Genetic Diversity and Genetic Vulnerability—An Appraisal[1]

WILLIAM L. BROWN[2]

During the past decade questions relating to biological diversity, genetic vulnerability, narrowing of the gene base of important cultivars and the loss of germplasm of both economic and noneconomic species have received increasing attention. Numerous studies, conferences, and symposia on these general subjects have spawned a flood of reports, proceedings, and scientific papers (Timothy and Goodman, 1979; Nat. Acad. Sci., 1972; Nat. Acad. Sci., 1978; U.S. Dept. of State, 1981). Many of these questions relate to the world's food supply, the future of which could depend upon the conservation and greater utilization of the reservoir of crop plant diversity (Biol. Diversity, 1980).

The Green Revolution has been criticized for its replacement of indigenous crop plants with high-yielding varieties that are alleged to be less dependable than those varieties they have replaced when grown under less than ideal conditions.

It has been suggested that the acquisition of seed companies by large, multinational corporations may result in a reduction in the number of varieties available to growers and in a possible monopoly of plant genetic resources (DeCrosta, 1980).

Without minimizing the importance of protecting noneconomic species and the environments in which they occur, I shall limit this discussion to questions of diversity and vulnerability as they relate to cultivated plants. Although no attempt will be made to treat specific crops in detail, my comments are in reference to major seed propagated field crops grown in the United States. It is mainly this group of cultivars about which there is much confusion today relative to the degree to which serious erosion is occurring in the gene base. There are conflicting viewpoints as to the amount of germplasm being lost and the biological and economic implications of that loss. There is also controversy over the alleged hazards associated with the widespread use of uniform cultivars.

For these reasons, an appraisal of the current situation relative to genetic diversity and genetic vulnerability of important economic crops seems appropriate. I hope to identify the more important needs still to be filled if the unused germplasm resources of cultivated plants are to receive the attention they fully deserve. I shall comment on those factors that lead to uniformity in modern high-yield varieties, and also consider the merits and disadvantages of uniformity. Finally, I shall describe my understanding of ways in which the modern seed industry relates to many of these matters.

RELATIONSHIP OF DIVERSITY AND VULNERABILITY

Much of the recent interest in genetic diversity developed as a result of the experience in the United States with southern corn leaf blight in 1969–1970. A

[1] Presented at the annual banquet, Society for Economic Botany, University of Alabama, Tuscaloosa, AL, June 16, 1982.

[2] Chairman, Pioneer Hi-Bred International, Inc., Des Moines, IA 50308.

Economic Botany, 37(1), 1983, pp. 4–12

new or previously undetected race of *Helminthosporium maydis* was first observed in Florida from where it moved rapidly northward, reaching the Cornbelt in 1970 (Tatum, 1971). It has been estimated that nationally corn production was reduced by as much as 15% because of this disease. The problem arose because of the cytoplasmic uniformity of a large proportion of the maize being grown at that time, and, for the first time, breeders came to realize that disease susceptibility is not determined solely by nuclear genes.

Genetic diversity is usually thought of as the amount of genetic variability among individuals of a variety, population or species. It is commonly believed that genetic vulnerability results from a reduction in genetic variability. For example, those varieties with a larger amount of genetic variability are thought to be less susceptible to the hazards of disease, insects, and other stresses than those with a small amount of genetic variability. It is this kind of thinking that leads to the assertion that modern agriculture, using uniform varieties and hybrids, reduces genetic diversity of our crop plants and causes them to be more susceptible to biological stresses. Such varieties are also said to be more narrowly adapted than varieties of greater genetic variability.

It is now clear that genetic diversity per se provides no insurance against genetic vulnerability. If it did, the American chestnut, *Castanea dentata,* would still be among the dominant species of the deciduous forests of eastern North America. No one familiar with *Castanea dentata* would question the breadth of genetic variability within the species, yet it was decimated by a single pathogen in approximately two decades, as a result of its uniform susceptibility to the chestnut blight fungus, *Endothia parasitica.*

Similarly, the highly variable American elm, *Ulmus americana,* has been shown to be highly susceptible to Dutch Elm disease fungus as that organism moved westward from the Atlantic coast.

