CHAPTER ELEVEN

Plant Introduction and Genetic Diversity

The movement of seeds and plants from one area of the world to another has been an important factor in agricultural development. The crops currently produced in a country often originated in other parts of the world. Plant introduction continues to be important in the identification of new crops and in obtaining new parental material for the development of cultivars of existing crops. This chapter will consider the overall concept of plant introduction; the procedures for securing, maintaining, and distributing plant introductions; and the techniques necessary to utilize them effectively for genetic improvement of a species.

ORIGIN OF GENETIC VARIATION IN NATURE

The center of origin for a crop is the geographical area in which it originated. A center of diversity is a location where there is extensive genetic variability among genotypes of the cultivated species and of related species. The center of origin and center of diversity for a crop may be the same or may be different.

The person credited with formulating and implementing the first large-scale program for germplasm collection is N. I. Vavilov. He was interested in obtaining germplasm with a broad range of genetic variability from throughout the world to use in improving cultivated crops in Russia. His work marked the beginning of a systematic approach to plant germplasm collection, maintenance, and utilization that has been vital to the improvement of crop species. On the basis of collections made by Russian scientists, Vavilov (1926, 1951) proposed eight centers of origin, two of which were later designated as subcenters (Table 11-1).

Detailed research on the origin of cultivated plants since the time of Vavilov has demonstrated that a center of origin cannot be defined simply by the genetic

Table 11–1 Centers of Origin of Plant Species, According to N.I. Vavilov (Vavilov, 1951)

	Centers of Origin	Examples of Cultivated Plants
I.	Chinese	Lettuce, rhubarb, soybean, turnip
II.	Indian	Cucumber, mango, oriental cotton, rice
IIa.	Indo-Malayan	Banana, coconut, yam
III.	Central Asiatic	Almond, cantaloupe, flax, lentil
IV.	Near-Eastern	Alfalfa, apple, cabbage, rye
V.	Mediterranean	Celery, chick pea, durum wheat, peppermint
VI.	Ethiopian (formerly Abyssinian)	Castor, coffee, grain sorghum, pearl millet
VII.	South Mexican and Central American	Lima bean, maize, papaya, upland cotton
VIII.	South American (Peruvian-Ecuadorian-Bolivian)	Egyptian cotton, potato, pumpkin, tomato
VIIIa.	Chiloé	Potato
VIIIb.	Brazilian-Paraguayan	Manioc, peanut, pineapple, rubber tree

diversity of a crop present in an area. Vavilov's original concept of eight centers of origin has been revised several times. The complexity of determining where a crop originated was described by J. R. Harlan (1971). He indicated that an assessment of the origin and dispersal of cultivated plants requires information from many fields of investigation, including genetics, chemotaxonomy, numer-

Table 11-2 Centers and Noncenters of Origin of Some Cultivated Plants, as Proposed by Harlan (1975)

	Center		Noncenter
A1:	Near East	A2:	Africa
	oat		sorghum
	cabbage		okra
	smooth bromegrass		sudangrass
	flax		oil palm
	cherry		watermelon
B1:	China	B2:	Southeast Asia and Pacific Islands
	rice		jackbean
	cucumber		eggplant
	soybean		coconut
	rapeseed		sugarcane
	peach		banana
C1:	Mesoamerica	C2:	South America
	maize		peanut
	squash		peanut
	upland cotton		tobacco
	sunflower		lima bean
	pineapple		pepper

ical taxonomy, ecology, geography, archeobotany, paleobotany, religion, history, art, and geology. Harlan suggested that the domestication of crop plants may have occurred in both centers and noncenters. In this case, a center is a limited geographical area where a crop was domesticated and from which it was disbursed to other regions of the world; a noncenter is a broad geographical area in which a crop may have been domesticated simultaneously in several different locations. Harlan proposed three centers and three noncenters. The centers are the Near East, China, and Mesoamerica and the noncenters are Africa, Southeast Asia and Pacific Islands, and South America (Table 11-2).

ACQUISITION OF PLANT INTRODUCTIONS

The procedures that have been used to obtain plant introductions for the United States are the same in principle as those that would be used in any country.

Germplasm Collection

The collection of plants in foreign countries has been an important method of obtaining plant introductions. Persons who make planned collections of plants are referred to as plant explorers or genetic resource collectors. They collect diverse genotypes of cultivated, wild, and weedy species that may have potential as breeding material in the future.

