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Working Paper 96-02

Understanding Global Trends in the Use of Wheat Diversity and International Flows of Wheat Genetic Resources

Melinda Smale

with contributions from

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CIMMYT

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Abstract: This paper discusses the centers of origin and diversity for bread wheat; sketches historical patterns in the sources and use of wheat genetic resources in modern plant breeding; identifies and compares indicators of genetic diversity used by social and biological scientists; reviews the relationship of wheat genetic diversity to yield stability and vulnerability to disease; develops a profile of the structure of genetic variation in wheat in the developing world today; and investigates how scientific plant breeding has influenced the structure of genetic variation among the major bread wheats grown in developing countries. Modern plant breeding appears to have contributed to genetic variation in several ways. The number of different landraces in pedigrees has steadily increased over the past 30 years, and the geographical origins of the landraces have broadened. The pedigree complexity of the more successful cultivars planted in the developing world has grown over time. Yield stability, both in terms of the performance of individual lines and in terms of regional yields, on farms, appears to have increased in the past decades. The diversity that confers resistance to the wheat rusts has also increased. Diversity over space and time varies among regions of the developing world. Spatial diversity, measured as the percentage area sown to leading modern cultivars, is lowest in West Asia and highest in Mexico/Guatemala. Temporal diversity is highest in Mexico/Guatemala, lowest in North Africa, and also fairly low in South Asia. However, both spatial and temporal diversity are fairly high for many developing countries compared to some of the major industrialized producers, such as Canada. Latent diversity, calculated from pedigree analysis, is fairly high across the developing world and does not appear lower than in the major industrialized wheat producers. Genetic distance measures calculated from genealogies demonstrate the comparative diversity among the top 10 bread wheats grown in West Asia and the marked similarity of wheats grown in Mexico/Guatemala and Canada. Numerous socioeconomic factors, which future research must examine more closely, have shaped the structure of genetic variation in farmers' fields. These factors are related to the adoption and diffusion of new varieties and include pricing policies for seed and associated inputs, and the structure of the seed multiplication and distribution system.

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Executive Summary

This paper, which presents initial results of CIMMYT's continuing study of wheat genetic diversity:

- summarizes the current scientific understanding of the centers of origin and diversity for bread wheat;
- traces historical patterns in the sources and use of wheat genetic resources in modern plant breeding;
- identifies and compares indicators of genetic diversity used by social and biological scientists;
- reviews the relationship of wheat genetic diversity to yield stability and vulnerability to disease;
- develops a profile of diversity among modern wheats in the developing world today, by applying indicators of genetic diversity to genealogical information and data on wheat releases and adoption; and
- investigates how scientific plant breeding has influenced the pattern of genetic variation among the major bread wheats grown in the developing world.

Our larger objective is to understand how international agricultural research can enhance the genetic diversity in wheat that may be of value to present and future generations of farmers in the developing world.

Centers of Origin and Diversity for Bread Wheats

Bread wheat (*Triticum aestivum*, a hexaploid) is a relative latecomer among cereals. The center of origin of diploids, tetraploids, and other relatives of bread wheat is believed to be West Asia, but the origin of bread wheats may be different, and more than one origin is possible. The origin of wheat has been characterized as "diffuse," and centers of diversity are thought to have evolved later as wheats dispersed. The evolution of the bread wheats is closely associated with social evolution, because bread wheat has been found only in domesticated form; it is one of the few crops grown today for which no wild forms have been identified.

How Worldwide Germplasm Flows Shaped the Evolution and Development of Cultivated Bread Wheats

International flows of genetic resources have long been multidirectional. By the second millennium, farmers had dispersed wheat cultivars from West Asia as far as Northern Europe, North Africa, the Asian Subcontinent, and China. From approximately 1500 to at least 1900, migrants and settlers from Eurasia and the Mediterranean carried seed to southern and eastern Africa, Australia, North and South America, and back again. Starting in the late 19th century, scientific plant breeders exchanged wheat seed. The varieties developed by early scientific breeding programs in Europe, India, Australia, North and South America, and China contain a similar core of landraces from six continents. These landraces were used and reused when wheat breeders exchanged germplasm.

The landraces most frequently appearing in the pedigrees of the bread wheat cultivars grown in the developing world today (low- and middle-income countries) originated in regions now considered part of the high-income world or in the Former Soviet Union and Eastern Europe.

A common popular misperception is that genetic narrowing in wheat began in the mid-1960s, when farmers worldwide adopted the semidwarf wheats developed by Japanese, U.S., and Mexican-based scientists. In the strictest sense, genetic narrowing actually began in wheat more than 9,000 years ago, when einkorn and emmer were domesticated. Ever since, genetic change has been intimately associated with changes in crop husbandry. Changes in farming systems were probably a major source of genetic narrowing in the wheat cultivars grown in the 19th century. In the early decades of the 20th century, farmers' fields came to be dominated by tall modern wheat varieties developed by professional breeders. In several major bread wheat producing nations, the area sown to just a few modern cultivars appears to have been greater than it is now. The commercialization of agriculture, the limitations of nascent seed industries, and government regulations were important factors affecting the distribution of scientifically bred cultivars. In a general sense, breakthroughs in achieving genetic "diversity" at one point in time are a potential source of genetic narrowing at another, precisely because scientific breakthroughs in wheat research often produce wheat cultivars that are attractive, widely adopted by farmers, and subsequently used as key breeding material.

It is important to remember that although most bread wheats grown today are modern cultivars, modern plant breeding itself can contribute to genetic variation. The number of different landraces in pedigrees has steadily increased over the past 30 years at least, and the geographical origins of the landraces have broadened. Various characteristics of wheat pedigrees suggest that the pedigrees of the more successful cultivars planted in the developing world have grown more complex. Large numbers of different landraces, generations, and crosses are now contained in the pedigrees of widely grown cultivars.

Measuring Genetic Diversity in Wheat

Unless we can measure genetic diversity, we cannot ascribe an economic value to it. A more comprehensive picture of genetic diversity in wheat can be developed through inspecting and comparing different indicators of diversity, but a preliminary step is to understand better what each indicator in fact measures, as well as its limitations.

Perspectives from breeding programs. Genetic variability is a vital issue for plant breeders because proper management of this diversity can produce a permanent gain in the performance of a plant. Biological scientists can measure many types of diversity in the context of breeding program activities, from the gene bank and laboratory to on-farm trials. Methods for detecting genetic diversity at the molecular level include the use of biochemical and molecular markers. Biochemical markers include isozymes. Isozyme techniques are comparatively inexpensive and powerful methods for measuring allele frequencies for specific genes, but because there are few isozyme systems per species (not more than 30), there are relatively few markers. Molecular markers are more expensive to use, but now thousands of known markers for several species enable a much larger number of genes to be studied, as well as other locations in noncoding segments of the chromosome. Molecular geneticists' techniques can be used to classify lines, populations, and landraces and to establish genetic links with traits of agronomic and economic interest and detect their genetic variation. Once genes and alleles related to the expression of a trait can be identified, the allele frequencies in a segregating population can be described by a standard set of summary statistics, and the apportionment of genetic variation within and between populations, races, or cultivars can be summarized and compared by multivariate analysis. However, despite its great power, the molecular study of plant genetic diversity is in its infancy, and detailed investigations of gene variation in wheat are still few.

Classical Mendelian genetic analysis can also be used to evaluate variation in single, known genes (qualitative traits), such as those conferring certain types of disease resistance. Forms of multivariate analysis can be used to analyze the variation in traits whose expression is governed by one or more gene loci. Pairwise coefficients of parentage can be calculated from pedigree information and used as indicators of genetic diversity. The coefficient of parentage has been described as an indicator of *latent genetic diversity;* it measures the probability that two cultivars are identical by descent for a character (observable or unobservable) that varies genetically and is not expressed as a result of intensive selection by plant breeders. Genetic distance measures can be calculated with molecular, morphological, or genealogical data. Often, however, the empirical relationship between molecular and other indicators is weak.

When they develop lines, scientific plant breeders seek genotypic variation for traits of economic value, such as yield. In trials on experiment stations and on farmers' fields, crop scientists use a number of statistical methods to separate the different types of variation observed in key traits by the sources of that variation — genotype, genotype-by-environment interactions, and environment.

Perspectives from social science. The focus of social scientists' concern is genetic diversity as it is recognized by farmers and as it is valued by different social interest groups. In the more detailed case studies that constitute an important part of research on genetic diversity in farmers' fields, human ecologists and anthropologists have attempted to understand and relate farmers' knowledge systems and taxonomic classifications to those recognized by biological scientists. In other studies, researchers have surveyed farmers to elicit information about the number of cultivars and area planted by source of seed, trait, and use.

At the other extreme from field-based studies are those based on secondary sources and published data. On the basis of broad distinctions such as cultivar names or classifications such as "modern" and "traditional," cultivar numbers or the percentage distributions of crop area by cultivar type have been used as measures of *spatial diversity.* Changes in these counts or area distributions over time provide measures of diversity in time. Other measures of *temporal diversity* include the average age and weighted (by area) average age of cultivars. Genealogical characteristics, such as the number and origin of landraces, and the number of breeding generations since the first cross, have also been used as indicators of diversity.

Genetic diversity and yield stability. In many developing countries, national food consumption depends largely on a small number of staple crops. Stability in national yields for the staple crops is generally believed to be beneficial under such conditions: not only do unexpected food imports place a burden on road and distributional systems, but imports often must be purchased under disadvantageous world market conditions. Unfortunately, discussions of "yield stability" among social and biological scientists are often hampered by language barriers, because they use the term to denote different phenomena. As a consequence, the impact of plant breeding on national crop yields relative to other determinants of yield is not easily understood.

When plant breeders test the lines they develop, they look for individual genotypes whose yields are stable over a broad range of environments. The most common method of assessing the yield stability of a genotype is to relate (through statistical regression) its mean yield by site to the mean yields for all genotypes by site. The mean yields for all genotypes by site, adjusted by the overall mean, is used as an environmental index. A regression slope of one implies that the genotype performs similarly across sites.

The expression of complex characters such as yield is heavily influenced by environmental conditions. Analysis of data from scientific trials often reveals that only a small proportion of yield variation is attributable to differences among genotypes, or even to genotype interactions with locations and years. Most variation results from differences among locations or years.

The variation in crop yields across regions is clearly influenced by many additional factors. Economists typically use the coefficient of yield variation, or the ratio of the standard deviation to the mean, as a measure of crop yield stability. They use time-series estimates of crop yield data, detrended to take out the effects of a rising mean over time, for given intervals. In this calculation, all wheat cultivars are grouped and yields are aggregated at the district, national, regional, or global level, depending on the focus of the analysis. Statistical regressions of the coefficient of yield variation on explanatory factors reveal that year-to-year variation in national yields primarily reflects changes in weather and the use of crop management inputs rather than varietal change. For social scientists and policy makers concerned about the stability of aggregate yields, the most important determinants to consider are thus price policies, input supply, and crop management practices.

Genetic diversity and vulnerability to disease. A common misperception in discussions of genetic diversity is that visible uniformity among cultivars is necessarily associated with *genetic vulnerability* to disease and other stresses. Crops can be relatively uniform in many respects and remain invulnerable to disease. Genetic diversity in and of itself provides no insurance against disease, because vulnerability can be latent, expressed only when new, virulent strains of pathogens evolve. Diversity can be hidden or expressed only in changing environments. Uniformity can also be hidden, when varieties that are visibly diverse are identical in the gene or genes that create the conditions for susceptibility.

What preoccupies most plant breeders and plant pathologists today is how to obtain disease resistance that endures through time. The rusts are historically the most important wheat diseases, as well as the best understood. Many scientists now breed for polygenic, durable resistance to rust by accumulating (in a single cultivar) genes from diverse sources and genes controlling various mechanisms of resistance. In the 1970s, as interest grew in agricultural systems that mimicked natural ecosystems, the possibility of combating disease through "alternative" genetic strategies of multiline varieties and varietal mixtures became increasingly popular.

Although susceptibility to disease affects the inherent resistance in a genotype(s), it is the extent of a genotype's contiguous cultivation that determines the probabilities of an epidemic. The principal strategy that plant breeders and pathologists pursue to forestall epidemics is to maximize diversity across space and time by recommending changing portfolios of cultivars. This preventive approach is influenced heavily by public policy. Public policy plays an important role in disease development and control, because the success of many control strategies devised by scientists depends on decisions by governmental or public institutions and the allocation of public resources for disease control.

Evidence on Genetic Variation among the Major Bread Wheats Grown in the Developing World

Empirical evidence on the structure of genetic variation in bread wheat, primarily in the developing world, was constructed by applying several indicators of diversity to data from genealogical information bases, global surveys, and trials.

Yield stability, both in terms of the performance of individual lines and in terms of regional yields, on farms, appears to have increased in the past few decades. One aspect of genetic diversity that has direct economic value in terms of yield savings — the diversity that confers resistance to the wheat rusts — has also increased over time.

In the developing world, bread wheats occupy far more area than durum wheats, and a greater area is sown to modern (tall and semidwarf) varieties of bread wheat than durum wheat. The more important a region is in terms of area sown to bread wheat, the less diverse it is in numbers of different crosses grown per million hectares. Spatial diversity, measured as the percentage of area sown to leading modern cultivars, is lowest for West Asia and highest in Mexico/Guatemala. The number of crosses per million hectares is very low in South Asia, one of the largest bread wheat producers in the developing world, and the percentage of area sown to only a few leading cultivars in this region is very high (for example, in Punjab, the major wheat-producing state of India).

Temporal diversity is highest in Mexico/Guatemala (primarily because of Mexico) and lowest in North Africa (a region where bread wheats are less important than durum wheats), but temporal diversity is also fairly low in South Asia. However, temporal diversity is fairly high for many developing countries compared to some of the major industrialized producers, such as Canada.

Latent diversity, as calculated from pedigree analysis, is fairly high for the regions of the developing world, and it does not appear lower in the developing world than in the major industrialized, wheat-producing countries of Australia, Canada, or the U.S. When the data are weighted by the percentage distribution of area planted to cultivars, they show even more clearly that average diversity decreases for all the regions in the developing world but that it decreases by a smaller magnitude than for Canada, for example. The socieconomic factors that affect adoption can strongly influence latent diversity in farmers' fields. Genetic distance measures, calculated from cluster analysis of pairwise coefficients of diversity among the cultivars grown in each region, demonstrate the comparative diversity among the top 10 bread wheats grown in West Asia and the marked similarity of those grown in Mexico and Guatemala as well as Canada. Again, South Asia ranks fairly low among the developing country regions for latent diversity indicators.

Conclusions

Genetic diversity is difficult to measure because it has many dimensions and is difficult to discuss because the biological and social scientists who study it may not share a common technical language, although they share common goals. Even within a single discipline, researchers may use various approaches to measure the same dimension of genetic diversity, without necessarily generating consistent results. If we do not understand the meaning of genetic diversity and the limitations of our measurement techniques, however, methods for valuing diversity and assessing policy tradeoffs will have no scientific basis. Without a scientific basis, economic analysis of genetic diversity issues will have at best little utility and at worst dangerous consequences.

