are recent introductions, and in many areas of the country the soybean is now pushing corn from its foremost position.

Man, in his migrations and travels, has introduced food plants into new areas ever since he became an agriculturist. Many of his plantings were complete failures or, at best, limited successes, but over many hundreds of years, natural selection, coupled with mass selections for desired types, has resulted in the widespread cultivation of several kinds of plants. Thus, rice and millets spread throughout Asia and Africa. The small grains were taken from the fertile crescent of the Middle East to many areas of the Old World. In the New World, corn, potato, and bean culture expanded throughout the hemisphere. The exploitation of the Americas and the circumnavigations of continents and the globe, led to a flurry of plant interchange which is still going on.

Introductions from the New World to the Old have had many successes and often unexpected results. The importation of the white potato from South America to Europe contributed indirectly to the large number of Irish

immigrants to this country. The spectacular growth of the potato in Ireland led to its becoming a staple, people had more to eat than ever, and the population increased. Then a fungus, for which the introduced potato had no resistance, struck and wiped out the potato plants. The Irish Potato Famine drove many people to our shore.

Table 1. A list of some major crop plants (after Harlan, 1956).

Gramineae	Solanaceae
Wheats, bread wheat, emmer, einkorn	Potato
Rice	Tobacco
Corn	Tomato, pepper, egg plant
Sugar cane	Cucurbitaceae
Sorghum	Pumpkins, melons, etc.
Barley	Euphorbiaceae
Milletts, Eleusine, teff, other grains	Cassava
Forages, Thatch bamboo	Convolvulaceae
	Sweet potato
Leguminosae	Malvaceae
Soybeans	Cotton
Beans, common, mung, lima, etc.	Palmaceae
Chickpea	Coconut
Cowpea	Date
Garden pea	Musaceae
Lentil	Banana
Peanut	Plantain
Alfalfa, clover, others	

That man was able to introduce crops to new areas and make selections of more desirable types was due to variability. A breeding program must be based upon variability to succeed. Without variation, there would be nothing to select for except new mutations - every plant would be the same. A breeder, therefore, must be concerned about the natural variation of a crop, where this variability came from and via what route - either by related species or direct transport. He must know of the primary centers of diversity and origin, as well as secondary centers of diversity. These centers are the fountain head of genetic material upon which plant improvement will succeed or fail.

Plant improvement, per se, is generally based on the inherent variation of genetic or inherited traits within a species and its relatives. Plant production is based on the genetic potential within a strain or variety, the environment in which that plant is grown, and the interaction of that genetic potential with differing environmental factors. In other words, the performance of a plant is a function of its genetic make-up and the environment.

Plant improvement or genetic progress is limited by the genetic variability of the species and its relatives, and further limited by the methods employed to manipulate the variability at our disposal. To increase variability, collections have been obtained by sporadic and insufficient expeditions, and by correspondence with collaborators at home and abroad. From such introductions, which represent a fraction of the species variability "in toto", only a few which superficially have the best characteristics are selected and incorporated into breeding programs. If the introduced material does not flower because of poor response to photoperiod, or if it is attacked by one of the prevalent diseases or pests, or if it just doesn't look good, it is often discarded. If interest in a particular entry is not high, the collection is also often lost by poor shelf life of the seed. For

cross-pollinated plants, the proof of the parent is its progeny, and yet, a great deal of material has been discarded on the basis of what it looked like.

Harlan (15) gives an excellent example of the value of collections and what happens when they are not maintained. The melon industry was seriously threatened by attacks of mildew. At the growers' insistence that something be done, a project was established for the exploration and assemblage of a world collection. Mildew resistant sources were found and the susceptible types were discarded. "After a period of breeding to introduce resistance into types that produced, shipped, and marketed well and which received good public acceptance, the problem was, in fact, rather satisfactorily solved. No sooner had the bulk of the susceptible material been thrown away than attacks of a virus began to threaten the industry. Much of the material had to be assembled a second time, and the entire procedure repeated to solve this problem. If, in the process of breeding for virus resistance the second collection is largely discarded, then still a third collection will no doubt be required to solve the next problem that comes up."

There are many difficulties encountered in maintaining a world collection. Individual plants may require a lot of space, and controlled pollination may be necessary to maintain the integrity of the varieties. "Plant exploration is relatively inexpensive, and it may be that the procedure just mentioned is really the most economical and efficient. Unfortunately, the geographic centers of diversity upon which we have depended so much in the past for our sources of germplasm are in great danger of extinction. Modern agriculture and modern technology are spreading rapidly around the world . . ." (14). New fertilizer-responsive and high yielding varieties are replacing the old mixed or unresponsive populations that have been grown, in some cases, for 2,000 to 5,000 years. Harlan (14) says of his exploration in southern Turkey

during 1958 ". . . I found great acreages of flax planted to a single variety. It was a selection of Argentine origin resistant to rust. From one end of Cilicia to the other I could not find a single indigenous variety although this very area had at one time been a center of diversity for flax." Another illustration is from Colombia. The Cauca Valley is roughly the size of Puerto Rico. It is of deep, rich, level soil, in which a corn race called *Comun* had been grown for many, many years. Yet in 1960, only 10 years after the Rockefeller Foundation and the Colombian Ministry of Agriculture initiated its agricultural program in that country, we could find only three small plantings of this variety. I have recently been told that the variety is presently not planted by any farmers; it has been replaced completely by improved varieties and hybrids (7). In this case, however, the germplasm had been collected and preserved, as it was one of the first steps in developing the Colombian corn program.

When the Rockefeller Foundation began its cooperative corn program with the Mexican and Colombian governments, it was readily apparent that a survey of the indigenous maize varieties was needed to serve as an inventory of available material for breeding. Out of this work and the interest of the National Academy of Sciences - National Research Council, funds were made available for the collection and preservation of as many native varieties of corn as possible (11). These are now preserved in germplasm banks in Brazil, Colombia, Mexico, and the United States, and total more than 12,000 collections. They represent what was deemed to best serve the indigenous needs of a traditional agriculture from sea level to 3,810 m. elevation near Lake Titicaca in Bolivia and Peru, from the dry tropics to those having rainfall up to 11,000 mm (30) along the west coast of Colombia, and from Lat. 45°S near Chiloe Island in Chile to almost Lat. 50°N on the Gaspé Peninsula of New Brunswick, Canada.

The value of these collections is readily apparent by the simple fact that they are already irreplaceable. Land reform, social changes, and new agricultural technology have altered the land use patterns so radically in the 15 or 20 years since the collections were made, that they could not be duplicated. The Germ Plasm Banks in which these collections are stored and maintained are already serving their purpose, as a repository of readily available living material. Exceptionally high resistance to the type of corn rust prevalent in Kenya was found in a Colombian variety (32k). An Ecuadorian collection has contributed greatly to increased yields in many areas when combined with local maize.

Table 2.

	kg/ha.	Yield in % of local variety
Kenya (23)		
Kitale II	3900	100
Ecuador 573	2780	71
Kitale II x Ecu. 573	5900	151
Indonesia (40)		
Indian var retz x Colombian variety	6528	144
Recommended variety	4519	100

An improved variety of the Mexican corn Tuxpeño was released in northern Honduras in 1963, and by the end of 1964 the native varieties had almost disappeared (34). Other areas where Latin American corns have been useful include India, Algeria, Thailand, and so on.

When the collections were begun in Mexico and compared for productivity, disease resistance and other agronomic characteristics, the need was apparent

for taxonomic order out of a bewildering array of diversity. With additional study it became possible to delineate similarities and relationships among these varieties, and to group them into definable and recognizable natural races. This outstanding work was published as "Races of Maize in Mexico" (32a). From that experience, similar collections were deemed necessary throughout the Western Hemisphere. This effort led to a series of monographs which, taken together, attempt to define and reduce to workable levels a cultivated crop upon which several civilizations had been built (32).