In 1916 and in 1935 wheat rust spread throughout the Great Plains, destroying hundreds of thousands of acres and numerous varieties of bread wheat, despite the fact that the amount of genetic diversity found among the varieties of wheat in use at the time was considerable.

In the early 1950s *Puccinia polysora,* a tropical rust fungus, spread across east Africa on highly variable hosts—the open pollinated maize varieties of the area. Yields were reduced significantly, and maize culture was in jeopardy until resistant genotypes were introduced from the Caribbean and Mexico. The local landraces of maize grown in east Africa at that time were extremely variable, yet they were all found to be uniformly susceptible to tropical rust.

The point with respect to disease and insect resistance is that genetic diversity alone is an inadequate defense unless that diversity includes genetic resistance to the organisms in question. What is important is diversity in those alleles that code for susceptibility or resistance to the pathogen or insect causing the problem.

This is not to say that the breeder should not increase the genetic diversity of those cultivars upon which we depend for our food, feed, and fiber. Neither should we allow landraces, old varieties, and primitive types, replaced by newly-introduced varieties, to become lost. To the extent it is possible to do so, all such sources of germplasm should be preserved for possible future use in breeding.

What are the circumstances that cause the breeder to be interested in increasing the gene base of our major crops? It is usually the presence of unusual biological or environmental stresses which result in noticeable yield reduction or crop failure. And to understand why problems of genetic diversity arise in cultivated species, some knowledge of how plant breeders operate is essential.

If the breeder is working with a species that has already undergone a considerable amount of selection and breeding research, the primary breeding materials are usually the elite varieties in current use. The usual practice is to intermate the best varieties available and select for superior genotypes within the progeny of such matings. It follows, then, that the continual use of the best varieties as breeding materials tends to concentrate in the breeding pool genes from limited elite sources. Thus, the repeated use of the best varieties for purposes of generating new varieties, lines and so forth tends to reduce the genetic variation within the breeding population.

The simplest way to alleviate this condition is to introduce into the breeding pool germplasm from unrelated sources. In simplest terms, the breeder is interested in introducing useful alleles which are different from those present in the populations in use. With present methodology there are no completely satisfactory ways of identifying new alleles of most of the genes which make up the species. However, since the breeding programs of most crops utilize only a small percentage of the total germplasm available, it is reasonable to assume that the elite breeding materials in use do not include all the desirable alleles present in the species. So, to increase genetic diversity, one has only to introduce new sources of germplasm which are not closely related to those in use.

For most crops there are vast stores of germplasm available in numerous gene banks, most of which consist of landraces, primitive varieties, etc. Many are from foreign sources which are not closely related to elite varieties in commercial use.

In the United States alone, there are more than 400,000 accessions of germplasm included in the National Plant Germplasm System. The USDA Small Grains Collection contains about 90,000 accessions of wheat, oats, barley, rye and rice. About 13,000 individual collections of maize are stored and maintained at the CIMMYT Seed Bank in Mexico. The accessions stored in the United States and most of those abroad are available to any bona fide plant scientist. Consequently, the breeder has access to a wealth of material if he wishes to increase the genetic diversity in the breeding populations with which he is working.

Under these circumstances, why then are we concerned about the erosion of the gene base in crop plants, and why is the genetic diversity of those crops less than desired? If breeders are not making full use of the germplasm available to them, why is this so?

The answer to the first question is that only limited use is being made of the vast germplasm sources available. The reasons for the limited use are somewhat more complicated; yet, there seem to be two primary reasons. First, although a vast amount of material is available, little is known about the major characteristics and potential usefulness of the individual accessions making up that store of materials. In other words, little of the material residing in the germplasm banks has been evaluated. In the absence of this knowledge, the breeder has no way of knowing which few among several hundred accessions will most likely provide the particular trait or traits needed in a breeding program. Since a systematic screening of accessions to locate the traits needed would require the full time of the breeder, he reluctantly chooses other sources in lieu of the accessions of the germplasm banks.