Several issues for future research emerge from this review. First, is it cause for concern that certain "blocks" of ancestors are common to the major wheat varieties grown in the developing world today? Second, the major wheats grown internationally have a relatively high similarity of parentage, owing to their common CIMMYT ancestry. Does this similarity of parentage matter, given that, because of international collaboration, the genetic base of CIMMYT bread wheats is so much broader than anything available within most national boundaries? Third, what if molecular analysis shows that the largest genetic contributors among landraces in the pedigrees of today's major wheats share the same DNA sequences because of earlier germplasm flows, even though the names and national origin of the major wheats appear distinct?

Finally, although this paper has examined the relationship between scientific wheat breeding and genetic diversity, it is important to emphasize that numerous factors play a larger role than scientific plant breeding in shaping the structure of genetic variation in farmers' fields in the developing world today. These factors are related to the adoption and diffusion of new varieties (such as pricing policies for seed and other inputs), to the mechanization of agriculture and industrial processing, and to the structure of the seed multiplication and distribution system. The positive influence of evolving seed systems on the diversity of wheats grown is shown clearly by the downward trends in area sown to leading cultivars and by the increasing temporal diversity during the 20th century in many industrialized countries. Another indication that factors other than breeding influence the diversity in farmers' wheat fields is the large difference between the average similarity of parentage of wheat releases and the weighted similarity of parentage of wheats grown in farmers' fields in India's Punjab. Yet it is also clear that maximizing spatial diversity in farmers' fields can have costs in terms of short-term yield losses, not only for a nation, but for individual farmers. These trade-offs will need to be investigated both empirically and theoretically.

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Introduction

The current debate over the role of scientific agriculture in reducing or enhancing biodiversity reflects a general concern for the "loss of complexity" in natural and agricultural systems (Dempsey 1990). The meaning of "complexity" differs by interest group. For example, ecologists express their concern in terms of the declining numbers of species that compose the natural resource base on which the livelihood of future generations depends. Philosophers question the ethics of policy decisions that influence the survival of species. Social scientists who study technical change in agriculture are concerned that specialization and commercialization will make rural communities vulnerable to sudden price swings, seasonal crop failures, or longer term shifts in the agricultural terms of trade. Plant pathologists focus on the probability of crop failure resulting from genetic vulnerability to disease, which is a particularly serious threat in countries where physical infrastructure or policies limit the government's capacity to respond to epidemics. Crop breeders are specifically concerned about the breadth of a species' genetic pool, because that is the reservoir they must draw upon in seeking continued gains in crop productivity and host plant resistance.

The sheer number of stakeholders and interest groups represented in the debate makes reaching a common understanding of genetic diversity difficult but essential. Defining terms and using them appropriately across disciplines is also a problem, even when the discussion is limited, as it will be here, to diversity within a species. For social scientists, the indicators used to gauge diversity within a given crop species in farmers' fields are the number of cultivars, the proportion of area planted to cultivars, and the rate at which farmers switch from one cultivar to another. Biological scientists use genealogical indicators, the analysis of morphological characteristics, and indices of gene frequencies constructed from biochemical or molecular markers. The indicators used by social scientists therefore measure different aspects of genetic diversity than those used by biological scientists. Not only do the indicators measure different phenomena, but the empirical relationship among them is sometimes weak. For example, the effect of genetic diversity on yield is complicated to determine because yield reflects the combined action of many genes. Once plants are grown in farmers' fields, variation in average yield is influenced not only by factors associated with plant breeding, but by agroclimatic circumstances and the economic factors and policies that affect the use of land, water, and other inputs.

Even within a single discipline, the discussion of genetic diversity challenges the frontiers of knowledge. For example, a crop is often assumed to be more vulnerable to evolving pathogens if many cultivars possess the same genes for disease resistance, but in fact pathologists recognize that the relationship between genes and disease resistance remains only partially detectable. Stem rust disease in wheat has been contained for about 40 years because a gene complex conferring resistance was bred into leading cultivars, but why this resistance has held is still not completely understood. Researchers have identified only some of the genes responsible for the resistance.

Another example concerns the role of biotechnology in wheat genetic diversity. On the one hand, biotechnology may expand the genetic variability of any species by introducing genes originating in distant species or even wholly synthesized in the laboratory. In this way, biotechnology helps researchers breach the "crossing barrier" that once limited conventional wheat breeding. On the other hand, a single isolated gene cannot be well understood as the basic unit of genetic resources, since a gene always acts in combination with other genes of the wheat genome, many of which may today be unknown. The potential contribution of biotechnological techniques to wheat genetic diversity is therefore best understood in combination with or in support of, rather than as distinct from, conventional breeding methods.

The preliminary work summarized here, which is drawn from CIMMYT's continuing study of wheat genetic diversity, has several purposes. One purpose is simply the identification, comparison, and application of indicators of genetic diversity used by social and biological scientists involved in crop research. A second purpose is to trace historical patterns in the sources and use of genetic resources in modern plant breeding. A third purpose is to characterize the structure of genetic variation among the major bread wheat varieties grown in the developing world today and to investigate how scientific plant breeding has influenced that structure. Our overall goal is to understand how international agricultural research can enhance the genetic diversity in wheat that may be of value to present and future generations of farmers in developing countries.

This paper gathers together the background material and analyses for our continuing study. The next section, intended primarily for readers who are unfamiliar with wheat science, outlines the current scientific understanding of bread wheat's centers of origin and diversity. The characteristics of these centers are distinct from those of the other major cereal crops such as rice and maize. The third section describes the movement of wheat germplasm across the millenia and discusses how this germplasm has been used and reused by farmers and modern plants breeders. The empirical information presented should be of interest to wheat scientists as well as other readers. The fourth section of this paper, "Measuring Genetic Diversity in Wheat," is largely intended for readers unfamiliar with wheat science. It defines genetic diversity, compares indicators of genetic diversity, and reviews the relationship of genetic diversity to yield stability and vulnerability to disease. The next section, "Evidence on Genetic Variation among the Major Bread Wheats Grown in the Developing World," applies several diversity indicators to genealogical information and data on releases and adoption of wheat cultivars in order to develop a profile of the pattern of genetic variation in wheat in the developing world today. The paper concludes by identifying some of the outstanding research issues raised by the analysis.

The scope of this background paper is necessarily limited by the information that is available. In the empirical analysis we have used various databases to characterize the global structure of within-species variation of the major bread wheats grown in the developing world. Although we have limited our analysis to bread wheat, we discuss the genetic contribution of durum wheat to bread wheat. We have constructed broad indicators among major bread wheat varieties grown today, although we have excluded cultivars that are grown on very small areas and which constitute some of the remaining diversity in farmers' fields. However, we mention the importance of these materials and the shrinking area they occupy in various microcenters throughout the world. By using genealogical analysis, we have started the genetic clock when pedigrees were first recorded by scientific plant breeders. Even so, we attempt to broaden our pedigree analysis with secondary information on the origins of landraces. We have focused on the major historical diseases of wheat, the rusts, because they are the best understood by science, although other diseases are gaining importance as cropping systems and environments change.[1]

The research described in this paper represents only one aspect of CIMMYT's current work on genetic diversity. We have also begun a systematic examination of issues related to the conservation of crops *in situ,* and we are attempting to develop methods for valuing certain aspects of genetic diversity. We believe that any economic analyses of wheat genetic diversity must be founded on an understanding of the scientific basis for measuring genetic diversity and a recognition of its scope and limitations. This paper is our first step in that direction.

Centers of Origin and Diversity for Bread Wheats

The Origins of Wheat

All of the wild and cultivated wheats we know may be classified into three groups on the basis of their genomes (AA, AABB, or AABBDD): (1) the diploid *Triticum monococcum* (einkorn); (2) the tetraploids *T. turgidum* (durum and emmer wheat); and (3) the hexaploid *T. aestivum* (bread wheat).[2,3] The source of the A genome is generally believed to be *T. urartu,* the source of the B genome is disputed, and the source of the D genome of bread wheats is generally understood to be *T. tauschii* (*Aegilops squarrosa*) (Mujeeb-Kazi, Rosas, and Roldan 1996).

Cultivated einkorn (AA), descended from a wild subspecies through mutation, still forms a component of the Zanduri wheat population found in Georgia of the Former Soviet Union (F.S.U.) and is a useful source of disease resistance (Zeven and de Wet 1982). The wild and cultivated emmer wheats (AABB) can be found in southern Turkey-Iraq-Iran, Israel,

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[1] See Appendix A for additional details on the sources of data for this paper.

[2] The exceptions to this classification are the tetraploid *T. timopheevi* (AAGG) and the hexaploid *T. zhukovskyi* (AAAAGG). *Triticum timopheevi* has a wild form that grows fairly widely in Southeast Asia and a cultivated form that is grown only in the Caucasus. *Triticum zhukovskyi* grows only in the Caucasus.

[3] Diploids, such as the wild grasses and primitive wheat that donated the genomes for durum and bread wheats, have seven pairs of chromosomes. The tetraploid wheats, including durum wheat, contain 14 pairs of chromosomes. Hexaploids have 21 pairs of chromosomes.

southern Syria, and Jordan, as well as in Ethiopia, India, and the Mediterranean countries. Emmer may have been domesticated earlier than einkorn and was the predominant type of wheat cultivated throughout Europe and the Mediterranean for thousands of years before durum wheat appeared. Farmers still sow the disease-resistant *khapli* (vernacular name of emmer) of India and Yaroslav emmer from the F.S.U.

Durum wheat (also AABB) is still grown widely in Italy, Spain, North Africa, West Asia, Ethiopia, the F.S.U., and the U.S. Bread wheat (AABBDD) is the most widely grown species of wheat. The cultivated bread and durum wheats are descendants of hybridized wild grass species. Durum wheat is a hybrid that occurred spontaneously between a wild grass and primitive diploid wheat. Bread wheat is the product of a later spontaneous hybridization between a tetraploid wheat and the diploid wild grass *T. tauschii* (*Ae. squarrosa*) (Figure 1), known as "goat grass" and found in the wheat fields of Asia Minor. Scientists speculate that events leading to the formation of today's wheats may have occurred many times in nature, rather than as a single hybridization event.

Knowledge of the ancestry of today's cultivated wheats is important for understanding the range of genetic diversity in their primary and secondary gene pools and the potential for incorporating useful genes or gene complexes, such as those that confer disease resistance or stress tolerance, into new cultivars. Bread wheat is one of the few crops grown today for which no wild forms have been identified, although bread wheat's primary gene pool contains species that have wild forms and continue to share a natural gene flow with wild grasses.

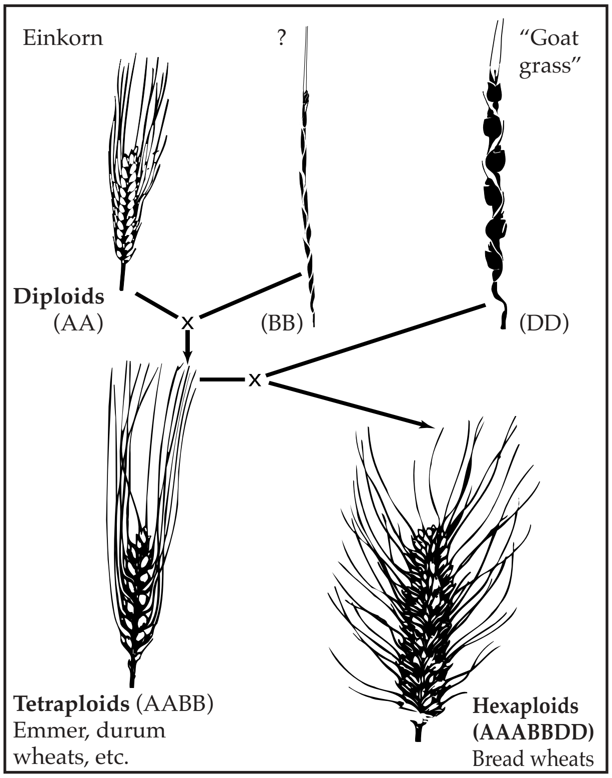


Figure 1. Origin of cultivated wheat types.
Source: Hancock (1994).

Bread wheat is a relative latecomer among cereals, and its domination of cultivated area in Europe and North Africa did not occur until historical times (Harlan 1987). Particularly during the Neolithic Dispersal of cereals that was associated with the evolution of stable food-producing economies between 6000 and 3000 B.C., wheats were distributed over Pakistan, the Indus Basin, China, Europe, and North Africa. Although evidence suggests that bread wheats were cultivated by that time in Asia, emmer and other wheat forms remained dominant in Europe and North Africa. Harlan (1987) has hypothesized that the food demands of the urban population in the Roman Empire, combined with the emergence of bakers' guilds, contributed to the conversion of Rome to baked bread and of the entire Mediterranean Basin to bread wheats by about 300 B.C.

If bread wheat has been cultivated since the hybridizations that produced it, then bread wheat has been relatively isolated from other species, and its genetic variation may be minor compared with the variation found in some of its wild progenitors and other relatives. According to some scientists, the utilization of bread wheat landraces maintained in collections offers only limited possibilities for breeding programs, because the gene pool was constituted after domestication (Jaaska 1993). Sharma and Gill (1983) conclude that durums, emmers, and other species and genera have contributed at least as much as bread wheat landraces to bread wheat breeding programs and appear to have received much more attention from researchers. An opposing point of view is that the wide range in growth habit, responses to environment, and disease among the cultivated bread wheats is evidence of considerable genetic variation (L.T. Evans, pers. comm.).

In any case, wild germplasm undoubtedly constitutes a valuable resource for bread wheat improvement (Cox, Murphy, and Goodman 1988; Mujeeb-Kazi and Hettel 1995). With special techniques, including wide crosses, genetic transformation, and other tools of biotechnology, genes from many species can be incorporated into bread wheat, thereby expanding the genetic base (see "Adding New Dimensions to Genetic Variability in Bread Wheats," later in this paper).

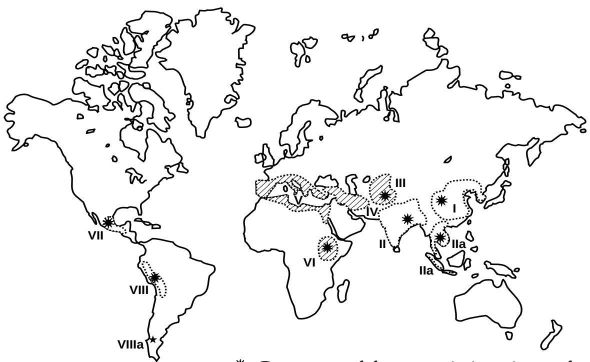
Geographical Centers of Origin and Centers of Diversity

Much debate has surrounded the identification of centers of origin and diversity for cultivated plants, including wheat. Russian scientist N.I. Vavilov pioneered the definition of crop origins. He identified geographical "centers of origin" for major crops based on patterns of variation observed in collections made from each species (Vavilov 1926, 1951; Figure 2). Vavilov's centers of origin and diversity have been used extensively in theories of crop evolution and, more recently, in devising strategies for collecting germplasm. In the early part of this century, Vavilov and his colleagues found that over most of Europe and Siberia, wheat cultivation was already based on a rather restricted number of bread wheats. Anatolia, Syria, Palestine, and Transcaucasia contained other forms and types of wheat (Zohary 1970). Vavilov and his colleagues also defined several other centers of variation, including the Ethiopian Plateau and Mediterranean Basin for durum wheats and Afghanistan for bread wheats.