Collections of a species or its relatives are made in areas in which a high level of genetic diversity is present. They also are made in areas with specialized environments in which unique genotypes may have evolved through natural selection.

A major concern today is the rapid loss of genetic diversity in crop species throughout the world. Extensive genetic diversity for a cultivated species occurs where a crop has been grown for a long time and where cultivars developed by plant breeders are not widely used. In such areas, the seeds or vegetative propagules planted by farmers may be a random sample of the previous crop that was subjected to natural selection. The farmer might perform some artificial selection by using seeds or propagules from a group of individuals with preferred characteristics. When a crop is heterogeneous and contains many different genotypes, natural and artificial selection result in the development of thousands of different cultivars, commonly referred to as landraces. If 100 farmers use seed from their own crop year after year without exchanging seed with each other, 100 different landraces can develop, each with a unique genetic constitution. Landraces are a valuable source of genetic diversity for improvement of a cultivated species. They are rapidly being lost as farmers are provided with improved cultivars developed by plant breeders.

It is important that landraces be collected and preserved throughout the world, particularly in areas where modern cultivars are replacing germplasm that has been used for crop production for a long time. Harlan (1975) found that widespread acceptance of semidwarf Mexican spring wheat cultivars in Asia, the center of diversity for the species, has caused the rapid elimination of many landraces of the crop in some regions. Political instability and crop failures also can eliminate valuable genetic resources.

Genetic diversity present in wild and weedy species is lost as the amount of land that remains undisturbed by people decreases and as the intensity of crop production increases. By definition, a wild species is one that grows in undisturbed areas. Genotypes of wild species are destroyed as previously undisturbed land is utilized for crop production, grazing, or industrial and domestic purposes. Certain types of environmental pollution also have caused the loss of germplasm of wild species.

Weedy species are uncultivated species that grow in areas that have been disturbed by agricultural production. The increased emphasis on weed control in cultivated crops has eliminated genotypes of species that previously were tolerated in agricultural production.

The collection of germplasm is difficult because it is not possible to sample every individual in a heterogeneous population of plants. The objective is to obtain a high level of genetic diversity with a manageable number and size of samples (Hawkes, 1981). The collector must determine if plants in a population will be sampled at random or if those with particular characteristics will be chosen. An appropriate distance between collection sites must be determined on the basis of variation in the environment to which plants are exposed, including such factors as cropping practices, soil, temperature, and moisture. For each sample, the collector records field information that will be helpful in preserving, evaluating, and utilizing the germplasm.

Exchange of Germplasm

The exchange of germplasm between countries is an important source of plant introductions. The genotypes contained in the germplasm collections of various countries may not be the same because of differences in the places from which samples have been obtained. The exchange of germplasm may involve entire collections of a species or only particular genotypes with special characteristics. One example of the benefits to be derived from international germplasm exchange is the development of semidwarf wheat cultivars in North America. Two dwarfing genes were found in a short, stiff-strawed Japanese wheat cultivar, which was crossed in Japan to the improved American cultivars 'Fultz' and 'Turkey.' A dwarf cultivar, 'Norin 10,' was released in 1935 to Japanese farmers. 'Norin 10' was brought to the United States in 1946. The use of 'Norin 10' in the wheat breeding program at Washington State University led to the development of the semidwarf wheat cultivar 'Gaines,' which was widely grown in the Pacific Northwest of the United States. A 'Norin 10' derivative from the Washington

State program was supplied to breeders in Mexico, who crossed it to indigenous Mexican cultivars. Several short-statured spring wheat cultivars selected from the crosses were first grown by Mexican farmers in 1962. Mexican wheat yields, which had leveled off in the late 1950s, began to increase with the introduction of the semidwarf cultivars. The same cultivars were introduced to India, Pakistan, the United States, and other countries. It is estimated that the dwarfing genes from 'Norin 10' have affected the food supply of one-quarter of the people of the world.

International germplasm exchange also can be valuable when a new pathogen or pest becomes a problem. Maize production declined in West Africa following the accidental introduction of maize rust (*Puccinia polysora*) in 1949. Beginning in 1952, when the rust was first observed in East Africa, plant breeders in Kenya screened 68 East African lines and found no resistance. Examination of herbarium specimens showed that the origin of the rust was Central and South America. Lines of maize from Central America and the Caribbean were brought to Kenya and 45 of the 203 lines screened were resistant. By backcrossing genes from the resistant lines into adapted African lines, maize lines with adequate rust resistance were available by 1956.