The second reason for the limited use of materials from the gene banks is more difficult to justify and has to do with the nature of unimproved germplasm.

As was pointed out earlier, most gene bank accessions consist of landraces and unimproved varieties. Such sources contain many undesirable traits which cannot be tolerated in modern cultivars. To eliminate such traits while retaining the few desirable genes that may be present in unimproved varieties is a formidable breeding task that requires much time and unlimited patience. It is not an activity from which rapid progress can be expected. Since the breeder is interested in efficiency, he is reluctant to spend time using germplasm that will require years to successfully incorporate into adapted genotypes.

This points up one of the most critical needs in germplasm resource management, that of evaluation. For reasons mentioned above, the bulk of germplasm resources now found in gene banks around the world will not be used until its potential value as breeding material has been determined. Until this is accomplished, it makes little sense to expand the present collecting activity beyond that required to salvage materials threatened with extinction. Within the United States, the National Plant Germplasm System should expand and concentrate its efforts on evaluation until those accessions now in storage are adequately screened and documented. Until this is done, and a catalogue of the evaluated germplasm made available, one of the most important sources of increased genetic diversity within cultivated plants will, in effect, continue to be unavailable to the breeder.

PROGRESS IN EXPANDING THE GENETIC BASE OF MAJOR CROPS

In 1972 a report was issued by the National Academy of Sciences on the genetic vulnerability of major crops. The report summarized the results of a study of a committee which, under the aegis of the National Research Council, had investigated the extent to which major U.S. crops were genetically vulnerable to epidemics and other biological stresses. The conclusion reached was that the genetic base of several important crops was sufficiently narrow to justify concern. A number of recommendations were made for increasing genetic diversity and, hopefully, reducing genetic vulnerability.

Ten years have elapsed since the publication of the NAS report. A recent survey by Duvick (1981) permits at least a partial comparison of the situation today with that of a decade ago. Duvick's survey included 87 breeding programs, 56 of which were public and 31 private. The crops surveyed included maize, sorghum, wheat, soybeans and cotton.

Without going into detail, the survey showed that the concentration of a few leading cultivars on U.S. farms, although still high, is less today than in 1970; that new cultivars in advance trials are numerous; that the average life of commercial varieties is 6–10 yr and growing shorter; that more diverse germplasm is present in current breeding pools than in those of former years. Still, superior new varieties tend to come from elite sources of germplasm with a relatively narrow genetic base.

With respect to maize, the survey indicated that more than 450 commercial hybrids were being offered the U.S. farmer in 1981. In addition, very large numbers of pre-commercial and experimental hybrids were in advance trials and in the final stages of testing.

In general, this survey suggests that considerable progress has been made in the past 10 yr in increasing the amount of genetic diversity available to U.S. agriculture. While these are encouraging signs, they provide no reason for a relaxation of efforts to continue to add to the gene base of our major crop species.

GENETIC DIVERSITY AND MODERN AGRICULTURE

The possible impact that plant breeding, plant variety protection legislation, and an expanding seed industry has on genetic diversity continues to receive much attention.

A number of authors (Wilkes and Wilkes, 1972: Paddock, 1970: Harris, 1972) have suggested that the replacement of genetically-variable, indigenous varieties with high-yielding, uniform cultivars entails considerable risk to those nations and farmers who have come under the influence of the Green Revolution.

Programs that introduce new, high-yielding varieties into areas where traditional agriculture depends upon the use of indigenous landraces have been criticized mainly on two counts. It is suggested that the introduction of new, high-yielding varieties into such areas results in the disappearance of the indigenous varieties and a resultant loss of potentially useful germplasm. It is also said that, while genetically uniform modern varieties produce high yields when combined with accompanying modern inputs such as fertilizers and chemical pesticides, they fail to perform as well as indigenous varieties under adverse environments and, therefore, lack the stability of performance required to provide a dependable, if minimal, food supply to the subsistence farmer.