Vavilov's central idea was that a cultivated plant species' place of origin would be found in the area that currently contained the largest number of varieties of the plant. This idea was based on the assumption that the selective forces of the environment operate in about the same manner through the evolutionary history of a given species. The longer a given species had occupied a given area, the greater the number of variations it would produce. Vavilov's work has since provoked controversy. Vavilov himself recognized that his original hypothesis was a simplification. In Ethiopia, for example, he found the greatest diversity in durum wheats without a single wild relative. Zhukovsky (1975) expanded Vavilov's centers into "mega-gene centers and micro-gene centers" in an effort to incorporate later evidence, but his classification has the analytical disadvantage of being all-encompassing. Since all regions of the world are included, centers are not sharply differentiated.

Another problem is that since Vavilov's initial proposition, the concepts of centers of diversity and centers of origin have often been used interchangeably. Researchers have applied statistical techniques to "test the Vavilovian hypothesis" by comparing the variation in observable (morphological) characteristics of wheat plants within so-called centers of origin and between these and other zones. Results have been mixed (for example, see Jain et al. 1975; Witcombe and Rao 1976; Witcombe and Gilani 1979; Porceddu 1976).

Scientists have also learned that, contrary to Vavilov's original assumption that selective forces remain constant over time, variation accumulates in species at different paces in different places. Topography and geographical isolation influence how rapidly plant populations diverge genetically from one another. Introgressive hybridization of plants, particularly when an area is disturbed by human populations or when new habitats are opened, may operate as a major evolutionary factor. Zohary has argued that a more logical approach to situating the place of crop origin is to explore the basis of genetic affinities with the wild progenitors of cultivated plants and to explore where these progenitors are geographically distributed (Harlan and Zohary 1966).



✷ Centers of form origination of the principal cultivated plants.

Vavilov (1951). World centers of origin of cultural plants.

Based on evidence from a number of disciplines, Harlan (1971) has proposed a classification for crop evolution based on "centers and non-centers." His theory is that agriculture originated independently in three areas. Each area comprised a system composed of a center of origin and a noncenter, in which activities of domestication were dispersed over a span of 5,000-10,000 km. One system includes a definable Near East center and a noncenter in Africa; another includes a North Chinese center and noncenter in Southeast Asia and

Zhukovsky (1975). Gene megacenters of cultivated plants.

Harlan (1971). Centers (A1, B1, C1) and noncenters (A2, B2, C2) of agricultural origin.

Figure 2. Centers of origin for wheat (▨).

the South Pacific; the third includes a Mesoamerican center and a South American noncenter. In each case, the center and noncenter interact. Crops did not necessarily originate in centers, nor did agriculture necessarily develop in a geographical "center."

Further, when crops are examined separately, it becomes clear that there are a variety of geographical patterns of origin and dispersal, depending on each crop's history, distribution, and wild progenitors (Harlan 1992). Some crops were domesticated several times, others only once. Some spread early and developed secondary centers; some spread recently and can be traced to their origins by historical data.

In the broadest sense, Vavilov, Zhukovsky, Zohary, and Harlan all concluded that what we know as the Fertile Crescent is the center of origin of agriculture and the region where the diploid grass progenitors of durum and bread wheats originated. But Zohary (1970) has referred to wheat's origins as "confused," and Harlan (1992) has described wheat as "diffuse" (neither centric nor noncentric). For example, although the geographical distribution of wild relatives of wheat and barley supports the idea of the Near East as a center of origin, cultivated einkorn and emmer (primitive wheats) are no longer widely found in that region (Harlan 1971). Einkorn is cultivated throughout Turkey but nowhere else, and emmer is primarily cultivated in the F.S.U., India, and Ethiopia. As wheat dispersed over vast geographic areas, new arrays of locally adapted cultivars evolved. Harlan's point of view is well expressed by the following:

> To say that "wheat" originated in the nuclear area which existed in 7000 B.C. would be misleading, to say the least. There is good evidence to suggest that hexaploid bread wheat originated outside of the nuclear area. To make any sensible statement about the place of origin of wheat, one would have to specify "what" wheat and "when." The famous Mexican wheats of Norman Borlaug originated in Mexico, not in the Near East nuclear area.
>
> Harlan (1971:469).

How Worldwide Germplasm Flows Shaped the Evolution and Development of Cultivated Bread Wheats

Historical Profile of Germplasm Flows

During their thousands of years of evolution B.C. and through about 1500 A.D., wheat populations spread with the extension of human settlement and cultivation practices but probably remained confined within the Afro-Eurasian landmass. According to Harlan (1987), the development of the use of pottery in the Near East and a stable food-producing economy provided a strong impetus for early flows of wheat germplasm. He calls the period 6000-3000 B.C. the Neolithic (ceramic) Dispersal. Traces of wheat in archaeological sites suggest that wheat spread into southern Europe by at least 5000-6000 B.C.; Pakistan by 6000 B.C.; Egypt by 4500 B.C. (and probably earlier); the Netherlands by 4000 B.C.; England and Scandinavia by 3000 B.C.; the Indus cultures by at least 3000 B.C. (evidence from Pakistan and Baluchistan suggests a much earlier date); and China by at least the second millennium (Harlan 1987). The Neolithic flow is considered to have constituted an "unprecedented evolutionary expansion" that resulted in a great degree of ecological differentiation as wheats adapted to local differences in aspect, altitude, soil moisture region, and cultural practices (Bennett 1970).

Another important juncture in the worldwide dispersal of wheat germplasm, roughly identified here with European exploration and later colonial periods, was motivated by the migration of farmers in search of new land and by governments in their quest for new sources of commerce (Figure 3). Spanish settlers planted the first wheat field in Mexico by 1529 (Heiser 1990), and the first recorded planting of wheat in Brazil occurred in that same century (Bastos-Lagos, n.d.). Australia's first wheat plot was reportedly planted in 1790 (Macindoe and Brown 1968). Other human migrations that spread wheat germplasm include the Mennonites' exodus into the Crimea and eventually to Kansas (described later). Secondary germplasm flows occurred within colonial empires and commercial spheres. Seed moved from Cape Town in South Africa to India and Australia, between South and North America, and between North Africa, East Africa, and other territories. During this period, seed was transmitted as cargo for food or in settlers' sacks, and wheat probably spread to almost all of what we now know as the wheat-producing world. No note is made here of human migrations originating in or directed over the broad expanse of Russia and China, but important transmissions of germplasm must also have occurred in these regions.

Although the colonial period extended into this century, 1880 marked the beginning of a new period in the flow of germplasm. The period was characterized by the development of scientific breeding programs throughout the wheat-producing world. For the first time, farmers and nonfarmers attempted to apply scientific principles to plant breeding, and the

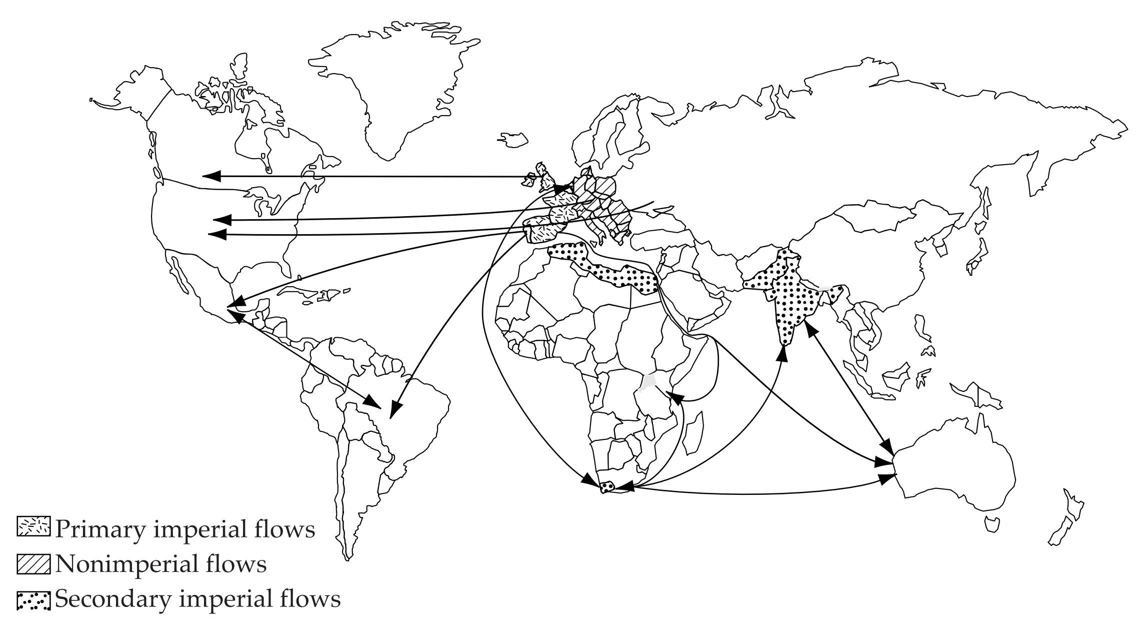


Figure 3. Imperial germplasm flows and migration, 1500-1900.

first plant breeding institutes were established. Figure 3 shows some of the major landraces, developed by farmers, that are (1) the most frequently used, (2) contribute the most in terms of Mendelian genetics to the modern bread wheats grown in the developing world today, or (3) have provided important genes or gene complexes for disease resistance. The approximate period in which they were first used by modern plant breeders, and their known origin, are also indicated. Farmers from most of today's major wheat-producing zones contributed important varieties of germplasm to the development of modern bread wheats.

Several landraces used by plant breeders before 1920 still figure heavily in the pedigrees of present-day bread wheats, including Zeeuwse Witte, Turkey, Blount's Lambrigg, Purple Straw, and Fife. Sherriff's Squarehead (popular from the mid- to late 1800s) was one of the earliest recorded products of modern plant breeding. Squarehead and its descendants, known to have originated in Great Britain, became a cornerstone of the early French, Belgian, German, Dutch, Swedish, and, indirectly, Italian breeding programs (Lupton 1987). Zeeuwse Witte, a Dutch landrace, was crossed with Squarehead to produce Wilhelmina. In the Italian breeding program initiated during the 1930s, Strampelli crossed Wilhelmina with the early maturing Italian landrace, Rieti, and top-crossed the F_1 progeny with Akagomughi, a Japanese dwarf variety. Two progeny of this cross, Ardito and Mentana, became the major progenitors of bread wheats throughout the Mediterrranean, South America, the FSU, and China (Lupton 1987; Dalrymple 1986; Yang and Smale 1996).

The movement of wheat seed from Turkey is one of the best-documented germplasm flows. Avoiding conscription by Frederick the Great of Prussia, Mennonite farmers settled on land ceded to them by Catherine the Great of Russia in the Crimea, recently seized from Turkey. The Mennonites adopted Turkish farmers' practice of sowing winter wheat. In the 1870s, again avoiding conscription (this time in the Russian army of Alexander II), the Mennonites migrated to Kansas. They carried with them the seed of "Turkey Red," the landrace ancestor of the hard winter wheats, named for the farmers who originally grew it and the color of its grain.[4] Later, wheat scientists from the Kansas Agricultural Experiment Station made selections from other landraces of the Crimea and Southern Russia (Flora 1988). Turkey wheat contained many different genotypes and was reselected to provide numerous cultivars which were then widely used in crosses (Reitz 1979). Not long after 1900, hard red winter wheat, mostly of the Turkey type, was grown on more than 20 million acres (more than 8 million hectares) across the U.S. (Quisinberry and Reitz 1974).

Blount's Lambrigg and Purple Straw were landraces used in Australian breeding work beginning with Farrer. Blount's Lambrigg is named for the farmer A.E. Blount in Colorado in the U.S. and for Farrer's farm, Lambrigg. Purple Straw is believed to have originated in the U.K., and Fife's origins are believed to be in the Polish region of Galicia. Selections from Fife are the building blocks of the North American spring wheats, the Australian wheats, and the bread wheats grown today in the developing world. Hard Red Calcutta (Pal 1966), whose name denotes only a commercial class of wheat exported from the port of Calcutta, is the

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[4] There is some disagreement about whether the Mennonites were the first to grow hard red winter wheat in Kansas, although they seem in any case to have played a prominent role in popularizing it (Stillbach 1988). The name "Turkey Red" probably refers to a group of landrace selections from the Caucasus.

other major parent of the North American spring wheats and the single most frequent female cytoplasm donor of bread wheats grown in the developing world (Nightingale 1996).

Major sources of disease resistance and other important traits introduced into breeding lines from 1900 to 1920 include the landraces Iumillo (durum wheat from Spain), Yaroslav emmer, Red Egyptian, Indian G, and Etawah. Indian G and Etawah figure heavily in the pedigrees of the Australian lines. Steinwedel, used for disease resistance by Australian breeders, is named for the German farmer who discovered it in his fields in Australia, but this landrace is believed to have reached Australia via South Africa (Macindoe and Brown 1968). Red Egyptian is of unknown African origin, usually attributed to either Ethiopia or the Republic of South Africa, although its name suggests that it originated in North Africa.

Alfredo Chaves and Polyssu, Brazilian landraces, were first crossed by Beckman in Brazil in 1935. One of the selections from that cross, Fronteira, is the probable source of a major gene complex for leaf rust resistance (Singh and Rajaram 1992). Although South American wheats were originally introduced from Europe, no known past or present European cultivars appear to carry similar levels of resistance to leaf rust. Leaf rust is endemic in the Southern Cone of South America (Samborski 1985). These two landraces are also among the most frequent female cytoplasm donors of bread wheats grown today in the developing world (Nightingale 1996). Americano 44d, an Uruguayan landrace of unknown origin (also known as Universal 2 in Argentina), was used by E. Klein in breeding some of the first Argentinean lines and is now considered to be a another important source of durable resistance to leaf rust (van Ginkel and Rajaram 1993).

The key landraces used in the breeding work that preceded the release of the first semidwarf wheats include Gaza, carried to Australia from Palestine by a soldier after the Second World War (Hanson, Borlaug, and Anderson 1982); Fultz, also known as "Mediterranean"; and Daruma, the Japanese dwarf wheat that carries the major dwarfing genes *Rht*1 and *Rht*2, which may actually have originated in Korea (Dalrymple 1986).[5] Daruma was one of the wheat varieties recommended in the Tokyo and Kangaw Prefectures around 1900, and it was first used by Japanese breeders in crosses with selections from Fultz in the early years of the 20th century (the Japanese government imported Fultz from the U.S. in 1887). Norin 10, derived from this breeding work and released in Japan during the 1930s, became the line through which *Rht*1 and *Rht*2 were bred into the Green Revolution semidwarf wheats in the 1950s and 1960s. Norin 10 became a major source of short stature in the world's wheat varieties but was never grown widely in Japan (for details, see Dalrymple 1986).

Several landraces not mentioned here (such as Criewener) have provided important traits for the semidwarf wheat varieties produced since the 1960s, including the widely grown Veery wheats. Petkus Rye was bred into the winter wheat parentage of the Veery lines via the variety Kavkas (details on the Veery pedigree appear later in this paper).

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[5] Dwarf wheats from Japan influenced Western wheat breeding as early as the 1860s, when short Japanese varieties were introduced into France. Dwarf varieties from Japan also featured in experimental breeding from 1930 to 1955 (particularly in Italy), but they apparently never featured in the parentage of significant commercial varieties (Dalrymple 1986).