Gifts of Germplasm

Plant germplasm has been used as political, scientific, and personal gifts between people from different countries. Germplasm that is obtained as a gift can be a useful source of plant introductions, if it is shared with the public agency responsible for germplasm conservation and distribution.

Purchase of Germplasm

The purchase of germplasm from another country generally applies to improved cultivars that may be of direct commercial value. The developer of a cultivar in one country may charge a fee to permit its use in another country.

MAINTENANCE AND DISTRIBUTION OF GERMPLASM

The international plant germplasm network includes the U.S. National Plant Germplasm System (NPGS), as well as the plant germplasm systems of other countries. The International Board of Plant Genetic Resources (IBPGR) coordinates the activity of all components of the international system. IBPGR is a center in the Consultative Group on International Agriculture Research (CGIAR), which is part of the United Nations Food and Agriculture Organization (FAO).

Besides national systems of germplasm collection and preservation, the CGIAR research centers, such as the International Center for Maize and Wheat Improvement (CIMMYT), the International Rice Research Institute (IRRI), and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) maintain extensive germplasm collections. The germplasm is available to scientists throughout the world.

Any individual in the United States can introduce seeds or propagules from another country if they comply with the requirements of the Animal and Plant Health Inspection Service of the U.S. Government. They have the choice of keeping the seeds for personal use or making them available to the public through the U.S. Plant Introduction system. Every individual who provides germplasm to the U.S. Plant Introduction system is contributing to present and future needs for genetic diversity.

Plant introductions are cataloged and assigned a plant inventory (PI) number by the Plant Introduction Office of the Plant Genetics and Germplasm Institute at Beltsville, Maryland (App. A). Introductions are then sent to the plant introduction station responsible for maintenance of the species. Most species are maintained at one of four Regional Plant Introduction Stations; however, some species are maintained at other sites. The environmental requirements a plant introduction has for seed production are the primary consideration in determining which station will be responsible for the plant's maintenance. Seed of plant introductions is maintained in long-term seed storage at the National Seed Storage Laboratory in Fort Collins, Colorado. Vegetatively propagated plant introductions are maintained at one of several National Clonal Repositories.

The NPGS maintains more than 400,000 accessions, both seeds and vegetatively propagated stocks. These are mostly landraces and unimproved germplasm from outside the United States. New accessions are added at a rate of 7000 to 15,000 per year.

Any individual in the United States can request and obtain seed of a plant introduction. The request can be made directly to the location that maintains the plant introduction or to one of the four regional stations. Requests are not sent to the National Seed Storage Laboratory because its seed supply is not available for routine distribution.

In 1984, the Germplasm Resources Information Network (GRIN) began operation. GRIN is a computerized data base containing information on the location, characteristics, and availability of accessions within the plant introduction system. Anyone with a valid need for information or for particular germplasm may obtain access to the system through the Database Management Unit of the Agricultural Research Service, Plant Genetics and Germplasm Institute, Beltsville, Maryland.

EVALUATION OF PLANT INTRODUCTIONS

Some characteristics of plant introductions are evaluated by the staff at the location where the plants are maintained, but the majority of the evaluation is done by other persons. Evaluation generally is the first step in the utilization of plant introductions. An individual interested in a particular characteristic from plant introductions often will evaluate part or all of the collection of a species. It may be a plant pathologist searching for disease resistance or a physiologist interested in variability for photosynthetic efficiency. Every individual who receives a plant introduction is requested to return information on the characteristics that were evaluated. The information becomes a part of the record of the plant introduction that can be shared with other interested persons. In such a manner, each person who uses plant introductions contributes to their evaluation.

UTILIZATION OF PLANT INTRODUCTIONS

When a new species is adapted for commercial production, plant introductions are used directly as cultivars. The general procedure is to introduce the best cultivars from countries in which the crop is grown commercially, evaluate their performance, and release the best ones to farmers. Plant introductions also may include experimental lines from countries where plant breeding programs for the species are conducted.

Heterogeneous plant introductions provide an opportunity for selection of superior individuals that are useful as cultivars. The evaluation and release of selections have contributed important cultivars of a new crop.

Plant introductions are one source of parents for hybridization in a cultivar development program (Chap. 10). A plant breeder responsible for cultivar development is interested in the ease and success with which genes can be transferred among genotypes. Scientific names provide a means of understanding the taxonomic relationship among plants that can be helpful as a starting point for selecting species from which useful genes may be extracted. However, the ultimate value of a species as a source of useful characteristics requires an understanding of the feasibility of gene transfer to cultivars of the cultivated species. In recognition of this fact, Harlan and de Wet (1971) proposed that species of plants be grouped into one of three gene pools.