Maize and the other cereal grasses produced over one billion tons of grain in 1965. The forage grasses supported over two and three-quarter billion animals (13). The grass family truly replenishes the world's feedbag.

It has been estimated that grasslands comprise 24% of the earth's vegetative cover (39). However, the grasses are geographically ubiquitous. In addition to their dominance in prairies and steppes, they are also found in forests, swamps, and deserts. As a group, they are significantly noteworthy in their ability to adapt themselves to diverse ecological conditions.

". . . It is a far cry indeed from tropical forests where grasses constitute less than 0.5% of the ground cover - and this mainly where some natural or artificial breakage has occurred in the tree canopy - to the prairies and pampas where grasses may make up 99.5% of the ground cover. In the former the grasses appear to have little obvious ecological significance; in the latter they are dominant and determine both the aspect and the economics of the vegetation." (16).

The ecological factors determining the occurrence of natural grasslands are still debated, and apparently vary among regions and types of grassland. Whether grasslands develop within very broad climatic limits ". . . is determined by many other factors, including microclimate (especially as affected by local topography), soil differences, and the effects of fire and grazing. Since these factors operate differently from place to place, and indeed from time to time, it is hardly surprising that no very satisfactory general relationship has been

determined between climate and grassland development, and it is questionable whether tropical grasslands, at least, can be regarded as climatically controlled. . ." (16).

Cultivated grasses are found well outside the climatic limits of their natural distribution since the cultivation process alters the environment, and the plants are not as dependent on the natural environment for growth and survival. Of perhaps 10,000 grass species, only about 40 are used on an important scale as cultivated pasture grasses. These are widely used outside their limits of natural distribution. Many of the grasses comprising the grasslands of the world have not been successful domesticates. They have evolved along with grazing animals. Their environment, at least when compared to cultivated grasses, is relatively stable. The most successful grasses as domesticates have been those occurring naturally in and around forest margins and woodlands. These areas are often disturbed sites - caused by flooding and washing, fire, uprooted trees, etc., and can be considered as floristic and ecological transition zones. The grasses which form a part of this sub-climax are opportunistic and aggressive, a highly desirable trait for any pasture grass.

The use of intensely managed pastures is a relatively new innovation of man, and has been going on for only a few hundreds of years. In this regard, the advances made with the grasses of temperate climates have been notable. Many of the Phleum, Festuca, Dactylis, Bromus, Poa, have been developed under the rigors of intensive agriculture, notably in Europe. Intensive grassland agriculture in tropical or sub-tropical areas has been non-existent until the last 50 to 100 years. Are we so naive to conclude that we have been as efficient in a century or so of selecting, domesticating, and improving wild forage grasses as our forebears, who, since the dawn of man, selected, domesticated and improved our food crops? I believe not. The exploitation of natural ranges on an extensive basis is another matter. But, assuming that we have not exhausted the possibilities of finding new domesticates of forage grasses for

intensive management, how do we go about it? It is impossible that we collect and preserve everything, yet every year that we delay, more of the marginal and transitional ecological areas are disappearing under increased agricultural pressures - areas in which many of the sub-climax grasses can be found.

One of the problems in plant introduction is in deciding which regions are most likely to contain useful material. Several schemes, based on agroclimatic homologues have been devised and suggested as guides for introduction (28,31). These have generally been based on temperature and rainfall patterns, day-degrees, length of growing season, and day length. An agrostological index has also been formulated, based on relative frequencies of grass species to determine the climatic and ecological conditions of a given region (15). From this, agroclimatic or bioclimatic homologues have been used for purposes of plant introduction. At the tribe level and in early phases of an introduction program they have been useful, i.e., Australia. There are weaknesses in the system, and at the generic and specific levels these schemes are not highly successful. The large amounts of genetic diversity within a genus or species, responding to various climatic and ecological conditions, negates the generalities of the above approaches. For example, 360 species of grasses have been found in North Carolina (4). They represent 13 of the 14 tribes of grasses of the world. However, there are 97 species of Panicum and 22 species of Paspalum (33% of the grasses in the state) from one tribe which is tropical in its origin and affinities. Yet one of the most promising experimental forage introductions in the state, Pennisetum flaccidum, originates from the Himalayan foothills at elevations from 1600 m. to 4300 m. To my knowledge, it has never been used anywhere as a seeded pasture, and only one accession has been introduced to the United States (10). Pennisetum is a tropical genus, and except for the above collection, we have found no other species that can survive the winters of North Carolina and is suitable for animals. There are other examples which illustrate that ecological and environmental generalizations, while help-

ful, are not sufficiently reliable to be used with any degree of confidence in agricultural development programs, except in very preliminary stages. Dactylis, orchardgrass, is usually thought of as a widely dispersed temperate grass used in Europe and the northeastern United States, flowering once early in the growing season and growing from basal tillers. Yet there is a subspecies from the Canary Islands, which has branched stems, initiates flowers from axillary buds, and has truly perennial stems. It flowers almost continuously during the growing season, and is killed by frost.

No predictive process or index will serve in lieu of on-site or adaptive research. In some cases, successful introduction almost appears to be a hit or miss situation, as in the previous example. One reason for this is due to the enormous plasticity with a genus and a species. This is readily apparent when the adaptive range of a cultivated species is considered. This is due to genetic variability, of which there may be considerable amounts within many locally adapted populations. Additional variation, as a consequence of genotype-environment interactions, is expressed when rooted cuttings are placed under various environmental conditions (12, 25, 26).

From the ecological point of view, flowering and seed production are a response to any one or a combination of factors such as photoperiod, temperature, or rainfall. In any given locality, ecotypes which best conform to local conditions have been selected for years or centuries. The ecology of such natural populations is entirely different from that of a cultivated monoculture of a food plant. Yet while most of the pasture grasses have not been completely domesticated, we attempt to impose upon them a set of biological conditions which have been used in growing our highly domesticated and cultivated food plants. The cultivated food plants may sometimes be seen as escapes in weed patches and disturbed sites for a few seasons, but they cannot persist outside the artificial environment that man has created for them and for which they have been selected and bred. On the other hand, the wild or semi-domesticates

such as forage grasses escape to adjacent sites and subsequently disperse over wider areas. They establish themselves as an integral part of the natural system, and persist in favorable niches in one or more of the vegetational levels of succession. Examples of this in the United States are Kentucky bluegrass, Poa sp.; orchardgrass, Dactylis; tall fescue, Festuca; Johnsongrass, Sorghum; bermudagrass, Cynodon; and in South America Kikuyu, Pennisetum; and guineagrass, Panicum. Some of these introduced grasses have become so successful and ubiquitous as to be declared noxious weeds. However, improved varieties of these same species form a major part of the beef and dairy industries of many of those same areas.

It is interesting to speculate what we might be able to obtain from forages if they were as developed in the "cultivated" sense as are our food crops. The latter are cultivated in a finely tuned ecosystem in which there is harmony between the genotype and environment. Elephantgrass, or napiergrass, Pennisetum purpureum, is not highly domesticated. However, under excellent growing conditions it will yield over 270 tons of green fodder per hectare (45,47). Assuming a dry matter content of 22.3% for napiergrass and 30.6% for green roughage corn (26), napiergrass has yielded 60 tons of dry matter. Corn would have had to yield 196 tons of fodder to equal that amount of dry matter. Unfortunately, dry matter alone is not critical. An important criterion of feeding value is total digestible nutrients, TDN. Using values of TDN of 15.0% for elephantgrass and 28.5% for flint corn with ripe kernels, (27), elephantgrass yielded 40.5 tons of TDN per hectare in the above example. Two crops of corn yielding 60 tons of silage per harvest -- 30 tons are now attainable and 40 tons might be anticipated in the future -- would yield 34.2 tons of TDN. Such a corn silage yield would approximate 600 bushels/acre of grain. These calculations are somewhat unrealistic and subject to serious criticism. They do, however, illustrate that forages are usually overlooked in development planning. They are also mismanaged at the production level.