The last period of worldwide germplasm flows is characterized by the prominence of international nurseries and national germplasm exchanges. In one sense, flows of genetic resources appear to have become more centralized during this period, as the financial resources and capacity to maintain diverse sources of germplasm have been concentrated in a few major banks and nurseries. Yet this impression is deceptive, because the flows are even more rapid and complex than in previous periods. As national programs have become stronger, more germplasm has been transferred between breeding programs in the nonindustrialized world (Byerlee and Moya 1993). Seed is now air-freighted from one place to another, and computers enable the pedigrees and selection history of any breeding line to be transmitted to scientific breeders throughout the world (see Skovmand et al. 1995). Another difference in the movement of germplasm in this most recent period is that industrialized countries increasingly seek to protect varieties from unauthorized distribution and use through intellectual property legislation, and pressure for similar protection is intensifying in developing nations.

The appearance and reappearance of landraces and wheat varieties in the genetic backgrounds of today's wheat cultivars have raised different concerns among different groups concerned about genetic diversity. Some fear that the genetic backgrounds of recently developed wheats have become too uniform. Others seek to confirm whether the landraces and varieties that constitute current wheats were originally reaped from the developing nations, to the unacknowledged benefit of industrialized nations. The next section discusses the issue of "genetic narrowing" in greater detail, and the following section will present quantitative evidence related to the geographic origins of bread wheats grown in developing and industrialized countries today.

"Genetic Narrowing" in the Bread Wheats

As we have said, the evolution of cultivated wheats is closely associated with social evolution. A common misperception is that genetic narrowing in wheat began in the mid-1960s, when growing numbers of farmers in industrialized and developing countries began planting the semidwarf wheats developed by Japanese, U.S., and Mexico-based scientists. In the strictest sense, genetic narrowing actually began in wheat more than 9,000 years ago, when einkorn and emmer were domesticated. Ever since, genetic change has been intimately associated with changes in crop husbandry (Fischer 1987).

The human selection pressures that accompanied domestication affected wheat physiologically. Farmers selected for plants that produced more seed and for spikelets with grain that was easily threshed but shattered less at harvest time (Harlan 1992). Today's bread and durum wheats have larger leaves and grain than wild forms of the diploid species, and the proportion of aboveground plant mass in the grain and the grain growth rate are higher (Evans and Dunstone 1970).

Porceddu et al. (1988) have argued that at least two major stages of genetic narrowing occurred in wheat in modern times. The first occurred in the 19th century when scientific plant breeding responded to the demand for new plant types. Farming systems emerged that were based on the intensive use of land and labor, livestock production, and the use of organic manure. Changes in cultivation methods favored genotypes that diverted large amounts of photosynthates to the ear and grain. A second stage of narrowing occurred in the 20th century with the utilization of genes determining major changes in plant type, such as the *Rht*1 and *Rht*2 dwarfing genes. These particular genes confer a yield advantage directly by reducing plant height and lodging problems; indirectly, they confer a yield advantage by reducing the plant's investment in stem tissue, thereby allowing greater storage in the grain. Given a certain combination of soil moisture, fertilizers, pesticides, and/or cultural practices, wheats possessing these dwarfing genes yield more than taller wheat types.[6]

Some analysts disagree about what constitutes genetic narrowing. For example, Hawkes (1983) views the crossing of the Japanese line Norin 10 with major Western breeding lines as an example of how diversity has been incorporated by modern plant breeding. However, a breakthrough in achieving genetic diversity at one point in time is also a potential source of narrowing at another, precisely because scientific breakthroughs produce wheat cultivars that are attractive and widely adopted by farmers. The 1B/1R translocation from rye widened the gene pool of bread wheats, expanded their adaptability by providing resistance to certain stresses (Villareal et al. 1991), and thus contributed to the popularity of the Veery wheats, which possessed the translocation.[7] Scientific plant breeding can also introduce new patterns of genetic variation within advanced lines. In some sense, over at least 200 years, wheat evolution has been passing into the hands of professional breeders (Simmonds 1979:11).

The first products of scientific plant breeding came to dominate cultivated area very early in the 20th century in Europe, India, Australia, and North America. Wilhelmina, released in 1901, dominated Dutch wheat area for 30 years and was also grown for hybridization in other countries. In Australia, Federation (1901) was the pre-eminent variety from 1910 to at least 1925 (Macindoe and Brown 1968). The variety Gentil Rosso, derived from an Italian landrace, accounted for more than 60% of the wheat grown in northern and central Italy in the early 1920s (de Cillis 1927).

Figure 4 shows that the percentage of wheat area planted to the dominant cultivar has declined since the early years of this century in Italy (durum wheat), France, the U.K., the Netherlands, Hungary, and Yugoslavia (winter wheats). The pattern is unclear and the time period covered by the data too brief for Sweden, Norway, Czechoslovakia, Poland, Spain, and Germany. In none of these countries, however, does the percentage distribution of leading cultivars appear to become greater over time (Lupton 1992). Downward trends are also found in the U.S. and in the Punjab of India, although the pattern in the Punjab fluctuates (Appendix C).

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[6] However, Austin et al. (1980) found that in the U.K., even before the introduction of *Rh*t1 and *Rh*t2, newer winter wheat cultivars were shorter, matured earlier, and often bore more spikes than older cultivars. Dalrimple (1988) recorded a similar pattern for U.S. wheats. Van Dobben (1962) found higher grain yield and lower straw yield when comparing 20th century cultivars to older Dutch cultivars, and Watson, Thorne, and French (1963) reported similar results when comparing the leading French cultivar of the 1950s, Cappelle Desprez, to the late 19th century English cultivar Squarehead's Master.

[7] The 1B/1R translocation refers to the translocation of the short arm of chromosome 1R of rye and the long arm of chromosome 1B of wheat.

The early phases of commercialization in agriculture in the industrialized countries during the 20th century undoubtedly contributed to narrowing the range of materials grown in farmers' fields. Nascent seed industries, and the relationship between government regulations and public- and private- sector breeding, clearly influenced the breadth of the materials available to farmers as well as breeders' activities. For example, the varieties bred by Henri Lévèques de Vilmorin and his son Philippe (Vilmorin 23, 27, 29, released in 1923, 1927, and 1929) dominated French wheat breeding for the first half of the 20th century. As the popularity of these varieties grew, protective legislation, introduced in the 1930s, restricted the number of varieties that seed merchants could sell (Lupton 1987). It is important to remember that in many countries of the developing world, some characteristics of emerging commercial seed industries may still play a major role in limiting the breadth of materials grown in farmers' fields.

Landraces by Source and Destination

Tables 1-3 present quantitative estimates of the geographical sources of the landraces in the pedigrees of bread wheats grown in the developing world today.[8] The first panel of each table shows the contributions of the regions of the developing world today (low- and middle-income countries) to bread wheat crosses grown in the developing world. The second panel shows the contributions of regions or countries that we now largely consider part of the industrialized world (high-income countries and the F.S.U. and Eastern Europe).[9] In the strictest sense, the term "landrace" implies here that no further information is known about the pedigree of the progenitor. Because information about the source of early progenitors is often incomplete, the data do contain measurement errors. Where possible, the information has been adjusted or extended by consulting various databases and secondary sources for the history of the major progenitors found in the pedigrees. Many of the major progenitors have been described and sources reported in the preceding section.

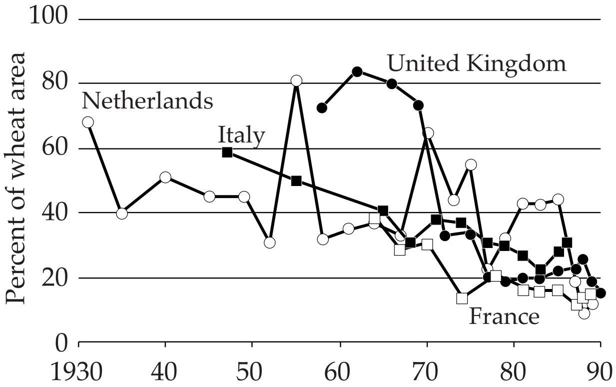

Figure 4. Area in dominant wheat cultivar, Europe, 1930-90.
Calculated from Lupton (1992).

Table 1 shows the percentage distribution by region of origin of all distinct landraces in the pedigrees of bread wheats grown in developing countries. In this calculation, each landrace is counted only the first time it appears in a pedigree. Only South Asia and the Southern Cone of South America have contributed the greatest number of landraces to the pedigrees of bread wheats now grown in their own region. For each of the other developing country regions, self-contributions are exceeded by contributions from the region composed of Poland, Germany, and the territories of the F.S.U.

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[8] Countries included in regions of the developing world are listed in Appendix B.

[9] The countries listed as "developing" in Tables 1-3 are classified by the World Bank as either low- or middle-income nations. Countries in the "industrialized" group, with the exception of the middle-income F.S.U. and Eastern European nations, are high-income countries.

Averaged over regions, the developing world contributed 47% and the industrialized world 45% of the distinct landraces found in the pedigrees of modern bread wheats. The origin of 8% of the landraces in those pedigrees is unknown.

In Table 2, the frequency of landrace use is calculated. Some major landraces may enter numerous times into the pedigree of one bread wheat cultivar (Figure 5). In terms of the frequency of landrace use, the contributions of Poland/Germany/F.S.U. and East Asia are magnified, and the proportional contribution of the industrialized world to modern wheats grown in the developing world appears higher than the contribution of the developing world itself.

For each landrace in each region of origin, the Mendelian contribution to all the crosses grown in 1990 was tabulated, by region of destination (Table 3). Each Mendelian coefficient was then multiplied by the hectares planted to the crosses in that year. The result is an estimate of the genetic contribution of landrace progenitors from each region to the bread

Table 1. Origin and destination of landraces in bread wheat crosses grown in the developing world in 1990

	Region of destination in developing world						
Region of Origin	Sub-Saharan Africa	North Africa	West Asia	South Asia	Mexico/ Guatemala	Andean Region	Southern Cone
	Percentage distribution of numbers of landraces in pedigrees						
Sub-Saharan Africa	12	9	7	9	10	12	7
North Africa	2	4	2	3	2	1	1
West Asia	2	1	7	2	1	1	1
South Asia	10	8	7	21	6	10	6
Mexico and Guatemala	4	3	7	6	9	7	5
Andean Region	0	0	0	0	1	1	1
Southern Cone of S. America	14	16	8	11	16	17	31
China	1	1	1	1	1	1	1
Developing world	**45**	**42**	**39**	**53**	**46**	**50**	**53**
North America	8	6	9	4	9	9	10
Northern Europe	10	8	5	6	9	8	6
Southern Europe	7	10	15	8	8	9	8
Poland, Germany, and F.S.U.	15	21	16	18	21	19	14
Japan and Korea	1	3	2	2	2	2	2
Australia	1	0	2	0	1	0	1
Industrialized world	**42**	**48**	**49**	**38**	**50**	**47**	**41**
Unknown	**13**	**10**	**12**	**9**	**4**	**3**	**6**
All	**100**	**100**	**100**	**100**	**100**	**100**	**100**

Source: CIMMYT Wheat Impacts Survey and Wheat Pedigree Management System; Macindoe and Brown (1968); Zeven and Zeven-Hissink (1976); Dalrymple (1986); Lupton (1987).

Note: All countries in "developing world" category are low- or middle-income countries . All countries in the "industrialized world" category, with the exception of the Former Soviet Union (F.S.U.) and Poland, are high-income countries.

wheat area of the developing world in 1990. The largest genetic contributors include the Southern Cone of South America, South Asia, and sub-Saharan Africa (in the developing world) and Poland/Germany/ F.S.U. and Southern Europe (in the industrialized world).

Several key points about these estimates need to be explained. First, much of the importance of sub-Saharan Africa as a germplasm contributor is a reflection of several Kenyan breeding lines, believed to have been derived largely from European and North African cultivars, for which the pedigrees are unknown. The first scientific wheat breeder in Kenya, G.W. Evans, used

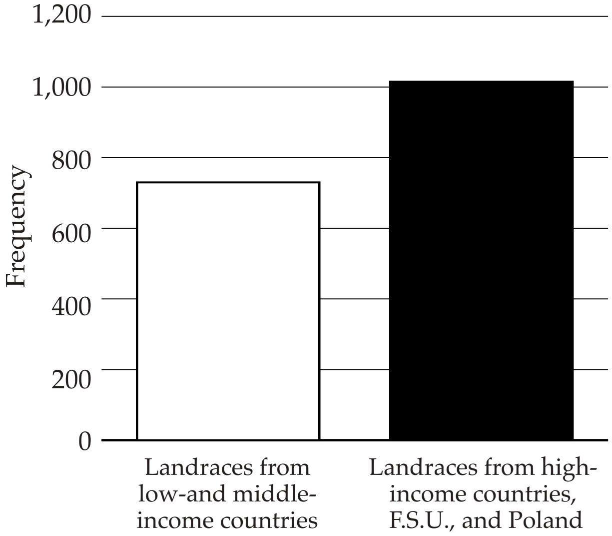


Figure 5. Frequency of landrace use in pedigrees of bread wheats grown in the developing world in 1990.

Table 2. Frequency of landrace occurrence in pedigrees of bread wheats grown in the developing world in 1990, by region of origin and destination

	Region of destination in developing world						
Region of Origin	**Sub-Saharan Africa**	**North Africa**	**West Asia**	**South Asia**	**Mexico/ Guatemala**	**Andean Region**	**Southern Cone**
	Frequency of use in pedigrees						
Sub-Saharan Africa	125	57	95	182	177	90	181
North Africa	4	3	2	12	2	1	3
West Asia	27	15	32	45	34	18	36
South Asia	102	59	83	211	116	75	122
Mexico/Guatemala	20	3	21	33	38	15	30
Andean Region	0	0	0	0	1	1	1
Southern Cone of S. America	193	96	186	299	318	152	356
China	23	13	18	34	35	15	31
Developing world	**494**	**246**	**437**	**816**	**721**	**367**	**760**
North America	49	19	36	50	55	27	67
Northern Europe	125	67	129	183	153	86	165
Southern Europe	156	91	189	266	219	119	231
Poland, Germany, and F.S.U.	319	193	311	524	428	253	437
Japan and Korea	51	33	65	90	70	38	80
Australia	2	0	2	0	1	0	2
Industrialized world	**702**	**403**	**732**	**1113**	**926**	**523**	**982**
Unknown	**45**	**13**	**31**	**52**	**31**	**10**	**21**

Source: CIMMYT Wheat Impacts Survey and Wheat Pedigree Management System; Macindoe and Brown (1968); Zeven and Zeven-Hissink (1976); Dalrymple (1986); Lupton (1987).

Note: All countries in "developing world" category are low or middle income countries . All countries in "industrialized world" category, with the exception of the Former Soviert Union (FSU) and Poland, are high-income countries

Rieti (Italy), Red Fife (of Polish origin), and varieties from Egypt and Australia. From 1920, G.I.L. Burton continued to develop a number of lines in Kenya; Norman Borlaug used these materials extensively in the breeding program in Mexico in the 1960s. Burton's records were lost in a fire (Dalrymple 1986).