1. *Primary gene pool:* The primary gene pool includes the cultivated species of a crop and related species from which useful genes can be most readily obtained for a cultivar development program. Species in the primary gene pool can be readily crossed, chromosome pairing during meiosis in F_1 plants is normal, and F_2 seed is produced. The segregation of genes in populations obtained from F_1 plants is predominantly normal.
2. *Secondary gene pool:* Species in the secondary gene pool include those from which genes can be transferred to the cultivated species, but not without difficulty. When genotypes of the cultivated species are crossed to those in the secondary gene pool, hybrid seed can be obtained, but the F_1 plants may be weak and difficult to maintain, chromosome pairing during meiosis in the hybrids may be poor or not occur at all, and the

hybrids tend to be sterile. Progeny that are obtained from hybrid plants may not exhibit normal gene segregation, and recovery of segregates with the desired genes from a species of the secondary gene pool may be difficult.

3. *Tertiary gene pool:* Gene transfer from a species in the tertiary gene pool to the cultivated species in the primary gene pool requires special techniques or may not even be possible with the techniques currently available. Crosses can be made between some species in the tertiary and primary pool, and fertilization may take place to produce a hybrid embryo. If mature hybrid seed cannot be obtained, it may be possible to use embryo culture to obtain a viable hybrid plant. If hybrid seed is obtained, the hybrid plant may die prematurely or be completely sterile. Grafting or tissue culture may be required to secure a viable hybrid plant. Chromosome doubling may be required to obtain some fertility in the hybrid.

Of the three sources of genes, the primary gene pool receives the greatest attention for cultivar development. A plant breeder will rely on genotypes of the cultivated species as the primary source of genetic variability. When a character is not available in cultivars or plant introductions of the cultivated species, related species in the primary gene pool will be evaluated for the characteristic. The related species in the primary gene pool may include the wild progenitor of the crop or weedy species. The wild and weedy species often have characteristics that are unacceptable in cultivars of the crop, including shattering, lodging susceptibility, colored seeds, and small seed size. Developing a cultivar that has a desirable characteristic from a wild or weedy species generally involves multiple backcrosses to a recurrent parent of the cultivated species. Linkage between genes controlling the desirable characteristic and those controlling undesirable ones may make the transfer difficult.

The secondary gene pool generally is not considered as a source of genes for cultivar development unless the desired genes are not available in the primary gene pool. Some genes that have not been found in the primary gene pool, but are present in the secondary gene pool, have proven to be useful in the improvement of cultivated species, particularly for pest resistance. The breeder who intends to use genes from a species in the secondary pool must consider such barriers as lack of vigor and a high degree of sterility in hybrid plants. In addition, the species would likely have numerous unacceptable characteristics that would have to be eliminated through repeated backcrosses to the cultivated species.

Use of genes from the tertiary gene pool generally is only considered if a characteristic is lacking in the primary and secondary pools. The breeder has to be willing to spend a considerable amount of time making the gene transfer. Specialized training might be required to obtain the skills needed to carry out certain procedures involved with gene transfer.

It should be emphasized that extensive experimentation is required to determine the species that fit in each of the gene pools. This is particularly true of the tertiary gene pool. Relatively few persons specialize in the basic research necessary to evaluate the feasibility of gene transfer from species that are not closely related to the cultivated one. Expanding research in tissue culture and molecular biology may expand the usable tertiary gene pool of crop species in the future.

CONSEQUENCES OF INSUFFICIENT GENETIC DIVERSITY

Two aspects of genetic diversity influence how cultivars are developed, how they are used in agricultural production, and what the consequence may be if sufficient diversity is lacking. One aspect is the genetic vulnerability of the crop to an unexpected production problem. The second relates to the continued improvement of cultivars for quantitative characters, such as yield.