Dairy production is usually limited to some degree of intensive management. Beef production is relegated to areas of marginal land, or land which can be put to no other use, and it is managed in an extensive fashion. This does not necessarily have to be so. On steep clay hillsides in the humid mountain area of Puerto Rico, an average gain of over one ton of beef per hectare was produced experimentally on elephantgrass (45). About one ton/ha of 14-8-4 was applied, and grazing was done on a three-week rotation. Similar intensively managed grass pastures in this area are being used in commercial operations. "On one farm....heavily fertilized, intensively managed Guinea, Pangola, and napiergrass pastures are carrying two steers per acre in the winter and three steers throughout the remainder of the year, and producing close to 1,000 pounds of gain in weight per acre yearly." (45).

The key here is intensive management based on adaptive concurrent research with forages and animals. It is expensive research in terms of land, animals and personnel. Cattlemen are notoriously poor agronomists, and agronomists are equally poor animal scientists, so the requirements for team research are essentially doubled in terms of personnel inputs. The philosophic differences of the agronomist and animal scientists, as ancient as the conflict between nomad and agriculturist, are not breached in most plans for development. Most of the research is on animals or on forages, but very little is on animals and forages. Just as plant breeders select varieties for response to fertilizers, it seems logical that animals might be selected which respond better to forages than to concentrates. Too much animal selection has been practiced using diets of high energy concentrates. One hopes that when the concentrates are needed to feed people, that the animals will perform equally well on a roughage diet. The situation has been promulgated in the United States by surplus grain, with prices such that grain can be fed economically. What the future holds is unknown, but on land not amenable for cultivation, forages and cattle can be used. It is a matter of determining how to use them best in any particular region.

To do this requires time and trained personnel.

Food needs over the next several decades will not wait the 15 to 25 years required to develop a corps of trained scientists in sufficient numbers to solve the problem. However, while they are being trained, interim programs of adaptive research can be initiated with experienced scientists and available germplasm. Of the several outstanding examples of this approach, the most noteworthy is that involving Dr. Norman E. Borlaug of the Rockefeller Foundation, the International Maize and Wheat Improvement Center (CIMMYT), and Pakistani scientists and officials. Borlaug's account (5) of this program, the 20 years' work in Mexico which preceded it, and subsequent programs in other countries is required reading for anyone interested or involved in producing more food. I have drawn freely from his presentation.

In 1961 and 1962, several young Pakistani wheat scientists who had received practical training in Mexico, returned to their country with many small samples of dwarf wheats from the Mexican program. Some of these were released varieties and others were still in the experimental stages. The best adapted germplasm was selected for further research and seed increase. "Perhaps 75 to 80% of the research done in Mexico on cultural practices and fertilizers was valid in Pakistan. Research done in Pakistan while the imported seed was being multiplied provided the necessary information to cover those gaps where the Mexican data were not valid." (5). In addition to having improved germplasm capable of responding to 120 kilos of nitrogen per hectare (the older varieties showed no response above 50 kilos of nitrogen because of lodging), an entire new technology was introduced as a package to the farmer. Within the package were included proper land preparation, date of seeding, depth of seeding, time and rate of fertilizer application, herbicide and pesticide use, etc. Perhaps just as important was that the scientists and extension people could and would do these things because they had been trained to do so. During the 1964-65 season, 10 hectares were planted with the Mexican wheats, 11,000 in 1966-67

and 3,000,000 in 1967-68. But what has happened to wheat production during this time? It rose from a previous high of 4.6 million tons in 1965 to an estimated 7 million tons in 1968 (5). Borlaug estimates that 43% of this harvest was due to the dwarf varieties and new technology on only 20% of the acreage sown to wheat. National average yields rose in the last year from 802 kilos per hectare to 1,167 kilos per hectare.

"Pakistan has achieved self sufficiency in three years after launching its accelerated wheat production programme, whereas it took Mexico 13 years to achieve this result. . . Moreover, it has the thrust, scientific knowhow, and technology to maintain self sufficiency for the next decade if aggressive leadership and sound fiscal policies are followed. . . Experience gained in Mexico, permitted holder action in Pakistan, and many of the pitfalls encountered in Mexico were avoided." (5). Similar efforts are now being exerted in India, Turkey, and Afghanistan.

I previously stated that varieties, technique, research, etc., could not be directly transported, and yet these above examples would seem to refute that statement. They do not, however, for several reasons: 1) The programs were directed by experienced, competent, mature scientists who intimately knew the technology needed and the genetic material at their disposal. 2) On-site research was done correctly as a screening procedure. 3) Additional on-site research was done to fill gaps where "transplanted" procedures or technique were not applicable.

Behind all this was 20 years of research in the Mexican wheat program. Many of the wheats in that program are now insensitive to photoperiod. In addition, they are widely adapted to other environmental conditions. To speed up the breeding procedure for improved varieties, two generations of selection are practiced in Mexico. The winter nurseries are in Sonora at 28° Lat. N., a few meters above sea level, and grown in the winter. The second generation is seeded in May near Toluca at 2600 m. elevation and 18° Lat. (5). At the winter

nurseries, daylength is about 10.4 hours on November 21 and then decreases to 10.2 on December 21. It begins to increase in succeeding months to 10.4, 11.1, and 12.0 hours. Near Toluca, daylength is 13 hours on May 21, it increases to 13.2 hours on June 21, then decreases each succeeding month to 13.0, 12.6, and 12.0 hours.

Two generations each year can be obtained with many crops within the tropics. Although there are consistent differences in daylength, temperature, rainfall distribution, etc. during the two seasons, selection for yield and other desired characters will tend to broaden the range of adaptability of those entries which come through the screening process. While some would argue that more progress toward greater yields would be obtained by selecting for a particular set of environmental conditions, i.e., a separate selection program for each growing season of the year, there is increasing evidence that homeostasis (a kind of physiological buffering system enabling the organism to perform equally well under reasonable environmental differences) occurs in plants. Furthermore, since it is impossible to breed varieties for the multitudinous environments which exist, it is foolish not to take advantage of a system which will halve the time lag until a variety release is possible. In addition, the life of a variety is relatively short, and will vary from three to five years. Perfection in a variety is impossible, so the plant breeder selects the best line/s available under the circumstances and releases it.

The wide scale use of a newly released variety does not call for the cessation of research for developing still more varieties. This is especially so with the use of modern cultural methods. Thicker plantings, denser stands, increased rates of fertilization, with or without irrigation, weed-free fields, all combine to create a new ecosystem. The microenvironments within this system may now be more favorable to the development of a new array of disease organisms and insect pests. If the organisms are able to establish and increase to what might be called a critical mass, a crop failure and perhaps famine, are

just around the corner. This phenomenon will become more important when a single variety, or a group of closely related varieties, is planted over a wide area. The researchers breeding new lines of corn, rice, or wheat at the international or regional centers are well aware of the danger, and they are continually recording insect and disease damage on breeding material. They are often able to forecast which diseases might become pandemic and then, given time, they change the genetic composition of the variety or release a new one. In some cases, a variety may be on the shelf for just such an event. In others, it may be necessary to screen the collections in the germ plasm banks to find the necessary tolerance or effective resistance to the organism in question, and then incorporate the resistance into an acceptable agronomic variety.

Just as man is stricken by different strains of influenza or encephalitis, so, too, are plants infected by different strains or races of disease. The causal organism of wheat stem rust has many different physiological races, expressed by differences in degree of pathogenicity on a set of differential host varieties. Once a race becomes established, its prevalence is determined by favorable environmental conditions, and the varieties being grown. Changes in race structure of the rust population can be very rapid. However, the devastating attacks of rust are not as capricious as they appear to be, once the underlying causes are known.