Second, although East Asia contributed only a few landraces (Akagomughi, Daruma, and one or two other landraces reputedly of Chinese origin) to the bread wheats grown in developing countries in 1990, these landraces were used frequently, and their Mendelian contribution is great. As explained earlier, Akagomughi and Daruma were sources of the dwarfing genes that had such a dramatic effect on wheat yields. However, it is important to recognize that the economic contribution of these and other landraces to yield or disease resistance is not expressed in any of the measures reported in Tables 1-3.

Table 3. Genetic contribution of landrace progenitors to 1990 bread wheat area, by region of landrace origin

	Genetic contribution to 1990 bread wheat area (in million hectares)[a]							
Region of origin of landrace progenitors	**Sub-Saharan Africa**	**North Africa**	**West Asia**	**South Asia**	**Mexico/ Guatemala**	**Andean Region**	**Southern Cone**	**Developing world**
Sub-Saharan Africa	0.0991	0.2603	0.629	3.4915	0.1593	0.0326	0.9981	**5.67**
North Africa	0.0006	0.031	0.09	0.0913	0.0002	0.0006	0.0043	**0.22**
West Asia	0.0091	0.0385	1.249	0.4434	0.0213	0.0032	0.1329	**1.90**
South Asia	0.0426	0.2038	0.273	4.6728	0.0499	0.0098	0.329	**5.58**
Mexico/Guatemala	0.0198	0.0046	0.25	0.1743	0.039	0.0027	0.1332	**0.62**
Andean Region	0.0	0.0	0.0	0.0	0.0	0.001	0.0017	**0.00**
Southern Cone of S. America	0.077	0.1439	0.809	3.3371	0.1239	0.0312	2.8966	**7.42**
China	0.0083	0.0242	0.052	0.2451	0.0148	0.0025	0.1857	**0.53**
Developing world	**0.26**	**0.71**	**3.35**	**12.46**	**0.41**	**0.08**	**4.68**	**21.94**
North America	0.0421	0.0752	0.296	0.1599	0.0158	0.0026	0.2443	**0.84**
Northern Europe	0.0319	0.0403	0.297	0.7229	0.0297	0.0066	0.3383	**1.47**
Southern Europe	0.0553	0.1503	1.147	3.338	0.1006	0.0185	0.6374	**5.45**
Poland, Germany, and F.S.U.	0.126	0.3129	1.813	8.4263	0.237	0.0461	1.3555	**12.32**
Japan and Korea	0.0363	0.0646	0.401	1.2633	0.0528	0.0115	0.4529	**2.28**
Australia	0.0001	0.0	0.08	0.0	0.0002	0.0	0.0	**0.08**
Industrialized world	**0.29**	**0.64**	**4.03**	**13.91**	**0.44**	**0.09**	**3.03**	**22.43**
Unknown	**0.0966**	**0.1577**	**0.613**	**2.4756**	**0.0285**	**0.004**	**0.3443**	**3.7198**
Total hectares planted to bread wheats released by breeding programs	**0.64**	**1.51**	**8.00**	**28.84**	**0.87**	**0.17**	**8.05**	**48.09**

Source: CIMMYT Wheat Impacts Survey and Wheat Pedigree Management System; Macindoe and Brown (1968); Zeven and Zeven-Hissink (1976); Dalrymple (1986); Lupton (1987).

[a] Includes only those cultivars for which pedigree information is available. Area is weighted by theoretical (Mendelian) contribution of landrace progenitors.

Note: All countries in "developing world" category are low- or middle-income countries . All countries in the "industrialized world" category, with the exception of the Former Soviert Union (F.S.U.) and Poland, are high-income countries.

The significance of the Southern Cone of South America reflects what little we know about cultivars that "migrated" to Brazil and Argentina long ago with European settlers. Around 1920, E. Klein began a scientific plant breeding program in Argentina. The pedigrees of the early scientific releases contain more than 50 varieties of distinct origins, including selections from Argentinean and Uruguayan populations, North American cultivars (such as Kanred, a selection from Crimean hard red wheat; Blackhull, a selection from Turkey wheat; and Marquis), and cultivars from France, Italy (such as Ardito and Mentana, both descended from Rieti, Akagomughi, Zeeuwse Witte, and Squarehead), Russia, Brazil, Germany, and Australia. Brazil also has a long history of scientific plant breeding, and one of the earliest and best-known cultivars bred there is Frontana, a cross of Fronteira and Mentana. Fronteira is a cross of Alfredo Chaves and Polyssu, both known as selections from the local wheats of Rio Grande do Sul (Kohli 1986).

Figure 3 and Tables 1-3 demonstrate fairly conclusively that germplasm flows for bread wheats have long been international and multidirectional. All regions are "indebted" to other regions for the landraces appearing in the pedigrees of their bread wheats. The largest contributor of landraces to a region is usually not the region itself. Furthermore, it is hard to distinguish the direction of germplasm flows because cultivars have moved from industrialized to developing countries at one point in time and vice versa at another. Finally, the known origins of most of the major landraces do not fit neatly within the categories of "industrialized" and "developing" nations used today. Major contributors are South Asia, Eastern Europe, the F.S.U., East Asia (for Daruma and Akagomughi, in particular), and the Mediterranean, but national boundaries and political configurations changed during wheat's long diaspora. Finally, our use of the term "landrace" is often a measure of our own ignorance. The progenitor may actually have been the result of a scientist's cross, a farmer's selection, or a commercial grain shipment.

How Breeding Programs Incorporate Landraces

Preserving landrace populations in their original form does not necessarily enable us to recapture their useful traits through recombination. For one thing, landrace populations continue to evolve with human populations. For another, conserving landraces either in gene banks or on the farm does not ensure that plant breeders will use them directly in their crossing programs. Plant breeders are sometimes reluctant to work directly with landraces because they "want the genes and not the linkages" (Harlan 1992:155). Molecular biology has the potential to assist in identifying genes and linkages present in landraces, but even techniques of molecular biology cannot identify all of the relationships.

Over time, pedigrees necessarily become longer as plant breeders continue to introduce new germplasm into their breeding programs. Most scientific plant breeders, however, do not know the genealogies of the new materials they borrow or obtain from other nations. Most new materials brought into a breeding program are advanced lines with long pedigrees that contain their own distinct landraces. Some of the new materials are advanced lines that have pedigrees similar to those of the breeder's older materials. Only a few are landraces that have never before been used in the genetic backgrounds of any of the breeder's materials. Although new materials are likely to contain new ancestors, many of the ancestors may be common to those already found in previously used materials.

The more international the breeding program, the more likely it is that new materials will contain ancestors that have not been used previously or do not occur in the genetic backgrounds of older materials. International plant breeding programs should be better placed than national programs to utilize landraces from diverse sources in developing new cultivars. Because they have greater access to a broader range of materials, international programs can assist national programs to use materials transmitted from one region to another, especially when funding constraints and the shorter planning horizons of national programs inhibit their capacity to search beyond national boundaries for potentially useful sources of germplasm.

Segments of the pedigrees of several of the leading cultivars grown in the developing world today are reproduced in Figure 6, illustrating the different ways that breeders incorporate new materials, as well as the sheer length and breadth of the pedigrees. A number of sources were used to label each landrace or farmer's selection in the pedigree with a probable or known country of origin and each scientific cross of selection with the country in which the line was produced and the approximate date.

Figure 6a shows most of the major segments of Sonalika, the bread wheat cultivar planted across the largest area in the world, mostly in South Asia. The pedigree is both wide and long, and includes landraces or farmers' selections from 17 countries. Breeders in 14 countries contributed lines to Sonalika's pedigree. Landraces and lines originated in six continents and most of the major wheat-producing nations of the world.

Mexipak (cross II8156, also released as Kalyansona and Siete Cerros), the most well-known of the semidwarf cultivars of the early Green Revolution period, still covers a large area of the wheat-producing world. Together with segments not expanded here, Mexipak's pedigree, like Sonalika's, also appears fairly wide and long (Figure 6b). The pedigree contains major European landraces (Squarehead, Fife, Rieti, and Zeeuwse Witte through Mentana), Kenyan lines of unknown origin, East Asian landraces (Akagomughi, Daruma, and Chino), landraces of the Southern Cone (such as Barleta and Pelon), and various other landraces, which enter through the Australian cross Gabo.

The pedigree of Veery is even larger, because it contains the II8156 and Bluebird pedigrees in their entirety more than once through one of its parents and one of its grandparents (Figure 6c). The Kavkas grandparent carries the 1B/1R translocation through a wide cross with Petkus Rye—a cross which occurred naturally in a farmer's field. One of Veery's ancestors is the famous F.S.U. cultivar Bezostaya, one of the few early scientific breeding lines that has been called a "wide" cross owing to the breadth of its ancestry (Lupton 1987). However, even Bezostaya reintroduces the familiar European and American (North and South) landraces into the pedigree.

In the development of Veery, II8156, and Sonalika, new landraces tended to be infused by crossing lines possessing distinctly different pedigrees. For example, the crosses and selections from Gabo in the II8156 pedigree bring in the genetic background containing Steinwedel, Blount's Lambrigg, and Gaza. The Kenyan lines bring in both unknown genetic backgrounds and landraces such as Red Egyptian. The well-known Norin 10-Brevor cross brings in Daruma. Strampelli's Mentana cross brings in Akagomughi. In Veery, the cross of Buho with Kavkas brought in a number of German, Russian, and F.S.U. landraces and lines. Veery's pedigree is in some sense a compound of other major lines, with new breadth introduced and old blocks reproduced through Kavkas.

The way that landraces are introduced in the pedigree of Gerek 79 is an exception among the top lines grown in the developing world and in general (Figure 6d). Gerek 79, a tall wheat, contains neither *Rht*1 or *Rht*2. Gerek 79's pedigree includes direct — and recent — introductions of Turkish landraces. One of Gerek 79's parents is a selection from a Turkish landrace, and one grandparent is a selection from a mixture of crosses between Mentana and Turkish landraces. On the other hand, Gerek 79's pedigree appears relatively simple compared to Veery's or Sonalika's. Through Mayo 48, Gerek 79 also carries the Newthatch and Florence Aurore pedigrees that are common to many advanced lines grown in both the developed and developing world today.

Measuring Genetic Diversity in Wheat

The previous sections of this paper described the long and extensive dispersal of wheat germplasm. We have also seen how farmers and breeders, seeking to incorporate exotic and new germplasm into their own wheat stocks, contributed to an unprecedented intermingling and movement of germplasm. How have these great germplasm flows and mixtures affected the genetic diversity — and vulnerability to disease — of wheat? Before these questions can be answered, some background information is required. In this section, we define genetic diversity and compare how biological and social scientists have approached the problem of measuring genetic diversity in wheat. The relationship of genetic diversity to yield stability and vulnerability to disease is also reviewed. With these issues clearly set out, we will proceed in the next section of this paper to assemble evidence on the genetic diversity of bread wheats currently grown in the developing world.

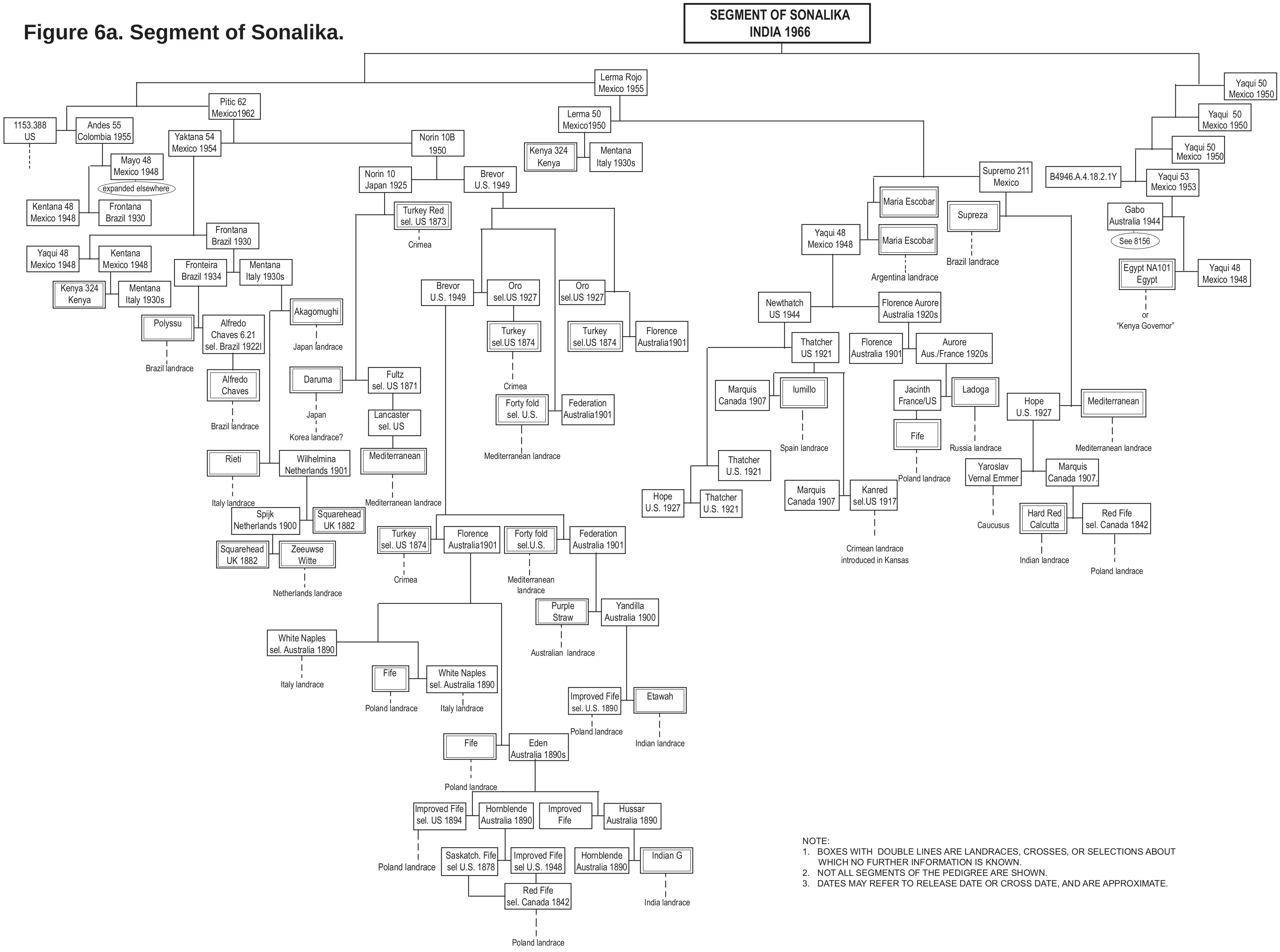
A Definition of Genetic Diversity

In simplest terms, the sources of variation in biological systems can be divided into what is inherited through genes and what is generated by the environment. "Environment" refers to all of the factors to which an organism is exposed. If the traits of two plants could be measured in identical environments, differences in expression would reflect only genetics. The proportion of total variation in traits caused by genetic differences is called *heritability.*

Several economically important, observable plant traits (such as yield, quality, and some types of disease resistance, including durable disease resistance) possess "low heritability." Low heritability implies that a greater proportion of total variation in the expression of these traits results from environment and from genotype-by-environment interaction, rather than genotype alone.