Genetic Vulnerability

Genetic vulnerability refers to the possibility that an unexpected problem could cause a major loss in the production of most or all cultivars of a crop. This possibility was highlighted by the epidemic of southern corn leaf blight that endangered maize production in the United States during the early 1970s. Hybrid seed maize was produced in the 1960s by use of cytoplasmic-genetic male sterility. All of the female parents used to produce hybrid seed maize had male-sterile cytoplasm derived from the same source, referred to as T cytoplasm. As a result, all maize hybrids, regardless of their diversity for nuclear genes, were related by a common cytoplasm. A race of the southern corn leaf blight developed that had the ability to attack maize plants with T cytoplasm, which meant that the entire U.S. maize crop was vulnerable to the pathogen. Hybrid seed companies rapidly increased seed of female parents with male-fertile cytoplasm (B lines) that were not susceptible to the pathogen. The female parents with male fertility were emasculated by detasseling in hybrid seed production fields. The conversion to male-fertile cytoplasm was rapid and loss from the disease was minimal. Nevertheless, the situation made the public aware of the danger caused by lack of genetic diversity. A subsequent study conducted by the National Academy of Science (1972) on the potential genetic vulnerability of major crops grown in the United States found most major crop cultivars to be genetically related and potentially vulnerable.

Limitation of Genetic Improvement

Insufficient genetic diversity in the parents used to form populations by hybridization may lead to a reduction in genetic variability for quantitative characters. As a result, improvement of the character may be difficult or impossible to achieve. This potential consequence of limited genetic diversity can be more difficult to evaluate and to overcome than that of genetic vulnerability. Many factors affect the degree of success from breeding in a crop, and it is difficult to identify clearly the effects of any one factor. It is difficult to determine whether a yield plateau has been reached in a crop, because yield improvement often does not occur at a constant rate. Breeders commonly conduct selection for several years before identifying a genotype that shows significant yield improvement. Because yield improvement often is sporadic and unpredictable, many years with no yield increase may be needed to be certain that a yield plateau has been reached. It also is important to determine whether a period without yield improvement is a result of the lack of genetic variability or due to insufficient emphasis on selection for yield. A breeding program that emphasizes improvement of characters other than yield can create an apparent yield plateau by restricting the parents that are used for crossing. Simultaneous selection for several characters also can restrict yield improvement, even though sufficient genetic variability for yield may be present.

MINIMIZING GENETIC VULNERABILITY

Systematic reduction of genetic vulnerability involves three interrelated steps: (a) the monitoring of pests or any other production problems that have the potential of becoming a threat to crop production, (b) the development of cultivars that will not be seriously influenced by the potential problem, and (c) the use of these cultivars for crop production.

Monitoring of Potential Problems

The systematic monitoring of crop pests is a worldwide project. Consideration must be given to new races of pests that are already in a country, and to new pests that may be introduced from other countries. The development of a cultivar with resistance to a pest can take many years. The early detection of a potential problem gives the breeder an opportunity to have appropriate cultivars ready, if they are needed.

Development of Cultivars with Increased Genetic Diversity

There is usually no simple way to increase the genetic diversity of cultivars of crops that already have been improved by plant breeding. The progeny of a cross between high-yielding parents are more likely to have superior yield than those from a cross between a high- and a low-yielding parent. For that reason, a plant breeder who is responsible for developing improved cultivars for yield and other quantitative characters in the immediate future will choose as parents those with the highest level of performance available. Plant introductions generally have poorer overall performance and may have major weaknesses not present in current cultivars. Populations developed from crosses between plant introductions and current cultivars generally are inferior to those available from crosses among

Table 11-3 Characteristics for Seed Yield of Five Soybean Breeding Populations with Different Levels of Plant Introduction (PI) Parentage

Population	Percent of PI Parents	Population $\overline{X}$ Yield (kg/ha)	Number of Superior Lines	Genetic Variability
AP1	100	2304b*	5	8,150 ± 4,783
AP2	75	2244c	1	24,234 ± 6,919
AP3	50	2293bc	7	29,185 ± 7,595
AP4	25	2338b	10	24,413 ± 6,942
AP5	0	2441a	22	13,926 ± 5,533

*Means followed by the same letter are not significantly different ($P > 0.05$) based on Duncan's multiple range test.

Source: Schoener and Fehr, 1979.

elite related parents. This has been illustrated by the performance of five populations of soybeans with different percentages of germplasm from plant introductions (Schoener and Fehr, 1979). The population with the greatest mean yield and the highest frequency of high-yielding segregates was the population that was developed from cultivars and elite breeding lines (Table 11-3).

A plant introduction may be desirable as a parent because it possesses an essential characteristic such as disease resistance. In this situation, it is a common practice to transfer the appropriate genes to local cultivars by backcrossing. Each generation of backcrossing reduces the likelihood that unique alleles for yield and other quantitative characters from the plant introduction will be present in the backcross progeny. It is doubtful, therefore, that plant introductions used as donor parents in a backcrossing program have contributed substantially to genetic variability for quantitative characters.

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