The wheat rust epidemic in 1916 destroyed about 300 million bushels of wheat in the United States and Canada (42). Rust resistant durum wheats were substituted for the susceptible hard red spring wheats. New rust races soon appeared, and the durums were then vulnerable. In 1926 a new wheat was released, and then in 1928 rust race 56 began to appear. It caused the rust epidemic in 1935. Beginning in 1934, a series of wheats resistant to the major rust races was released, and except for 1935 and 1937 there was no serious outbreak of rust for many years. "These new varieties were highly resistant to

all the North American races of rust. During this period the number of prevalent races decreased to three or four, and no major epiphytotics occurred" (1). But during this time small quantities of several rust races had been observed on or near the alternate host of the pathogen, barberry. One of these races, 15 B, observed since 1938 in the northern United States, ..." suddenly exploded in the United States and Canada in the summer of 1950 and ruined late fields of varieties that had been immune for almost a decade. High winds carried race 15 B into Mexico in the fall of 1950; it survived the winter on fall-sown wheat in a few places, then multiplied fast on spring-sown wheat in the exceptionally wet summer of 1951... Race 15 B had smashed the Hope and New thatch types of resistance" (41).

The necessity and usefulness of having diverse and broad samples of germ-plasm available in a breeding program was readily apparent in 1951. "Some 60,000 varieties and lines from the Mexican program and another 6,000 from the World Wheat Collection of the United States Department of Agriculture were grown and evaluated at..." four locations in Mexico... "In this vast test, only four varieties grown commercially in North America were resistant to stem rust, and all were Mexican made... and they all have Kenya-type resistance." (41).

Unexpectedly, race 139, known for 20 years, struck these varieties in 1953. This race had been rare and "...unimportant practically, although it had excited curiosity because of its exceptionally weak parasitism and its persistence in minute quantities in northern Mexico. But it now demonstrated far more strength than it had shown previously; it knocked out varieties that the generally stronger race 15 B could not hurt. Race 139 (and possibly the closely related 49) had the weapons for breaking through the Kenya-type resistance, just as 15 B had the weapons for breaking through the" Hope and New thatch resistance.

"But stem rust was not yet finished. Races 29 and 48, long known in

certain areas of the United States but not in Mexico, made threatening gestures in 1953, provoking Borlaug to write in 1954: 'The varieties now being grown commercially must be replaced by newer varieties with different types of stem rust resistance. This is necessitated by three major changes in rust races which have occurred since 1950... Varieties resistant to some or all of these races, as well as to the races formerly prevalent, have been developed by the cooperative program... The constant shifting in population of stem rust races illustrates the necessity of a continuous breeding program to combat this parasite which is constantly a threat to the wheat crop.'" (41).

Another dramatic illustration is available from rice (8). In 1962 the average rice yield in Southeast Asia was about 1,500 kilograms per hectare, while Japan was producing about 5,000 kilograms per hectare. Research was obviously needed, and the International Rice Research Institute began collecting germplasm and crossing types which had various desirable attributes. From among the hundreds of segregants of the eighth cross, they selected the now famous IR-8. One of its parents was a semi-dwarf variety from Taiwan and the other was a tall variety developed in Indonesia. IR-8 was semi-dwarf and fertilizer responsive, enabling it to utilize fertilizer without lodging. It was highly tillered and had upright leaves, which permitted more heads per plant and more efficient light interception. Equally important, it was insensitive to photoperiod and could be planted at low elevations within the tropics around the world. The wide adaptability of IR-8 and the versatility of some of the improved varieties from Taiwan have been demonstrated in Africa, Asia, and Latin America. Yields of 4,000 to 6,000 kilograms per hectare are not uncommon, and yields over 10,000 kilograms per hectare have been obtained (9).

The success of the above program has been due primarily to the isolation and use of two genetic systems. Genetic studies indicate the semi-dwarf

character is controlled by a single major recessive gene and modified slightly by minor genes. By putting the gene in a homozygous condition and selecting progenies with the appropriate modifiers, a range of short-statured plants can be obtained. The shortest types could then be used where water control and cultural management were very precise. The taller forms of the semi-dwarfs might be recommended in other areas where water control was less precise or erratic and cultural practices less refined (3). Photoperiod-insensitivity is the other genetic system, and it contributes immeasurably to the adaptability of the varieties. Sensitivity to photoperiod is apparently controlled by one or two dominant genes (9).

Varieties with these two genetic systems can be used as a base for further improvement and environment-specificity within a country. In Colombia, for example, rice is grown from near sea level in the Sinu Valley along the northern coast to over 1000 meters elevation in the Cauca Valley. Climatic factors, while similar, are sufficiently different to affect most crops. Mean annual temperature differs by only 2°C , at the lower altitude the mean is 28°C , and the high humidity such that it is oppressive to many people. By contrast, the Cauca Valley is held to have a comparatively salubrious and invigorating climate. Both areas have a bi-modal rainfall distribution. By contrast, the grassland plains of the Llanos, extending eastward from the foothills of the Eastern Cordillera into Venezuela, have one rainfall period per year.

Biotic differences among these three areas are great indeed. Edaphic characters can be ameliorated largely by fertilizers. Climatic differences in the environment are vast. For practical purposes, field beans cannot be grown in the Sinu. Also, the complex of disease organisms on corn is distinct in that area. From this, as well as all past experience in plant breeding, it is almost a foregone conclusion that different varieties of rice eventually will be grown in these three areas. The varieties might differ in reaction to

a range of insect or disease organisms. They might also differ in maturity, or response to heat by having different rates of respiration. In any case, better performing varieties than the widely adapted IR-8 type can be created for more environment-specificity or ecological specificity. With proper cultural procedures, three crops a year may be possible.

These accounts illustrate several important features necessary for successful utilization of germplasm. First, that while a problem may exist at the local level, the underlying causes or solutions may be of a regional or international nature and interest. Second, that the collection of germplasm available was sufficiently large to contain a broad base of diversity, thereby giving a reasonably good chance of isolating the desired plant characteristics for incorporation into an acceptable variety. Third, the desired characters are often contained in exotic material. Fourth, success was a result of continuous team effort. A breeder or pathologist or agronomist or soils man alone could not have been successful within the time allotted. Nor could the team effort have been successful on a stop-start series of short term effort and funding.

From these examples we might conclude that science can be transported. The technology or applied science, however, cannot be transported per se, but must be adapted to fit the myriad conditions in which it will be used. This has been the key to success with the rice and wheat varieties emanating from the research centers in Mexico and the Phillipines, where the variety remained constant and cultural conditions were modified. In corn, photoperiod-insensitivity has not yet been found. So, in addition to localized cultural modifications, germplasm from the large research centers is usually modified at the local level by hybridization. Occasionally a synthetic variety with a broad genetic base can be used without modification in areas not greatly dissimilar to that in which the variety originated. In this case, the heterozygous state

of a broad genetic base permits good performance under slightly different environmental conditions. Results with corn have not yet been as spectacular as those with rice and wheat, but as new germplasm resources are identified and new broad base gene pools are formed, corn yields will continue to increase.

These yields already attained indicate, to some at least, that we can produce sufficient food over the next quarter century to feed the predicted 6 or 7 billion people. Others believe that associated inputs, such as fertilizers, pesticides, herbicides, etc., cannot be economically produced in the required quantities to make use of known technology and germplasm. Whatever the outcome, we must depend upon agricultural resources as prime food needs for some time to come. Short term prospects for staving off the impending famine over the next several decades must be geared and dependent upon regional centers, such as CIMMYT (The International Center for Wheat and Maize Improvement) and IRRI (International Rice Research Institute). Others, now in operation or contemplated, could be listed, but these two are probably the most widely known and serve as excellent examples.

Much of the broad technology and germplasm that determines the fate of millions will originate from these centers. Hopefully, many individual nations will then be able, with proper assistance and encouragement, to improve on these techniques and germplasm. To date, most national programs have demonstrated their inadequacies to solve their food problem. Our foremost hope is that the regional concept is successful. If not, famine appears certain to strike. If successful, we have only bought time until population control can reduce food demands to supply capabilities. Either way, food demands will be increased in the future.