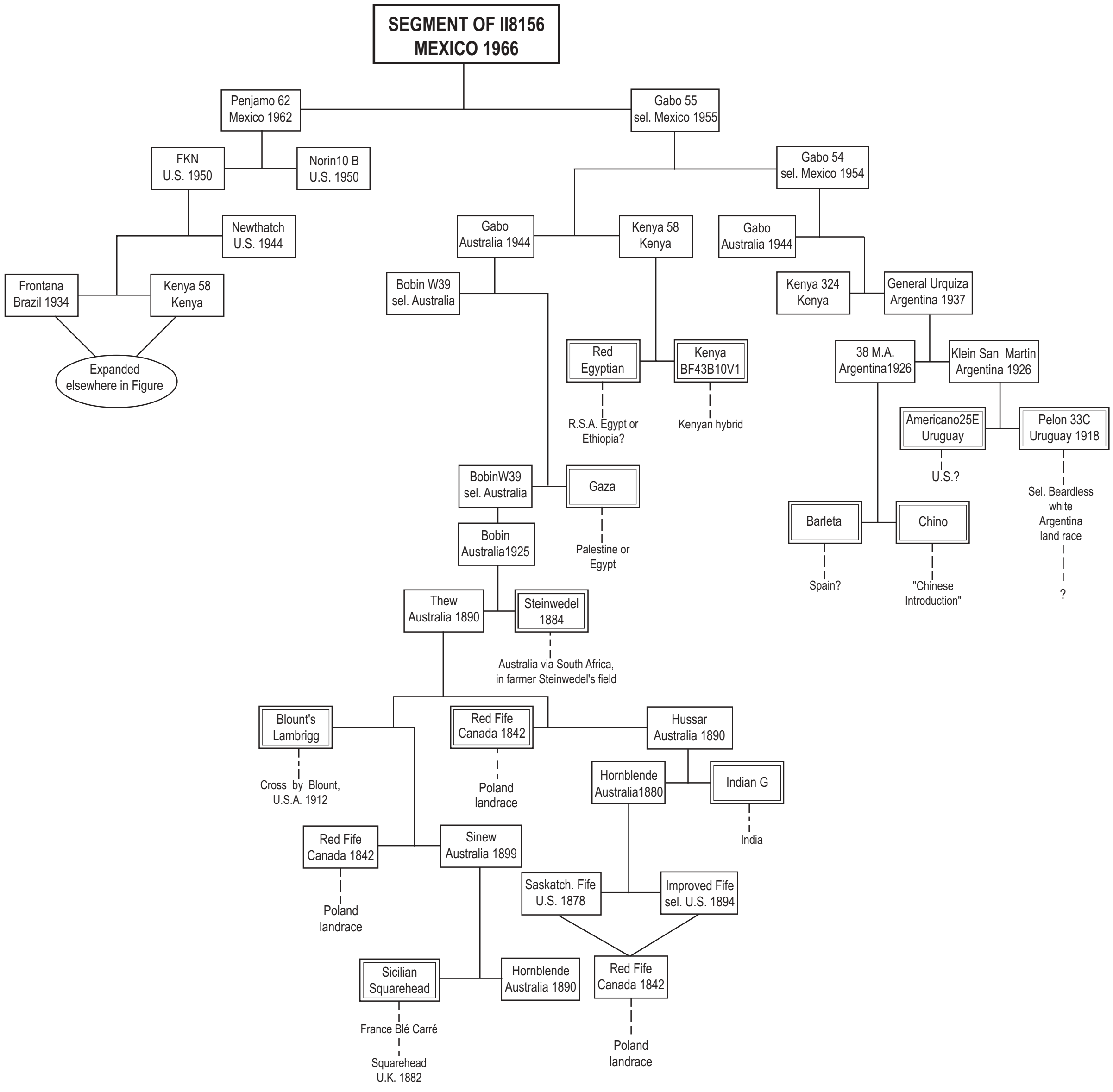
Genetic diversity is genetic variation, but it can be measured in a number of ways, such as among alleles at a single gene locus which may be recessive or dominant, or in terms of visible differences in the expression of traits that are conferred polygenically, or in terms of

Figure 6a. Segment of Sonalika.



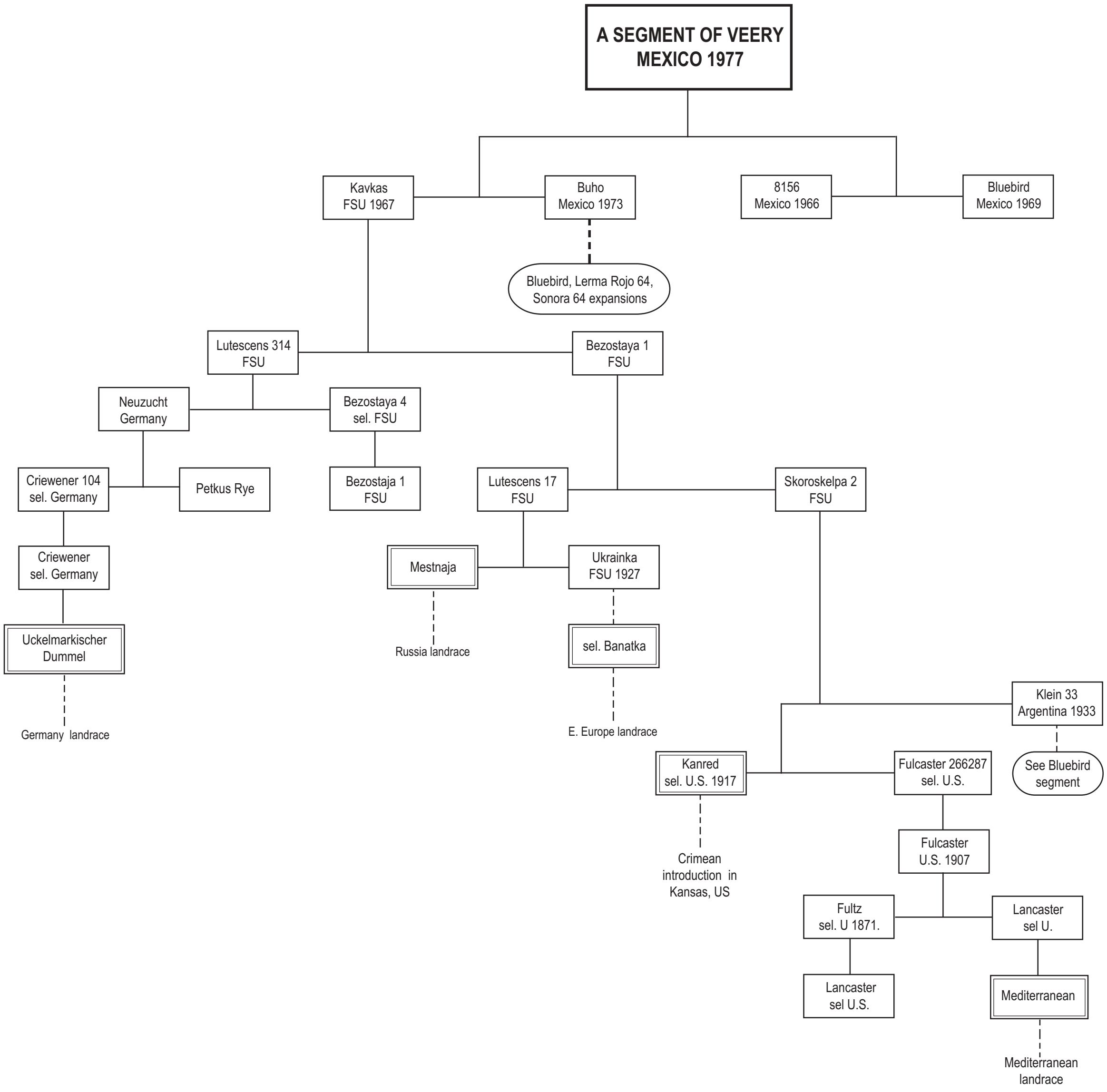
NOTE:
1. BOXES WITH DOUBLE LINES ARE LANDRACES, CROSSES, OR SELECTIONS ABOUT WHICH NO FURTHER INFORMATION IS KNOWN.
2. NOT ALL SEGMENTS OF THE PEDIGREE ARE SHOWN.
3. DATES MAY REFER TO RELEASE DATE OR CROSS DATE, AND ARE APPROXIMATE.

Figure 6b. Segment of II8156.



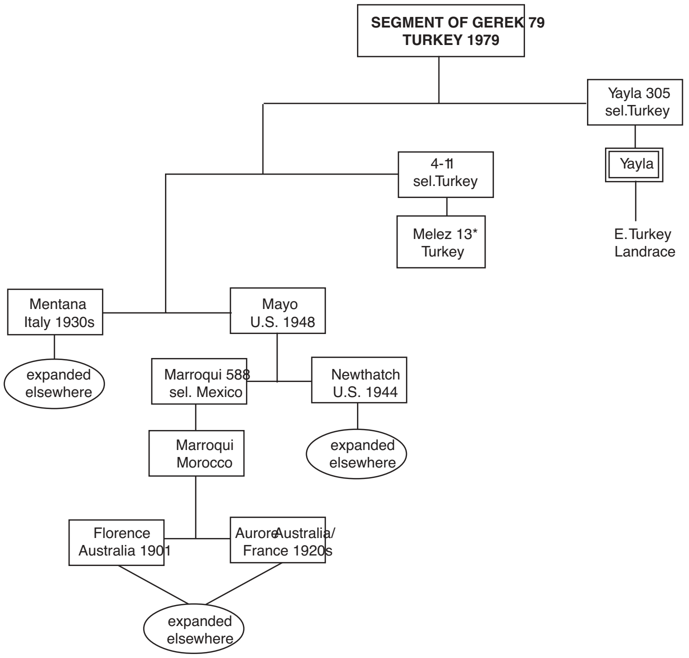
NOTE:
1. BOXES WITH DOUBLE LINES ARE LANDRACES, CROSSES, OR SELECTIONS ABOUT WHICH NO FURTHER INFORMATION IS KNOWN.
2. NOT ALL SEGMENTS OF THE PEDIGREE ARE SHOWN.
3. DATES MAY REFER TO RELEASE DATE OR CROSS DATE, AND ARE APPROXIMATE.

Figure 6c. Segment of Veery.



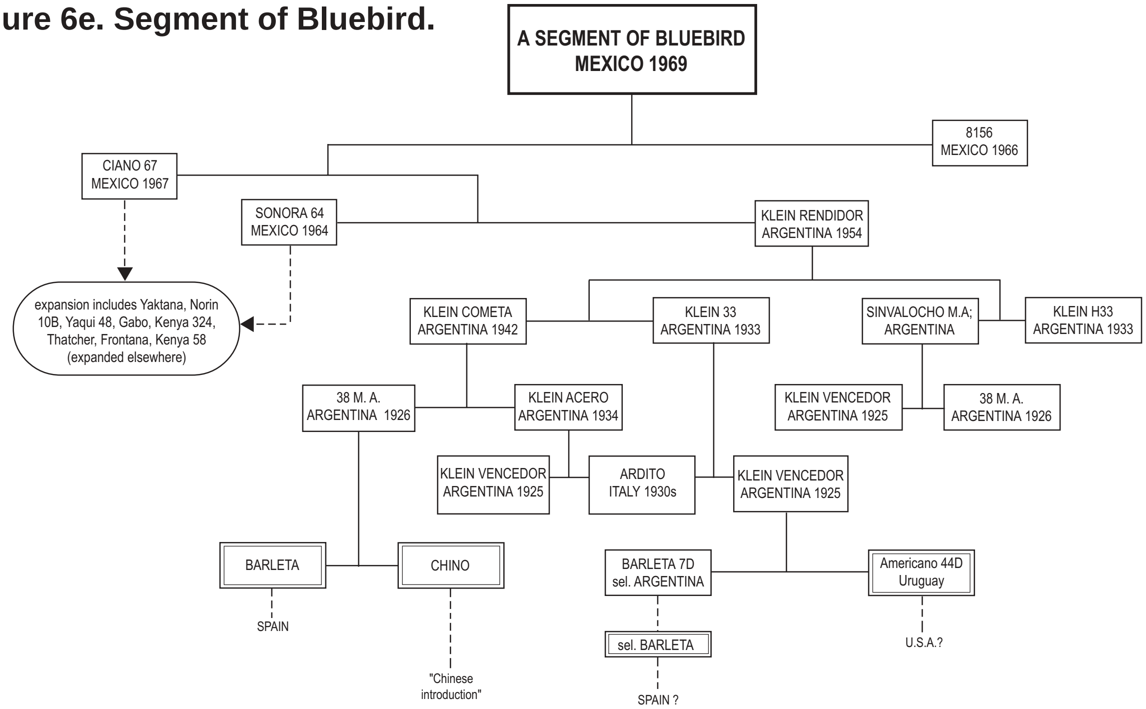
NOTE:
1. BOXES WITH DOUBLE LINES ARE LANDRACES, CROSSES, OR SELECTIONS ABOUT WHICH NO FURTHER INFORMATION IS KNOWN.
2. NOT ALL SEGMENTS OF THE PEDIGREE ARE SHOWN.
3. DATES MAY REFER TO RELEASE DATE OR CROSS DATE, AND ARE APPROXIMATE.

Figure 6d. Segment of Gerek 79.



* A mixture of crosses between Mentana and Turkish landraces.

Figure 6e. Segment of Bluebird.



NOTE:
1. BOXES WITH DOUBLE LINES ARE LANDRACES, CROSSES, OR SELECTIONS ABOUT WHICH NO FURTHER INFORMATION IS KNOWN.
2. NOT ALL SEGMENTS OF THE PEDIGREE ARE SHOWN.
3. DATES MAY REFER TO RELEASE DATE OR CROSS DATE, AND ARE APPROXIMATE.

the numbers of genotypes planted in a farmers' field. The *potential for genetic diversity* can be defined as the *inherited genetic variability* present in a population, race, species, or genus. In its broadest sense, genetic variability in wheat refers not only to the cultivated, primitive, and wild forms of wheat, but also to wheat's close relatives (rye, barley) and to any other source of genes that could be introduced into wheat. Biotechnology may expand the classical boundaries of the genetic variability of any species by creating the potential to introduce genes that originate in distant species or that have been wholly synthesized in the laboratory.

Inherited variability. Inherited variability in a species results from mutations in DNA, which is formed of pairs of different amino acids, known as base pairs. Genes are composed of coding sequences of base pairs, which means that they confer expression of traits in plants by transcribing information into RNA, which then translates the information into proteins. Variants of a genetic locus or gene are called alleles. Although we can measure the variation in both coding and noncoding sequences, it is differences in allelic frequencies that have the potential to create the genetic diversity we can observe in plant populations. On the other hand, different alleles may be expressed similarly. Further, many traits of economic value are polygenic, which means than more than one gene is associated with their expression. Some genes code for proteins that are regulatory, and their effects may be unobservable. The unique association of an allele with a trait is therefore often impossible.

Wheat is also an allopolyploid species, which means that it has multiple sets of chromosomes, each of which is donated by a different grass species. In and of itself, polyploidy would seem to permit relatively great genetic variability through the presence of multiple chromosome copies and possible recombinations. Yet cultivated wheats have been found to exhibit only limited intraspecific variability, in part because they originated from chance crosses of unique individuals of diploid (duplicate chromosome) genome donors (Jaaska 1993). Furthermore, less than 10% of the DNA in the bread wheat genome consists of coding sequences. The genetic basis of variation in bread wheat is therefore based on genetic differences in only a minor portion of the bread wheat genome.