The first criticism is a perfectly valid one with which no responsible biologist should disagree. If newly introduced varieties are accepted by farmers they will, indeed, result in a decline in use, and possibly ultimate disappearance of local landraces unless the latter are salvaged. However, there are no a priori reasons why this should happen. The old landraces of crop species are valuable resources which should not be allowed to disappear. It is the responsibility of governments, genetic resource organizations, and plant breeders, both public and private, to salvage germplasm before it is lost and to assure its introduction into appropriate germplasm banks. If this is done, and done properly, the introduction and adoption of new varieties will not result in the loss of older ones. Moreover, it does not seem right that the farmer should be deprived of the use of better performing crop varieties simply because, by chance, he happens to reside in an area of the world rich in plant genetic diversity.

The conclusion that the introduction of high-yielding, uniform cultivars necessarily results in a wipe-out of indigenous varieties fails to recognize the intelligence and sound judgment that is characteristic of most farmers. I have yet to encounter a farmer, either in the developed or developing world, who has ever completely replaced his traditional crop varieties with newly-introduced ones before having had some experience with the new introductions. This is true regardless of the claims made for the new varieties. Farmers, generally, are anxious to try new strains of plants, but initially will do so only in a small way and in comparison with the varieties with which they are familiar. It is only after he has demonstrated to his own satisfaction over a period of years that the new introductions are superior that the farmer will switch varieties completely. If a substitution of varieties is made, it will likely benefit the farmer and is justified. But fortunately, his conservative and sound approach to switching varieties provides some insurance against the sudden loss of indigenous germplasm and provides some lead time in which to salvage replaced varieties before they disappear.

The second criticism leveled at the introduction of high-yield varieties into areas of primitive agriculture is much more controversial. Statements similar to the following frequently appear in the literature: "Given ideal conditions, and large amounts of fertilizers and chemicals, green revolution seeds will respond well and provide high yields. However, if any required inputs do not arrive on time, or are absent altogether, farmers may experience extensive crop failure" (Mooney, 1979).

The validity of such assertions, usually made in the absence of any supporting data, need to be seriously questioned. It is true, of course, that any variety, be it primitive or modern, will perform better under favorable conditions than under unfavorable ones. But it is also true that high-yield varieties tend to outperform primitive varieties under all conditions, even though yield levels of both categories of varieties will be lower when grown under unfavorable conditions.

The critical point here has to do with relative yield stability of genetically-uniform and genetically-variable varieties. This is a question of variety × year and variety × location interactions, commonly employed statistical measures of the stability of genotypes when exposed to fluctuating environments.

Some of the best information on the relative stability of genetically uniform and genetically variable genotypes comes from experiments with maize (Eberhart and Russell, 1969). For many years following the development of hybrid maize, the hybrids used were double crosses. This type of hybrid involved 4 inbred lines as grandparents and 2 single crosses as parents (a single cross being the progeny of a mating of 2 inbred lines). The doublecross hybrid, therefore, was a population exhibiting considerable genetic variation. As further breeding produced more vigorous and higher-yielding inbred lines it was shown in the 1960s that it was practical to produce singlecross hybrids for commercial use. It had long been known that the best single crosses were higher yielding than the best double crosses but because of the genetic uniformity of single crosses, it was believed that they would lack the stability and consistent performance over years and environments that was characteristic of good double crosses. To obtain answers to this question, a number of experiments were carried out comparing variety-by-year and variety-by-location interactions in single and double crosses (Eberhart and Russell, 1969). The resulting data showed clearly that, on the average, estimates of variety-by-year and variety-by-location interactions were larger among single crosses than double crosses. Yet, it was also shown that, despite the averages, the variety-by-year and variety-by-location interactions in the best single crosses were no higher than in the best double crosses. This suggested that the performance of the best highly uniform, high-yielding single crosses might be expected to be as stable and consistent as the best double crosses. Experience has borne this out, and today the single cross is the predominant type of hybrid in use in the United States.