Among biologists, collecting and maintaining germplasm of cultivated plants is easily understood, appreciated and justified. Justification before

budget committees, planners, and legislatures is somewhat more difficult. However, when the uncultivated wild relatives are mentioned, resistance to the program is often impenetrable, unless, of course, a disease or pest is threatening to wipe out the crop and its associated industries.

It is true that we usually don't know the genetic characteristics of wild species or whether they will be of value for unforeseen circumstances in the future. However, since many of them are in danger of disappearing, it behooves us to collect and preserve them before it is too late. Wild relatives have not been used often, but a few instances in which they were used have resulted in sufficient economic benefit to justify a vigorous program of collection. Several wild diploid (two sets of chromosomes) relatives have been used for bringing disease resistance into commercial tobacco, (four sets of chromosomes) N. longiflora and N. plumbaginifolia for black shank resistance, N. glutinosa for mosaic virus resistance and N. debneyi for wildfire resistance. Crown rust resistance in oats has been transferred from the 14 chromosome species of wild oats to the commercial 42 chromosome varieties (36). The commercial tetraploid cotton, TH-149, has increased lint strength which came from a wild diploid, Gossypium thurberi. Most of the US acreage now is planted with this or similar varieties. Yet the increased lint strength came from a wild relative which has no lint, only seed fibers a few millimeters long. There are other examples in sugar cane, melons, potatoes, and forage grasses. The value of collections, as insurance for the future, is difficult to assess. The time when any particular one may be useful is equally obscure. But, "A crop worker made a small collection of cottons in Acala, Mexico, in 1906. No one thought much of the collection at the time, and it was only through luck that it was preserved. A single selection . . . developed from this same collection was worth 300 million dollars to California farmers in 1952" (33). Preservation of germplasm, including wild relatives, is too com-

plex to be handled by any one nation. One country might be able to maintain viable material of a portion of the variability, but the ecological requirements of an entire widely spread genus or species are such that many types would be lost through natural selection. The Maize Germplasm Banks in Brazil, Colombia, Mexico, and the U. S. were organized so that each center was responsible for germplasm collected within a specified geographical area. Even here, there are serious difficulties.

Many of the races were highly artificial in the sense that they had been selected by man for specific purposes, e. g. dyes, fermented drink, religious ceremonies, etc. However, that they also were confined to certain environmental limits is undeniable. Some races are restricted in their adaptation to altitude, which is a function of temperature, light intensity, and photoperiod, while others are more flexible (32a). In Colombia, a race usually grown above 1,800 m will not produce seed below 1,000 m. Likewise a race from 0-800 m shows extreme lack of adaptation above 1,800 m (32c). A compensatory effect of latitude and altitude is apparent in that maize from 1,500 m at 6° N in Colombia can be moved to 25°-30° N or S if used at lower altitudes (32k). Some, such as Cuba Yellow Flint (32b) can be used in breeding programs around the world below 1500 ft and at latitudes 30° or less (32k). The interrelationships of altitude and latitude are not simple and not clear.

The maize from Chile is stored in the Colombian or Andean Center. Because of photoperiod response, most of the Chilean material cannot be grown and replenished in Colombia, so it must be sent to other areas. The lowland races were grown in Iowa and Mexico on occasion for seed increase and maintenance of germination level. High altitude Chilean races were grown in the mountains of Mexico. FAO has recently initiated programs for germplasm maintenance, in which cognizance is given to the biological requirements of the plant. Early indications with some of the forage grasses are encouraging.

While it is in the national interest of many governments to maintain broad collections of their most important crops, it is not possible or reasonable for every country to attempt to maintain complete collections of every crop and its relatives. A regional or ecological approach is called for.

The way in which individual lines or samples of germplasm are maintained is extremely important. Asexually propagated plants (many of the tubers, fruit trees, grapes, sugar canes) have usually been maintained as vegetative stock, although the danger of a virus being spread by cutting is very high. Means and feasibility of perpetuating vegetative stocks in national repositories are being discussed (22). It is presently necessary for the interested researcher to maintain his own collection or arrange for new material through correspondence with associates. The efficiency of such systems is very low and limited by the inability of individuals to collect and maintain sufficient collections.

The seed sown crops are of two principal categories, based on mode of reproduction: 1) Cross-fertilizers, in which the female is pollinated by male gametes from other plants. This system insures that natural populations are in a continual state of hybridization and heterozygosity. 2) Self-fertilizers, where females are pollinated by male gametes from the female parent. Most plants in these populations are genetically identical or they may be a mixture of pure lines. In either case, the genes are generally all in the homozygous condition. However, if a cross has occurred, about 97% of all the genes in the population is returned to homozygosity in five generations.

The integrity of the self-fertilized strains is easily maintained by planting each sample in a row and harvesting the seed. Since no crossing has occurred, there will be no recombination. All progeny will resemble the parent.

Cross pollinators maintained without pollen control beget progeny with half of their genes from the female and the other half from various strains

throughout the plantings. Half the parentage is unknown. Unfortunately, many of the collections have been maintained in this fashion, especially for ages. Pollination control in some species, such as corn, is relatively easy because of flower structure, and those collections have been maintained with a greater degree of integrity. Many of the problems associated with germplasm conservation were discussed at a 1967 FAO (Food and Agricultural Organization of the United Nations) technical conference on "Exploration, Utilization and Conservation of Plant Gene Resources" in Rome (In Press). The conference was in cooperation with the International Biological Program (IBP) sub-committee for Plant Gene Pools on the Use and Management of Biological Resources Section. These organizations and UNESCO have expressed interest, concern, and, in some cases, initiated or aided programs of germplasm collection and preservation.

Ideally, every collection would be maintained as a separate entity, and measures taken to insure its genetic integrity whenever it was planted for increase or maintenance purposes. The expense, facilities, and personnel required for sizeable collections of cross-pollinators often preclude exercising the ideal. Furthermore, controlled-pollination progenies are the best indication of a parent's worth. Any decent sized collection then becomes unmanageable, and complete evaluations are beyond the realm of imagination. The number of possible crosses among n objects is equal to $\frac{n(n-1)}{2}$, or 499,500 crosses for a collection of 1000 strains. To drive the point home, almost 50 million crosses would be required for 10,000 strains. There are about 12,000 entries in the maize collection, over 3000 in the cotton collections (S. G. Stephens, personal communication), about 2,000 soybeans (C. A. Brim, personal communication), 18,000 wheats, including released varieties, lines, and collections (C. F. Murphy, personal communication), 15,000 peanuts (D. A. Emery, personal communication). Although many of these are cross-pollinated, herculean effort is required to hand-cross the self-pollinators, in order to obtain new genetic recombinations.

Compromise of the ideal with practicality has usually been exercised in germplasm maintenance. The Andean Maize Germ Plasm Bank in Medellin, Colombia, had, by 1961, received 5,482 indigenous strains from Colombia, Bolivia, Chile, Ecuador, Peru, and Venezuela. A severe strain was placed on facilities, budget, and personnel by maintaining the collections in viable condition and simultaneously carrying on a high calibre improvement program for the entire country. Furthermore, it is not possible to evaluate collections of this size in all environments against all the plagues and vagaries of nature. To facilitate maintenance, evaluation, and use of the germplasm bank, a biologically systematic compositing of material was begun. The indigenous strains of each Andean country had been classified into races (32). From an almost unmanageable collection of over 5,000 indigenous strains, 191 races have been described for the Andean zone. Ear and grain character measurements were taken from the original ears grown in their native environment. Physiological, morphological, and chromosome data were obtained in Colombia, Mexico, or Iowa from nurseries at suitable altitudes. Some strains, usually three to five, were chosen as "type" or "typical" examples of a race, and these were individually maintained and increased. Other collections which were equally as representative of the race, were classified as "others". Briefly, the compositing system consisted of mixing together equal numbers of viable seeds (as determined by germination tests) of all collections classified as race "A". Race "A" composite included the "typical" strains as well as the "others". A second mixture was made of those classified as race "B", and so on. Some races contain sub-groups differing, for example, in grain color or kernel characteristics. Therefore, if race "C" had both yellow and white grain types, and also flour and flint starch texture, there may have been five different composites made for this race: white flint; yellow flint; white flour; yellow flour; mixed or segregating for starch and color. Likewise, the collections intermediate between races "A" and "B"

were composited to form one population of "A-B" germplasm. The intermediates of "E" and "F" were composited into a "B-F" complex.