The relationship between noncoding sequences and coding sequences (genes) is not fully understood, however, and may be potentially important. The way that single genes interact with other DNA sequences is also likely to be complex. Allelic variation occurs at most if not all of the postulated thousands of genes that condition the phenotype of wheat.

Factors that condition the range of inherited variability. Patterns of genetic variation in cultivated plants are determined by a wide variety of factors that interact "intricately" (Bretting and Goodman 1989), including the history of cultivation, ecological and cultural diversity, and introgression with wild and weedy relatives or between different races of a crop (Harlan 1992). Human migration and trade led to exchange of genetic material and, in the particularly varied habitats of primitive agriculture, to introgression from extraneous gene pools. Other biological and political factors have also played their part (Frankel and Bennett 1970). These patterns are not well understood (Harlan 1992), and the distribution of genetic variation in any large geographical region may take a number of forms. It may even resemble "a mosaic, where no association among particular genetic variations and any ecogeographical factor can be discerned" (Bretting and Goodman 1989).

The properties of the environment that influence the ranking of the performance of genotypes are defined as “selective.” Since bread wheat has always been cultivated, most of the selective pressures conditioning its evolution occurred through domestication and cultivation.[10] When a plant is cultivated, certain adaptation pressures automatically begin; in cereals, these include selection pressures associated with harvesting and seedling competition. Throughout the process of domestication, deliberate human selections have been superimposed on these automatic pressures. The effects of seed selection practices may be extremely powerful. Although the plant populations of traditional cultivators may be rich in variation because the farmers often use mixtures, the mixtures will still conform to whatever criteria an individual selector chooses. The total potential range of variation will still be fragmented into limited subpopulations that are grown for different purposes to fit different ecological niches of the agricultural system. In traditional farming communities, farmers’ breeding strategies are based on local genetic resources, their selection strategies are aimed at adaptation to specific niches and heterogeneous varieties, and their selection methods are “moderately efficient” (Berg 1993).

Close adaptation of scientifically bred cultivars to specific niches is difficult to attain because the environments that crops occupy are more numerous and diverse than the environments of the relatively few centers where they originated. In industrialized economies, the breeding of cultivars to meet the quality standards for processing and numerous end uses also implies greater phenotypic uniformity within market classes. Scientific wheat breeders utilize the world’s genetic resources with controlled crossing. They attempt to develop cultivars possessing phenotypic uniformity and broad adaptation within regions and in industrialized markets, and their selection methods are “efficient” (Berg 1993).

The genetic differences concealed by phenotypic (visible) uniformity may be released under the stimulus of environmental change. While phenotypic uniformity may be an indication of a closely adapted population, it may, and very frequently does, conceal considerable potential for genetic variation (Bennett 1970). We can observe a lack of (or much) genetic variation that hides much (or a lack of) potential for genetic variation.

How Biological and Social Scientists Measure Genetic Variation

Perspectives from breeding programs. Genetic variability is a vital issue for plant breeders because proper management of this diversity can produce a permanent gain in the performance of the plant. In some sense, an understanding of the existing structure of genetic variation in the expression of plant traits is the cornerstone of conventional plant breeding. The plant breeder assembles genetic variation and attempts to alter, by selection, the average expression of a wide range of plant traits. Increasing the potential for genetic diversity, or genetic variability, however, has not always been and is not yet a primary concern of all scientific plant breeding programs.

Today’s scientific plant breeders work not only with visible variation in plant characteristics through conventional genetic analysis, but increasingly with parent-offspring studies,

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[10] When a crop is domesticated, there are two populations. One population is wild, and the other is harvested and planted. Very different kinds of selection pressure govern their development.

pedigree analysis, and information provided to them by molecular biologists. There are many types of diversity that biological scientists can measure in the context of breeding program activities — from the gene bank and laboratory to on-farm trials (Table 4).

Methods for detecting genetic diversity at the molecular level include the use of biochemical and molecular markers. Biochemical markers include isozymes, which are proteins with a common enzymatic function, and seed storage proteins. Isozyme techniques are comparatively inexpensive and powerful methods for measuring allele frequencies for specific genes, but because there are few isozyme systems per species (not more than 30), there are relatively few markers. Molecular markers are more expensive to use, but there are now thousands of known markers for several species, which enables the study of a much larger number of genes, as well as other locations in noncoding segments of the chromosome.

Techniques used by molecular geneticists can be used to classify lines, populations, and landraces and to establish genetic linkage with traits of agronomic and economic interest and detect their genetic variation. Once genes and alleles related to the expression of a trait can be identified, the allele frequencies in a segregating population can be described by a standard set of summary statistics, and the apportionment of genetic variation within and between populations, races, or cultivars can be summarized and compared by multivariate analysis.

Table 4. Indicators that plant breeders and social scientists use to measure genetic diversity in crop plants from genes to fields

Conceptual measure	Operational measure
1. Diversity in single genes	Biochemical analysis (isozymes and seed storage proteins) of variation in alleles for a single gene; classical Mendelian analysis
2. Polygenic diversity	Multivariate analysis of morphological variation in traits whose expression is determined by multiple genes
3. Latent diversity of genome	Genealogical analysis; analysis of cytoplasm donors; molecular (DNA) analysis and probes
4. Pedigree complexity	Genealogical characteristics
5. Performance-based diversity	Analysis of genotypic variance and genotype-by-environment interactions; analysis of yield variance at farm, district, national, or regional level
6. *Ex situ* diversity	Analysis of numbers of accessions within and among species; analysis of morphological characters of accessions
7. Spatial diversity	Number of cultivars by source, use, or trait; percentage distibution of area planted to cultivars
8. Temporal diversity	Average age of cultivars per time period; rate of cultivar replacement

Despite its great power, the molecular study of plant genetic diversity is in its infancy, and detailed investigations of gene variation in wheat are still few. Molecular biology has shed some light on the actions of specific genes and portions of genomes, but scientists still know little about the interactions of identifiable genes and other DNA sequences. DNA analysis is perhaps best classified as the analysis of latent diversity, in that it is most powerful when combined with conventional plant breeding methods, in testing for the presence or absence of traits that have economic value, or in seeking new ways to incorporate useful diversity from other species.

Classical Mendelian genetic analysis can also be used to evaluate variation in single, known genes (qualitative traits), such as those conferring certain types of disease resistance. Forms of multivariate analysis can be used to analyze the variation in traits whose expression is governed by one or more gene loci. Pairwise coefficients of parentage can be calculated from pedigree information and used as indicators of genetic diversity (Cox, Murphy, and Rodgers 1986). Souza et. al. (1994) have described the coefficient of parentage as an indicator of *latent genetic diversity.*[11] Genetic distance measures can be calculated with molecular, morphological, or genealogical data (see Dudley 1994; Weitzman 1992). Often, however, the empirical relationship between molecular and other indicators is weak. For example, some recent research on wheat has shown a fairly close relationship between morphological and parentage measures (van Beuningen 1993) but not necessarily between molecular and morphological measures (see Cox et al. 1985; Sorrells et al. 1993).

When they develop lines, scientific plant breeders seek genotypic variation for traits of economic value, such as yield. In trials on experiment stations and on farmers' fields, crop scientists use a number of statistical methods to separate the different types of variation observed in key traits by the source of that variation — genotype, genotype-by-environment interactions, and environment.

Perspectives from social science. Social scientists are concerned with genetic diversity as it is recognized by farmers and as it is valued by different social interest groups. In the more detailed case studies that comprise an important part of research on genetic diversity in farmers' fields, human ecologists and anthropologists have attempted to understand and relate farmers' knowledge systems and taxonomic classifications to those recognized by scientists (examples include Bellon 1990; Brush, Taylor, and Bellon 1992; Sperling, Loevinsohn, and Ntambovura 1994; Dennis 1987; and Richards 1985).

In other studies, researchers have used farmer surveys to elicit information about the number of cultivars and area planted by source of seed, trait, and use. The seed may be inherited from the farmer's parents, purchased commercially, purchased from other farmers, exchanged between farmers, or obtained as payment for labor. The trait may be plant height, ratio of grain to stover, grain color or texture, maturation period, or yield.

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[11] In wheat, the coefficient of parentage measures the probability that two cultivars are identical by descent for a character (observable or unobservable) that varies genetically and is not expressed as a result of intensive selection by plant breeders.

The grain or stover of the cultivar may be of particular value for commercial purposes or for direct or indirect household use (examples include Byerlee, Iqbal, and Fischer 1989; Husain 1987; and Smale et al. 1991). Research by Meng, Taylor, and Brush (1995) in Turkey and similar research in Mexico are examples in which molecular, cultivar, and household survey data are combined.

At the other extreme from these field-based studies are those based on secondary sources and published data. On the basis of broad distinctions such as cultivar names or classifications such as "modern" and "traditional," cultivar numbers or the percentage distributions of crop area by cultivar type have been used as measures of *spatial diversity*.[12] Changes in these counts or area distributions over time provide measures of "diversity in time" (Duvick 1984). Other measures of *temporal diversity*, such as the average age and weighted[13] average age of cultivars, have been proposed and used by Brennan and Byerlee (1991). Genealogical characteristics, such as the number and origin of landraces, and the number of breeding generations since the first cross, were used for the first time by Gollin and Evenson (1990), who have employed the term *pedigree complexity* to describe these characteristics of genetic resources.

Genetic Diversity and Yield Stability

National food consumption in many developing countries depends largely on a small number of staple crops. Stability in national yields for the staple crops is generally believed to be beneficial under such conditions: not only do unexpected food imports place a burden on road and distributional systems, but imports often must be purchased under disadvantageous world market conditions. How yield stability affects the income of individual farmers depends on the composition of their farm and nonfarm activities and the completeness of the market for their resources and products.

Unfortunately, discussions of "yield stability" among social and biological scientists are often hampered by language barriers, because they use the phrase to denote different phenomena. As a consequence, the impact of plant breeding on national crop yields relative to other determinants is not easily understood.

When plant breeders test the lines they develop, they look for individual genotypes whose yields are stable over a broad range of environments. The most common method of assessing the yield stability of a genotype is to relate (through statistical regression) its mean yield by site to the mean yields for all genotypes by site. The mean yields for all genotypes by site, adjusted by the overall mean, is used as an environmental index. A regression slope of one implies that the genotype performs similarly across sites.

The expression of complex characters such as yield is heavily influenced by environmental conditions. Analysis of data from scientific trials often reveals that only a small proportion of yield variation is attributable to differences among genotypes, or even to genotype interactions with locations and years. Most variation results from differences among

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[12] Similar measures of spatial diversity are the Herfindahl and dynamic Herfindahl indices used by Pardey et al. (1996).

[13] Weighted by area.

locations or years. The extent to which new varieties contribute to changes in yield variability, however, will differ greatly among regions (Arnold and Austin 1989).

The variation in crop yields across regions is clearly influenced by many additional factors. Economists typically use the coefficient of yield variation, or the ratio of the standard deviation to the mean, as a measure of crop yield stability. They use time-series estimates of crop yield data, detrended to take out the effects of a rising mean over time, for given intervals. In this calculation, all wheat cultivars are grouped and yields are aggregated at the district, national, regional, or global level, depending on the focus of the analysis.

Statistical regressions of the coefficient of yield variation on explanatory factors reveal that year-to-year variation in national yields primarily reflects changes in weather and the use of crop management inputs rather than varietal change (see Anderson and Hazell 1989; Singh and Byerlee 1990). The spread of irrigation has reduced the influence of weather conditions, but input use is very much influenced by input supply and pricing policy. For social scientists and policy makers concerned about the stability of aggregate yields, the most important determinants to consider are thus price policies, input supply, and crop management practices.

Genetic Diversity and Vulnerability to Disease

A common misperception in discussions of genetic diversity is that visible uniformity among cultivars is necessarily associated with *genetic vulnerability*. Crops can be relatively uniform in many respects and remain invulnerable to disease. Genetic diversity in and of itself provides no insurance against disease, because vulnerability can be latent, revealed only as new, virulent strains of pathogens evolve over time. Diversity can be hidden, expressed only in different environments, and uniformity can be hidden as well, when visibly diverse varieties are actually identical in the gene or genes that create the conditions for susceptibility (see BOA/NRC 1993; NRC 1972).

Three aspects of the vulnerability problem are particularly important for those who are not plant breeders to understand. First, resistance is not an absolute quality but ranges from partial resistance to near immunity.[14] Second, because the pathogen population constantly evolves in a complex interaction with the host, "resistance" may be of short, but unpredictable, duration. The genetic variation in the pathogen is of great importance, because a host may be resistant to some forms of a pathogen but completely susceptible to others. (For instance, new races of the pathogens causing the rust diseases of wheat develop relatively easily.) Third, genes for resistance may respond differently to varying environmental conditions.

The rusts are historically the most important diseases of wheat, as well as the best understood, although other diseases are becoming more important as cropping systems change. What preoccupies most plant breeders and plant pathologists today is how to obtain resistance that endures through time. Many scientists now breed for polygenic,

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[14] The complexity of the topic is exemplified by the fact that plant pathologists have used more than 30 terms to characterize resistance (Thurston 1971).

durable resistance by accumulating, within a single cultivar, genes from diverse sources and genes controlling various mechanisms of resistance. Breeding for this type of resistance is more time-consuming and expensive for a research program but is a longer lasting insurance against vulnerability to disease.[15] Two basic strategies can be pursued to utilize genetic diversity in a way that supports the goal of enhancing durable, host-plant resistance to the rusts in wheat cultivars. The first strategy is to maximize the number of effective resistance genes in a genotype or set of genotypes. The second is to promote, via government institutions, the reduction of contiguous areas of land planted to the same varieties or to varieties possessing the same resistance genes.

In the 1970s, as interest grew in agricultural systems that mimicked natural ecosystems, "alternative" genetic strategies of multiline varieties and varietal mixtures became increasingly popular concepts. The individual lines in a multiline variety differ in the specific resistance genes they carry. Varietal mixtures are combinations of the seed of cultivars that have already been released which possess different resistance genes.

The primary constraints to the diffusion of these control strategies have been economic. Both multilines and varietal mixtures pose problems when uniform grain quality is important to the farmer in marketing the crop, as is often the case for wheat used to make bread. Multilines take a long time to develop, with the result that they yield as much as the lines from which they are derived but less than other varieties that are currently available (Figure 7). Consequently they have not proven very profitable for seed companies or very attractive to farmers. The principal advantage of multilines and mixtures is that they mimic a more natural agricultural system, in which host plants are not genetically identical and the pathogen population can be stabilized at intermediate levels and numbers (Roelfs, Singh, and Saari 1992).

While susceptibility to disease affects the inherent resistance in a genotype(s), it is the extent of a genotype's contiguous cultivation that determines the probabilities of an epidemic. The principal strategies that plant breeders and pathologists pursue to forestall epidemics are to maximize diversity across space and time by recommending changing portfolios of cultivars. These preventive approaches are influenced heavily by public policy.

Public policy plays an important role in the course of disease development and control, because the successful implementation of many of the strategies devised by scientists depends on decisions by governmental or public institutions and the allocation of public resources for disease control (NRC 1972; for an example, see Dubin and Torres 1981). Regional gene deployment is next to impossible because it requires close cooperation among breeders and agreements that hold over decades. "Curative" strategies are also essentially matters of public policy. Disease reconnaissance and monitoring are important for enabling rapid responses to outbreaks, and the best way to prevent disease from spreading (through chemical or other methods of control) once an epidemic is diagnosed is increasingly a source of policy debate.