There are no genetic reasons why the best genetically-uniform varieties of wheat and rice and other self-fertilized species should be less stable and less consistent in performance than uniform single crosses of maize. If those who continue to refer to the erratic performance of high-yield, uniform varieties expect to be taken seriously, they should at least provide data from which they draw their conclusions. In the absence of such data one should continue to view with skepticsm those references to the high risks associated with the use of uniform cultivars.

Before leaving the matter of genetic uniformity it is appropriate to consider the reasons for the dominance of uniform cultivars in the developed world. While it is often assumed that the breeder is responsible for the uniformity of varieties, there are, in fact, many other forces in agriculture which encourage uniformity.

Some degree of uniformity is essential for the satisfactory utilization of mechanical harvesting equipment and certain processing equipment used in the food industry. Farmers tend to associate uniformity with "good breeding" and seem to prefer it to variability that is apparent in the field. Prescribed levels of uniformity are necessary to meet the requirements of seed certifying agencies.

In parts of Europe the requirements of "inscription" are such as to eliminate effectively variability in the varieties approved for sale. Thus, although the breeder develops genetically-uniform varieties, he does so primarily because of pressures from users and agencies which either control or influence the introduction of new cultivars. If the decision was left to the breeder he would prefer to have the option of complete flexibility with respect to genetic uniformity. The breeder also recognizes that genetic vulnerability can be reduced through inter-varietal as well as intra-varietal variability. Availability of several varieties or hybrids of different genetic backgrounds but adapted to similar ecological zones probably provide more protection against damage from pests than one quite variable variety. The breeder often uses this option to counter the requirement of intravarietal uniformity and to protect the user.

THE SEED INDUSTRY AND GENETIC DIVERSITY

The following examples are fairly typical of statements purporting to associate a decline in genetic diversity with practices within the seed industry:

"For commercial reasons, transnational corporations are concentrating on fewer varieties of seeds which they can market worldwide, thus eroding the genetic diversity of plants" (Hurtado, 1982).

"By controlling seed companies, multinational corporations have the potential to control the food producing resources of this country . . . . Multinational corporations, many of which are chemical companies, could then develop varieties that are coated with fungicides and depend on the companies' own fertilizers for good yields. They could also tie up the market and raise the price of seeds to many times what they usually sell for" (DeCrosta, 1980).

Statements such as these cause concern, not only amongst laymen but also among biologists. It is sometimes difficult to know what the facts are relative to such statements unless one has detailed knowledge of the observations in question.

The rapid movement of large chemical, pharmaceutical, and energy companies into the seed industry has happened and seemingly is continuing. It is too early to know the effects of this change in ownership in the seed industry. One might logically assume, however, that the recent acquisitions would eventually result in greater competition in the industry. The increased competition, if it occurs, would be because of the development and release of more and better varieties. Such an occurrence would increase genetic diversity as opposed to reducing it.

The fear that large corporations may concentrate on fewer varieties and market them worldwide, thereby eroding genetic diversity, makes little sense biologically. While there is some flexibility in the longitudinal adaptation of plants, most species are quite sensitive to photoperiodic and temperature changes associated with latitudinal differences. These factors place severe constraints on the movement of cultivars to environments which differ from those under which they were developed. Also, many diseases and insects are location-specific which, when breeding for resistance, requires selection to take place in the area in which the variety is to be used. These requirements, in addition to the varietal preferences of the user, place severe restraints on the degree to which varieties can be successfully used worldwide.

Those groups that are concerned about the impact of multinational companies on genetic diversity seem also to fear the effects of plant variety protection legislation. No doubt some of the fear must result from a failure to distinguish between American legislation and that of the Common Market countries of Western Europe where a system of "national lists" has been developed which prohibits the use of varieties not included in the lists. The Plant Variety Protection Act of the United States is quite different in nature and effect. It was developed to discourage the pirating of varieties and to preserve the rights to the variety by the developer of the variety. Its use is voluntary, and it has no effect whatsoever on the marketing or use of new varieties. Protected varieties are available for use in research. Moreover, they may be multiplied by farmers for their own use or for sale to neighboring farmers.