This system, which still maintains typical individual collections, permits maintenance of large seed supplies of composite races. 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, disease resistance, and other economic characteristics.

Certain races have no immediately apparent economic characteristics, but they may prove to be valuable in the future. Other races which look highly desirable do not contribute appreciably to increased yields, while others, extremely undesirable on esthetic grounds and low yield, exhibit considerable amounts of hybrid vigor when crossed. All these types of corns - good and bad - make up the collections which are the world's only real source of material for the development of superior corns. By growing the races, alone and in crosses, patterns of adaptability and good combining emerge. Certain races then become identified by their outstanding performance as varieties. Some are exceptional sources of inbred lines or new variability and diversity at the local and international level. The long range problem is determining how these really superior corns were made or evolved.

Understanding more of the evolutionary history of the species and varieties we work with would certainly contribute to more judicious use of exotic germplasm than the often wasteful and haphazard usage of it practiced in the past.

There is evidence that good material has complex and diverse origins, although diversity per se is not the answer. The evolutionary histories of truly outstanding germplasm have similarities which cannot be ignored (44). There are several examples in maize: the Corn Belt Dents of the United States; the Tuxpeno race from Mexico; Eto from Colombia, the Cuban Yellow

Flints. A good example in self-pollinated crops is Composite Cross II in barley. There is even an example from an undomesticated apomictic polyploid perennial forage grass, Bothriochloa ischaemum. The essential feature in the formation of these superior gene sources is that after diverse germplasm had been brought together, no stringent selection for "desirable" types was practiced by man. Natural selection undoubtedly occurred among the various genotypes in the population, but it is a slower process than that exercised by man. There was time for genetic linkages to break up and recombination of genes to occur; time for the different genotypes in the population to reach a state of dynamic equilibrium in which their frequencies fluctuate within certain limits according to environmental conditions. Periodic infusions of new germplasm may amplify the genetic base, and the process is repeated. Most of the failures in the use of exotic germplasm are probably due to premature attempts at selection in newly created populations. Another reason for failure in the use of local-exotic crosses is that they have been prematurely discarded on the basis of appearance.

One wonders at the irreparable genetic damage or loss perpetuated over the years for appearance's sake. The old corn shows were marvellous examples of much-ado-about-nothing. Prizes were given for the best appearing and most uniform corn ears. The prize really went to those who spent the most time sorting through mounds of corn. There was no regard for performance or yield. Many farmers soon realized they could often get better yields from non-show-type corn and the corn shows, as sources for seed, were soon discontinued. Vestiges of this outmoded, refuted, and useless custom still continue to this day. Walk through the exhibit halls at state fairs. Look in the arenas or show rings where beef, dairy, and swine are judged. The custom has unfortunately been accepted by many underdeveloped countries. Many a show animal, often with unknown prepotency as a sire or performance as a dam, has been imported at a cost of thousands. The animal may win many ribbons, yet be com-

pletely unsuited for the environment, and worse, contribute nothing of real value to the herd or country.

When I was Director of the Colombian-Rockefeller Corn Program, our corn was often criticized by visiting U. S. colleagues for being "shaggy" or "lousy" looking. The plants were tall with ears high on the plant. Many of the varieties and hybrids had a few diseased leaf spots or pustules, the plants weren't as uniform as those in the States, and so forth. Given an acceptable industrial or comestible quality, the only important matter is really yield - nothing else. It would take five generations to incorporate resistance into a line used for hybrids. In the same five years, an entirely new hybrid with new lines could also be released. Therefore, minor disease and insect reaction were not stressed, especially when the new hybrids would yield more than their predecessors by 15 to 40%. (Unpubl. annual reports Instituto Colombiano Agropecuario, Maize Section). In corn, a hybrid or varietal population is not homozygous, such as is the case with wheat. The implications of disease and insect problems were less important in corn because they were not critical or limiting. The heterozygous state and diverse parental germplasm of the maize populations were apparently sufficient to prevent the explosive epidemics so common with self-pollinated crops such as wheat.

To many, uniformity is a necessary requirement for appearance, and the way to phenotypic uniformity is through genetic uniformity. This is an erroneous conception leading to restricted germplasm and the discarding of many genes. Uniformity of phenotype is needed for grain or fruit quality or machine harvesting, and used in varietal identification or seed laws. There also appears to be uniformity for uniformity's sake, perhaps unconsciously from the influence of genetics. Studies of Mendelian genetics require genotypic and phenotypic uniformity. In plant breeding, the more genotypically homogenous the variety becomes, the more it is restricted in its ecological

tolerances. Performance is also restricted since micro-environment, edaphic, and climatic differences exist within the areas in which a variety is planted. Phenotypically homogeneous populations with genotypic heterogeneity will probably be used more in the future.

The use of double-cross hybrids, three-way hybrids, varietal crosses and synthetics of cross-pollinated plants also utilize genotypic heterogeneity, although those breeding methods were not developed with that in mind and the point is usually overlooked. Ample evidence favoring genotypic heterogeneity within phenotypic homogeneous populations of cross-pollinators is available in the Colombian corn improvement program. Isolation of inbred lines in open-pollinated varieties begins with a self-pollination. Some of the resulting seed were planted in special crossing blocks to determine the worth of the line. The remaining seed of the line would ordinarily be kept in storage for two planting seasons until the worth of the line was determined by yield tests. Without facilities in the humid tropics, seed storage is difficult, and in some cases, almost impossible. However, we were able to obtain reasonable germination if the seed were not stored for more than one growing season. So my predecessors figured that the only way to maintain the line was to plant it before its worth was known. They developed the following system: In a plot of some 60 plants of the S_1 line, five of the best appearing plants were self-pollinated for the S_2 generation. Ten to 15 other plants in the same plot were sib-mated. After harvesting the controlled pollination seed, the five S_2 lines and the S_1 -sib $_1$ line were planted and individually crossed onto a tester to determine the worth of each of the six lines. The process was then repeated. Much of this was lost effort if the original S_1 line was discarded, but there was no alternative, as time was important for the release of improved corn. If, however, the line was selected on the basis of yield trials, we had several different advanced generations on hand to continue. The upshot of this was that most all lines, perhaps more than 95% of those in

released or experimental hybrids, did not have many generations of self-pollination in their pedigrees. Furthermore, the selfed generations were usually interspersed and separated by several generations of sib-mating. I have not studied the pedigrees lately, but such was the situation up to 1961.

The most obvious explanation is that self-fertilization and accompanying selection is a very drastic procedure. Each generation, one-half of the remaining heterozygous genes, are fixed in equal proportions, 25% as homozygous recessives and 25% as homozygous dominants. Selection of a plant for continued selfing, with a gene in the homozygous recessive state, permanently eliminates the possibility of obtaining the dominant gene in later generations, and vice versa. With continued selfing then, many genes are essentially eliminated before they can be evaluated. Sib-mating offers a slower approach to homozygosity, and by the system used, there was selection for major genes effecting easily recognized characters. Sib-mating among such plants would tend to delay the fixation and chance discarding many of the genes effecting quantitative characters. The lines developed by the self-sib system were phenotypically homogeneous but genotypically heterogeneous and in some cases heterozygous. Although these lines did appear to be very uniform, it was possible to select for and fix genes for certain characters in late generations, e.g., grain color, disease and insect reaction, fertility restorers for cytoplasmic sterility. The system also delays the chance discarding of new genetic recombinations which occur as a result of crossing over between linked genes.

Even with self fertilized crops, considerable evidence indicates that genotypic heterogeneous populations will be widely used in the future (14,38, 20,2), although the concept has often been maligned and overlooked. There have been a number of reports where multiline or composite varieties have yielded more than the average of the lines making up the composite. There are also cases where heterogeneous population yielded more than the highest

yielding individual entry (38, 20).

The most striking evidence of the above is from populations composited by bulking F_1 lines, and then seeding and harvesting year after year without rigorous selection. The most notable population, Composite Cross II, has slowly increased in yield from about 74% to 104% of a commercially grown variety (14). This has been over a period of 28 generations, but after the initial crosses were made, no special methods or skills were used. These kinds of populations are extremely variable, even in late generations (14, 2). At any time they can be sampled for extracting commercial types. In fact, a significant number of commercial barleys can be traced to such populations, and some selections from the F_{24} generation yielded 56% more than the commercial variety, Atlas (14).

Such populations have enormous adaptability, variability, and potential, limited by the numbers of crosses which can be made. This problem has recently been circumvented. The "American collection of spring barleys gleaned from all parts of the world. . ." was crossed onto male sterile females to form Composite Cross XXI (43). A tremendous array of variability has been combined. The male sterile gene will insure many generations of additional hybridization and genetic recombination. The diversity of segregations and types which might be selected from this composite stagger the imagination. But, based on experience with earlier composites, this one should be a splendid future source of new material for many parts of the world.

The agricultural advancements associated with hybrid corn in the United States have been remarkable. Yet, the success of hybrid corn has done a great deal of philosophic harm. It created a condition of hybridomania throughout the world. It is true that hybrids can and should be produced in numerous areas of undeveloped nations. It is equally true that there are other regions where they are unsuitable, such as many of the isolated mountainous zones and/or lowland fringe areas. Farmers with small land holdings often replant

seed from their harvest, or sell it to neighboring farmers for planting. This practice greatly reduces yields in the case of hybrid corn. For such areas and conditions as these, there is a real need for improved varieties or synthetics. These possess a broad genetic base, enabling them to perform well over more varied environmental conditions than can double-cross hybrids. The use of synthetics does not require as sophisticated and elaborate a seed industry for producing and distributing seed as does the use of hybrids. In addition to commercial use, synthetics may also be used as source material for inbreds whenever hybrids are feasible.

Some recent studies have indicated surprisingly high yields of synthetics. In one case, after four cycles of selection, the synthetic yielded 3% less than the highest yielding hybrid developed for the area (21). In another, the fourth cycle synthetic yielded only 5% less than the hybrid check (46). In both studies, gains in yield were about 10 to 12% each selection cycle. Similar advances are being obtained in Kenya, Ecuador and Colombia (19). The synthetic populations still contain variability, and further advances should be possible.

The heart of these programs is the maize germplasm collection, twenty years of experience with them, dedicated personnel, and innovation in technique and method of breeding. Varietal crosses have been released as hybrids. Occasionally, when the advanced generation of the cross did not have the usual drastically reduced yields, it was released as a synthetic. Hybrids have been made with lines inbred only one generation - heresy to a classicist, but it improved local yields. Visual selection for multiple ears has resulted in a released variety 20% better than the original source. Varietal and racial crosses are widely used, often as a basis for compositing germplasm for regional programs throughout the world. Experience with these germplasm pools is such that it will soon be possible to prescribe which pools should be used as an initial base for improvement in specific parts of

the world (19).

The success of the regional corn programs is notable. Yields have increased slowly and steadily, but without the benefit of major genes, such as stiff straw and photoperiod insensitivity, which led to the break-throughs with wheat and rice. A comparable event or break-through in corn, superimposed on yields already attainable, would be astounding.

Certain items of this presentation have been stressed, perhaps too much, while others have been glossed over. I do not advocate one breeding scheme over another, but do wish to emphasize a philosophy which usually seems to escape many of those responsible for planning, financing, and executing programs of development. To others, whose lot it is to become involved in development programs, I recommend reading the various annual reports, symposia proceedings, and publications of the Ford and Rockefeller Foundations, in addition to reports from International Maize and Wheat Improvement Center (CIMMYT) and the International Rice Research Institute (IRRI). In these, the philosophy, accomplishments, and hopes for man and his nations are stated more eloquently and completely than I am capable of doing here.

The world's immediate and short term needs can be met only by utilizing a system similar to the regional approaches mentioned. The great mass of germplasm and technology must come from these centers. With the centers as a base, competent local effort of other individual governments should contribute additional increments of benefits, if adequately supported.

Each nation cannot be efficiently and economically self-sufficient in all foodstuffs. Certain foods can be produced more economically in some areas than others and they could serve as a source of foreign exchange. Other countries could best concentrate on production of different crops. We don't need a world economy based on the systems and policies of the present day markets in coffee, cocoa, sugar, and the like --- even though the future commodities may be corn, wheat, manihot, millet and rice.

Individual national commitment will be needed to develop and promote new commodities. Perhaps specialized markets could be developed by promoting plants presently used in an indigenous or dooryard agriculture. Examples might be tubers or relatives of the cultivated potato; Oxalis sp.; Ulloca sp.; quinoa, Chenopodium quinoa; teff, Eragrostis abyssinica; amaranth species; taro; arracacha. The list could go on and on. Some of these have never really been investigated for commercial agricultural potential, but they are all already domesticated. Medicinal and industrial crops may also serve as foreign exchange items. There are several excellent examples of research pay-offs that resulted from changing plants to fit the requirements of commercial and industrial operations; soybeans, castor beans, safflower, and sorghum. Other possibilities have certainly not been exhausted.

With this gazing into the crystal ball, I am very much concerned about germplasm preservation. Premature or indiscriminate bulking and compositing of individual collections must be avoided. Compositing should be done only after a systematic study of the material has been completed. All individual collections should be maintained separately, if possible. The composites could be used for preliminary adaptive studies or source material established breeding programs. This would meet most requirements. Individual collections could be reserved for special cases of highly refined and sophisticated studies. The composites and germplasm complexes will be the base upon which we will modify and build to satisfy our future food needs.

Only four crops, wheat, barley, maize, and rice, represent over 80% of the world's cereal production. If we include potatoes, sweet potatoes, yams, pulses, and consider one-third of the oil seeds as edible, then those same four cereals represent almost 70% of the crop production of the world (13). This percentage will undoubtedly increase to avert famine. But, then what; is man to exist on these few plants? Physically he can exist, but by his very humanity, he desires and, perhaps, deserves more.

LITERATURE CITED

1. Allard, R. W. 1960. Principles of plant breeding. John Wiley & Sons, New York. p. 364; 485 pp.
2. Allard, R. W. and S. K. Jain. 1962. Population studies in predominately self-pollinated species. II. Analysis of quantitative genetic changes in bulk-hybrid population of barley. *Evolution* 16:90-101.
3. Aquino, R. C., and P. R. Jennings. 1966. Inheritance and significance of dwarfism in an indica rice variety. *Crop Sci.* 6:551-554.
4. Blomquist, H. L. 1948. The grasses of North Carolina. Duke University Press, Durham. 276 pp.
5. Borlaug, Norman E. 1948. Wheat breeding and its impact on world food supply. *Proc. Third Internat'l. Wheat Genetics Symposium*. Adelaide, Australia. (In Press)
6. Braidwood, Robert J. 1960. The agricultural revolution. *Scientific American* 203:130-148.
7. Cassalet, D. Feb. 1968. Climaco personal comm.
8. Chandler, R. F., Jr. 1968. The case for research. *In Strategy for the Conquest of Hunger*. The Rockefeller Foundation Symp. N.Y. pp 92-97.
9. Chang, T. T. 1967. The genetic basis of wide adaptability and yielding ability of rice varieties in the tropics. *Internat'l. Rice Commission Newsletter* 16:4-12.
10. Chatterji, A. K. and D. H. Timothy. Microsporogenesis and embryogenesis in *Crop Sci.* (In Press).
11. Clark, J. Allen. 1956. Collection, preservation and utilization of indigenous strains of maize. *Economic Botany*. 10:194-200.
12. Cooper, J. P. 1954. Studies on growth and development in *Lolium*. IV. Genetic control of heading response in local populations. *J. Ecol.* 42:521-566.
13. Food Agricultural Organization of the United Nations. 1966. Production Yearbook. Vol. 20.
14. Harlan, Jack R. 1956. Distribution and utilization of natural variability in cultivated plants. *Genetics in Plant Breeding*. Brookhaven Symposia in Plant Breeding, No. 9. 191-208.
15. Hartley, W. 1954. The agrostological index. A phytogeographical approach to the problems of pasture plant introduction. *Aust. J. Bot.* 2:1-21.
16. _____. 1964. The distribution of the grasses. *In Grasses and Grasslands*. C. Barnard (Ed.) MacMillan and Co. Ltd. London. 29-46.
17. Helbaek, Hans. 1959. Domestication of food plants in the Old World. *Science* 130 (3372):365-372.