It is yet too early to know the extent to which this legislation provides protection to the breeder. There seems little doubt, however, that it has resulted in additional breeding and the introduction of a larger number of varieties, particularly varieties of self-fertilized species. In this way the legislation tends to increase rather than decrease genetic diversity.

SUMMARY

1. Plant germplasm is among the most essential of the world's natural resources. Its conservation merits far greater attention than it is now receiving.

2. Total genetic diversity does not provide insurance against genetic vulnerability. To be of use to the breeder, sources of genetic diversity must include useful alleles not present in elite populations that carry resistance to pests and other stresses that adversely affect productivity and quality.

3. Breeding programs of the most important crops include only a small percentage of the total germplasm available within each crop. The major reason for this limited use of the stores of germplasm found in gene banks is the lack of evaluation data on such material. Until a gene bank's accessions are evaluated and documented they will continue to be of limited value to the breeder.

4. The results of a recent survey indicate that the genetic base of several important crops has increased during the past decade.

5. Several criticisms of the Green Revolution (used in the broadest sense) are considered. Introductions of new, improved cultivars do tend to replace indigenous varieties containing potentially useful germplasm. Expanded efforts are needed to rescue such varieties before extinction.

Research does not support the contention that modern, genetically-uniform cultivars are necessarily less stable and less dependable than genetically-variable cultivars.

6. With respect to the impacts of a changing seed industry on genetic diversity, it is suggested that these changes will not result in a concentration of fewer varieties used worldwide. The movement of pharmaceutical and chemical companies into the seed industry has occurred too recently to permit an evaluation of the effects of such moves. It will likely result in greater competition which, in turn, will stimulate more breeding and the introduction of a greater number of varieties than have been available in the past.

Plant variety protection legislation in the United States has also served to stimulate additional breeding in self-fertilized species and has resulted in an increase in the amount of genetic diversity available to the farmer.

LITERATURE CITED

Biological Diversity. 1980. Reprinted from 11th Annual Report of Council on Environmental Quality. p. 2–44. Supt. of Documents, U.S. Govt. Printing Office, Washington, DC.

Committee on Genetic Vulnerability of Major Crops. 1972. Genetic Vulnerability of Major Crops. Natl. Acad. Sci., Washington, DC.

Committee on Germplasm Resources. 1978. Conservation of Germplasm Resources: An Imperative. Natl. Acad. Sci., Washington, DC.

DeCrosta, A. 1980. The real scoop on the plant patent controversy. Organic Gardening, May. p. 108–113.

Duvick, D. N. 1981. Genetic diversity in major U.S. farm crops—on the farm and in reserve. XII Int. Bot. Congr. Abstr. p. 216.

Eberhart, S. A., and W. A. Russell. 1969. Yield and stability for a ten-line diallel of single-cross and double-cross maize hybrids. Crop Sci. 9: 357–361.

Harris, M. 1972. How green the revolution. Nat. Hist. 81: 28–30.

Hurtado, M. E. 1982. Lifeline for the world's threatened seeds. South: The Third World Magazine. Issue 17.

Mooney, P. R. 1979. Seeds of The Earth. Canadian Council for International Co-operation, Ottawa.

Paddock, W. C. 1970. How green is the green revolution? Bioscience 20: 897–902.

Tatum, L. A. 1971. The southern corn leaf blight epidemic. Science 171: 1113–1116.

Timothy, D. H., and M. M. Goodman. 1979. Germplasm preservation: The basis of future feast or famine. Genetic resources of maize—an example. *In* Plant Seed, Development, Preservation, and Germination. ed. I. Rubenstein, R. L. Phillips, C. E. Green, B. G. Gengenbach. Academic Press, New York.

U.S. Department of State. 1981. Proc. strategy conference on biological diversity. Publ. 9262. Washington, DC.

Wilkes, H. G., and S. Wilkes. 1972. The green revolution. Environment 14: 32–39.