18. Hopper, W. David. 1968. Investment in agriculture: The essentials for payoff. In Strategy for the Conquest of Hunger Symp. Proc. The Rockefeller Foundation, N. Y. 102-113.
19. International Maize and Wheat Improvement Center (CIMMYT) Report. 1966-67. Mexico, D.F. 103 pp.
20. Jensen, N. F. 1965. Multiline superiority in cereals. Crop Sci. 5: 566-568.
21. Johnson, E. C. 1963. Agronomy Abstracts. Amer. Soc. of Agron.
22. Laison, R. E. 1961. Perpetuation and protection of germ plasm as vegetative stock. In. Germ Plasm Resources. Publ. No. 66, AAAS 327-336. Washington, D. C.
23. Maize Research Section. Annual Report. National Agricultural Research Station, Kitale, Kenya.
24. Mangelsdorf, P. C. 1966. Genetic potentials for increasing yields of food crops and animals. Proc. Nat'l. Acad. Sci. Symposium "Prospects of World Food Supply". 56(2) 370-375.
25. McMillan, C. 1965. Grassland community fractions from Central North America under simulated climates. Amer. Jour. Bot. 52:109-116.
26. Miller, D. F. 1968 (Ed). Composition of cereal grains and forages. NAS-NRC Publ. 585. Washington, D. C. 663 pp.
27. Morrisson, F. B. 1940. Feeds and feeding. 20th Ed. Morrisson Pub. Co., Ithaca, N. Y.
28. Nuttonson, M. Y. 1948. Preliminary observations of phenological data as a tool in the study of photoperiodic and thermal requirements of various plant material. In Vernalisation and Photoperiodism. A. E. Murneek and R. O. Whyte (Eds). Chronica Botanica. 129-143.
29. Paddock, William, and Paul Paddock. 1964. Hungry Nations. Little Brown & Co., Boston. 344 pp.
30. Patiño, Victor Manuel. 1956. El Maiz Chococito. Noticia sobre su cultivo en America Ecuatorial. America Indigena. 16:309-346.
31. Prescott, J. A., J. A. Collins, and G. R. Shirmurkar. 1952. The comparative climatology of Australia and Argentina. Geog. Rev. 42:118-133.
32. Races of maize in Latin America.
 - a. Welhausen, E. J., Roberts, L. M. and Hernandez X., E. in collaboration with Mangelsdorf, P. C. Races of maize in Mexico. The Bussey Institution, Harvard Univ., 1952, pp. 1-223.
 - b. Hatheway, W. H. 1957. Races of maize in Cuba. Nat. Acad. Sci.-Nat. Res. Council, No. 453.
 - c. Roberts, L. M., Grant, U. J., Ramirez, 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. Council, No. 510.
- d. Wellhausen, E. J., Fuentes, O. and Hernandez, Corzo A., in collaboration with Mangelsdorf, P. C. 1957. Races of maize in Central America. Nat. Acad. Sci.-Nat. Res. Council, No. 511.
 - e. 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. Council, No. 593.
 - f. Ramirez, E. R., Timothy, D. H., Diaz, B. E. and Grant, U. J. in collaboration with Nicholson, G. E., Anderson, E. and Brown, W. L. 1960. Races of maize in Bolivia. Nat. Acad. Sci.-Nat. Res. Council, No. 747.
 - g. Brown, W. L. 1960. Races of maize in the West Indies. Nat. Acad. Sci.-Nat. Res. Council, No. 792.
 - h. Timothy, D. H., Peña, V. B. and Ramirez, E. R. in collaboration with Brown, W. L. and Anderson, E. 1961. Races of maize in Chile. Nat. Acad. Sci.-Nat. Res. Council, No. 847.
 - i. Grobman, A., Salhuana, W. and Sevilla, R. in collaboration with Mangelsdorf, P. C. 1961. Races of maize in Peru, their origins, evolution and classification. Nat. Acad. Sci.-Nat. Res. Council, No. 915.
 - j. Timothy, D. H., Hatheway, W. H., Grant, U. J., and Torregroza, C. M., Sarria, V. D., and Varela, A. D. 1963. Races of maize in Ecuador. Nat. Acad. Sci.-Nat. Res. Council, No. 975.
 - k. 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. Council, No. 1136.
- 33. Robertson, D. W. May 10, 1955. Testimony at hearing of Agricultural Appropriations Subcommittee. House of Representatives.
 - 34. Rockefeller Foundation. 1964-1965. Program in the Agricultural Sciences. The Rockefeller Foundation, New York.
 - 35. Report of the Panel on World Food Supply. "The World Food Problem" a report of the President's Science Advisory Committee. May, 1967. Vols I, II, III. The White House. U. S. Gov't. Printing Office.
 - 36. Sadanaga, K., and M. D. Simons. 1960. Transfer of crown rust resistance of diploid and tetraploid species to hexaploid oats. Agron. J. 52: 285-288.
 - 37. Schultz, Theodore, W. 1965. Economic Crises in World Agriculture. Univ. of Michigan Press, Ann Arbor. 114 pp.
 - 38. Schutz, W. M., C. A. Brim, and S. A. Usanis. 1968. Inter-genotypic competition in plant populations I. Feedback systems with stable equilibria in populations of autogamous homozygous lines. Crop Sci. 8:61-66.

39. Shantz, H. L. 1954. The place of grasslands in the earth's cover of vegetation. Ecology 35:143-51.
40. Sprague, E. W. 1964. Research to improve production of corn in Asia. In Agricultural Science for the Developing Nations. A. H. Moseman (Ed.). Amer. Assoc. Adv. Science Publ. No. 76:53-68.
41. Stakeman, E. C., Richard Bradfield, Paul C. Mangelsdorf. 1967. Campaigns against hunger. Belknap Press. Cambridge, Mass.
42. Stakeman, E. C., and J. G. Harrar. 1957. Principles of Plant Pathology. P. 25. Ronald Press, N. Y. 581 pp.
43. Suneson, C. A., and G. A. Weibe. 1962. A "Paul Bunyan" plant breeding enterprise with barley. Crop Sci. 2:347-348.
44. Timothy, D. H. 1966. Considerations on the use of exotic germplasm, genetic recombination, and natural selection. Proc. IX Internat'l. Grassl. Congress. 175-177.
45. Vicente-Chandler, J., Caro-Costas, R., Pearson, R. W., Abruña, F., Figarella, J., and Selva, S. 1964. The intensive management of tropical forages in Puerto Rico. Univ. Puerto Rico Agric. Exp. Sta. Bull. 187. 152 pp.
46. Wellhausen, E. J. 1965. Exotic germ plasm for improvement of corn belt maize. Proc. 20th Hybrid Corn Industry-Research Conference. 31-45.
47. Whyte, R. O., T. R. G. Moir, and J. P. Cooper. 1959. Grasses in agriculture. FAO Agricultural Studies. No. 42. FAO. Rome. 417 pp.