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[15] Breeders typically work from advanced lines, and most advanced lines are already relatively uniform with respect to single, known resistance genes.

Evidence on Genetic Variation among the Major Bread Wheats Grown in the Developing World

Evidence from Farmers' Fields [16]

In the developing world, bread wheats are sown on a far greater area than durum wheats. South Asia, the Southern Cone of South America, and Mexico/Guatemala produce primarily bread wheats. Probably less than 20% of the bread wheat area in the developing world is still sown to unimproved cultivars, many of which are found in parts of West Asia. Durum wheats are more prominent in some regions, and the proportion of area sown to traditional cultivars is greater for durum than for bread wheats, which has important implications for their genetic diversity. North Africa, Ethiopia, and some parts of West Asia (Syria, Jordan) have proportionally more area planted to durum wheats (CIMMYT World Wheat Impacts Survey, summarized in Byerlee and Moya 1993).

The text that follows will focus on bread wheats. We use the term *modern* to denote both tall and semidwarf varieties that are products of a plant breeding program. We base much of our analysis on the number of distinct crosses rather than the number of cultivars, since several varieties can result from the same cross and any one of these varieties can be released and grown under different cultivar names. The latter happens, for example, when national programs re-release (and rename) a line obtained from an international research institution or another national program. The most precise level of detail for identifying a unique product of a breeding program—a variety—is given by a combination of cross information and selection history. Unfortunately, that level of detail is not available for all varieties in our databases. In these tables, and in the reported calculations of coefficients of parentage, selections from the same cross have been treated as the same cross. This slightly overstates the similarity of parentage and understates the diversity.

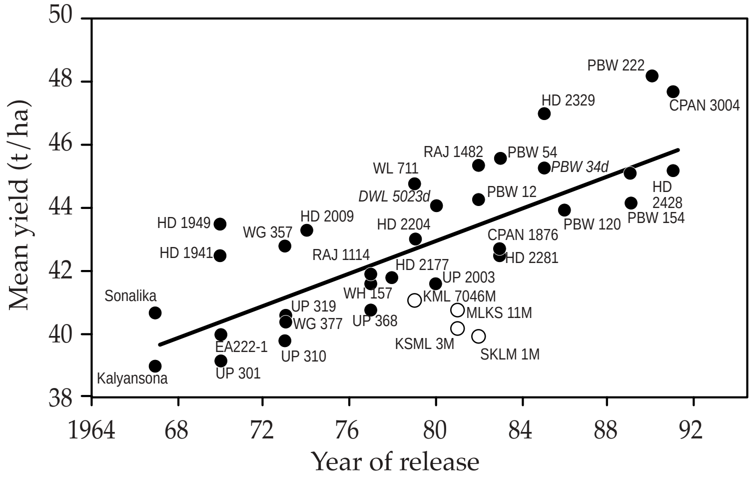

Figure 7. Yield trend in wheat varieties (black dots) and multilines (white dots) released for India's northwestern and northern plains zones, 1967-91 (crops were grown under irrigated conditions and sown in a timely fashion).

Source: K.B.L. Jain (personal communication).

Indicators of spatial diversity. The more important a region is in terms of area sown to bread wheat, the less diverse it is in terms of the number of crosses grown per million hectares.

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[16] The People's Republic of China is the largest national producer of wheat in the developing world, but the Wheat Impacts Survey contains wheat cultivar data from only one region of China. The CIMMYT Economics and Wheat Programs are improving the coverage and quality of data on wheat releases and pedigree information for China. Some preliminary findings on germplasm use, genealogies, and area distributions by cultivar are reported in Yang and Smale (1996). Appendix B lists the countries from which data were available.

Among regions of the developing world, those with the greatest number of bread wheat cultivars and crosses planted in farmers' fields in 1990 were South Asia and the Southern Cone of South America (Table 5). South Asia, the Southern Cone, and West Asia, which contain the largest area planted to bread wheats, have the lowest number of crosses per million hectares sown. The fewest bread wheat crosses were found in North Africa, where durum wheat is more important, and the Andean Region, where traditional cultivars still cover a significant portion of the bread wheat area. The Andean Region, with its small wheat area and many microclimates, has the greatest number of crosses per million hectares of bread wheat grown.

As noted, the percentage of area planted to leading cultivars is an indicator of *spatial diversity*. The percentage of area planted to the top five unique crosses ranges from 43% in the Southern Cone to 71% for Mexico/Guatemala and the Andean Region (Table 5). In each region, after the top 5-10 crosses are considered, the percentage of bread wheat area sown to each cross diminishes rapidly, which implies that the remainder of the bread wheat area is distributed among large numbers of crosses. West Asia has a relatively high level of spatial diversity, which may reflect in part the relative importance of traditional bread wheat cultivars in that region.

The figures in Table 5 appear high, but it is important to recognize that the area sown to leading cultivars is probably lower today than in earlier decades of the 20th century (see above, "Measuring Genetic Diversity in Wheat"). Since the beginning of the Green Revolution in the mid-1960s, the percentage of area planted to leading bread wheats has also changed. At least twice as many cultivars derived from the Veery cross were released in developing countries, compared to the number derived from the II8156 cross, but the Veery cultivars occupy only about one-fifth the area once sown to II8156 (Byerlee and Moya 1993).

Table 5. Indicators of spatial diversity among bread wheats grown in the developing world in 1990

	Sub-Saharan Africa	North Africa	West Asia	South Asia	Mexico/ Guatemala	Andean Region	Southern Cone	Developing world
Number of modern cultivars	39	28	51	64	42	27	64	310
Number of crosses from which cultivars were selected	30	23	47	51	36	25	54	234
Area in modern cultivars (million ha)	0.7	1.8	8.4	29.2	0.9	0.2	8.8	49.8
Modern cultivars as percentage of area in bread wheats	86	83	53	93	94	87	93	82
Crosses/mill ha modern cultivars	45	13	5	2	41	145	6	5
Top five crosses as percentage of area in modern cultivars	64	62	48	59	71	71	43	36.4

Source: Calculated from CIMMYT Wheat Pedigree Management System and data from CIMMYT Wheat Impacts Survey (summarized in Byerlee and Moya 1993).

Note: Regional numbers of cultivars and crosses do not total to "developing world" because the same cultivar or cross may be grown in more than one region. "Developing world" category excludes China. "Modern" cultivars include semidwarf and tall improved varieties.

Indicators of temporal diversity. The average age of crosses in farmers' fields, weighted by the area planted to each cross, is a measure of the *temporal diversity* of cultivars. The weighted average age of crosses ranges from about eight years for Mexico/Guatemala to about 15 years for North Africa (Table 6). The rapid rate of change among crosses grown in Mexico/Guatemala reflects in part the high rate of change in the virulence of leaf rusts in that zone. As a point of comparison with these figures, Brennan and Byerlee (1991) have estimated the weighted average age of cultivars for a number of specific wheat-producing zones of the industrialized and developing world, over several decades. Among the zones they examined, the Yaqui Valley of Mexico had the highest temporal diversity (a weighted average age of only 3.1 years) and the Punjab of Pakistan, the lowest (a weighted average age of about 11 years). Wheat-producing zones in Brazil, Argentina, the U.S., Australia, New Zealand, and the Netherlands had an average over time of 7-10 years. By contrast, Canada has a relatively low level of temporal diversity for an important industrialized wheat producer, ranging from about 10 to 13 years over the past 20 years (unpublished data from N. Thomas, see Thomas 1995). In 1990 in the developing world, the cultivars with the oldest weighted average age (surpassing 16 years) were found in Colombia, Ecuador, Jordan, Lebanon, Myanmar (Burma), Nepal, and Yemen (Byerlee and Moya 1993).

The age of crosses planted by farmers has implications for their resistance to both known and unknown pathogens. Using data from a number of countries, Kilpatrick (1975) estimated that resistance in a cultivar lasts 5-6 years for leaf and stripe rusts, when resistance is monogenic. Based on

Table 6. Temporal diversity of bread wheat crosses grown in developing countries in 1990

Region	Country	Weighted average age (years) of cross in 1990
Sub-Saharan Africa		**11.30**
	Burundi	9.00
	Ethiopia	13.40
	Kenya	13.30
	Sudan	10.38
	Tanzania	6.71
	Zambia	5.00
	Zimbabwe	6.76
West Asia		**10.64**
	Iran	8.87
	Jordan	12.00
	Lebanon	20.22
	Saudi Arabia	9.97
	Syria	12.66
	Turkey	11.23
	Yemen Arab Republic	12.00
North Africa		**14.66**
	Algeria	14.80
	Egypt	13.72
	Libya	16.00
	Morocco	13.60
	Tunisia	24.80
South Asia		**12.84**
	Bangladesh	10.71
	Burma	30.33
	India	12.54
	Nepal	17.81
	Pakistan	13.20
Southern Cone		**9.20**
	Argentina	11.25
	Brazil	7.02
	Chile	6.35
	Paraguay	8.42
	Uruguay	3.72
Andean Region		**13.69**
	Bolivia	6.08
	Colombia	21.84
	Ecuador	18.28
	Peru	11.05
Mexico/Guatemala		**7.97**
	Guatemala	6.85
	Mexico	8.01

Source: Calculated from CIMMYT Wheat Impacts Survey and CIMMYT Pedigree Management System.
Note: Weighted by the percentage of area planted to cross.

that estimate, none of the regions of the developing world, and only a minority of countries, had desirable levels of varietal turnover in 1990. But the longevity of a cultivar's rust resistance is very specific to the environment in which it is grown, and the socially optimal period for cultivar replacement is a function of many economic and biological factors, of which resistance to pathogens is only one (Heisey and Brennan 1991). There is a need for higher rates of varietal turnover in more favorable production environments, because the conditions conducive to high productivity also encourage diseases to develop. Historically, of course, some individual cultivars dominated the wheat areas of industrialized countries for decades — such as Wilhelmina and Juliana in the Netherlands, the Vilmorin crosses in France, and Federation in Australia. More recently, the fact that Neepawa occupied over 50% of the wheat area in Canada for years has contributed to a relatively low measure of temporal diversity (Thomas 1995).

Indicators based on genealogies. As calculated from the coefficients of parentage, the *latent diversity* of the top 10 cultivars planted in the developing world in 1990 appears to be fairly high, although the average coefficient of diversity varies by geographical region (Table 7). Among regions of the developing world, the average coefficients of diversity are significantly higher among the top 10 lines grown in West Asia and the Southern Cone of South America than in South Asia and Mexico/Guatemala.

As a point of comparison, the same indicators are presented for three of the four major bread wheat producers of the industrialized world and for the top 10 spring wheat crosses. In Australia average and weighted coefficients are almost equal, which implies that the top 10 crosses are distributed equally as a percentage of national area. Each state of Australia has a different set of leading cultivars, and the environment is more heterogeneous than in the U.S. or Canada. The top 10 crosses grown in Canada are statistically less diverse than the top 10 in any of the developing or industrialized regions considered. The minimum diversity among pairs of crosses is also near zero in Canada, whereas the maximum diversity is lower than for the other industrialized producers and the developing regions.

An estimate of "genealogical distance," suggested by the work of Weitzman (1992), is also shown in Table 7.[17] As compared to a simple average of the coefficients of diversity for each group of 10 cultivars, this indicator represents the sum of the distances of each cultivar from all other cultivars in the set, based on the pairwise coefficient of diversity as a measure of distance. Once again, Canada's leading spring wheats appear markedly less diverse than those of either the other major industrialized wheat producers or the developing regions.[18] Mexican wheats, grown in a small, relatively homogeneous

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[17] The sum of the branch lengths of the dendrogram constructed from Ward's cluster analysis of pairwise, ultrametric distances. Here, the pairwise distance measures are coefficients of diversity. Any pairwise distance measure that satisfies ultrametric properties can be used as the basis of analysis. A distance has ultrametric properties if $d(i,j) \geq 0$; $d(i,i) = 0$; and $d(i,j) = d(j,i)$—where *d* represents distance, and *i* and *j* represent points or individuals.

[18] France, the fourth major producer in the industrialized world, is not represented, although some well-known aspects of the history of wheat breeding and patenting in that nation suggest that latent genetic diversity may be fairly low. As shown earlier, area sown to the top cultivars declined rapidly in recent years.

production environment, also appear considerably less diverse — a result that is not as clear with a simple average of coefficients of diversity. The top 10 bread wheats of West Asia appear to be among the most diverse for the developing regions.

These data, and data presented for the Indian Punjab in Appendix C, show how the variables that affect the distribution of planted area among cultivars influence both temporal and latent diversity. The difference between the weighted and unweighted measures of diversity crudely reflects the effects of factors related to varietal adoption and, in particular, seed distribution systems. Farmers will choose to grow the variety that is most attractive to them (in terms of profits or other measures of economic value), but the range of their choice is often limited by the few seed types marketed locally. Policy factors that affect the rate of release of cultivars, and the adoption factors that affect farmers' choice of varieties and the rate at which varieties are replaced in farmers' fields, are major determinants of a crop's diversity that are outside the influence of plant breeders.

The top 10 wheat cultivars in the developing world in 1990 are described in terms of *pedigree complexity* and other characteristics in Table 8. Sonalika, Veery, II8156, and Bluebird have been released by various names in different countries. The dominance of South Asia in terms of wheat area, numbers of wheat producers, and the longevity and productivity of the research system is reflected in the fact that seven of the top 10 cultivars were released

Table 7. Latent diversity of top 10 bread wheat crosses grown in the developing world and selected industrialized nations in 1990

Region/country	Average coefficient of diversity	Average coefficient of diversity weighted by cultivated area	Minimum pairwise coefficient of diversity	Maximum pairwise coefficient of diversity	Genealogical distance
Developing world	0.78	0.70	0.43	0.98	8.18
Sub-Saharan Africa	0.79	0.77	0.28	0.99	8.29
North Africa	0.79	0.73	0.57	1.00	7.88
West Asia	0.84a	0.80	0.67	0.99	8.11
South Asia	0.72b	0.63	0.35	0.96	7.70
Mexico/Guatemala	0.69b	0.63	0.57	0.88	5.80
Andean Region	0.80	0.72	0.41	0.99	7.89
Southern Cone of S. America	0.82a	0.80	0.69	1.00	7.78
Selected major industrialized bread wheat producers					
Canada (spring wheats)	0.48e	0.22	0.01	0.80	4.71
Australia (spring wheats)	0.74b	0.72	0.30	0.98	8.63
U.S. (hard red spring wheats)	0.84a	0.79	0.53	1.00	8.71

Source: Calculated from CIMMYT Wheat Impacts Survey and CIMMYT Wheat Pedigree Management System.
Note: Coefficient of diversity=1-coefficient of parentage. Genetic distance is measured as total branch length of dendrogram constructed from Ward's cluster analysis of coefficients of diversity (Weitzman 1992). Average coefficients of diversity with different letters are statistically different, using a nonparametric test. China is excluded from the "developing world" category.

first in India and Pakistan, and most of the area planted to those cultivars is found there. Klein Chamaco, an Argentinean cultivar; Gerek 79, a Turkish cultivar; and Veery, released first in Mexico and Pakistan and subsequently in other countries, are the other three of the top 10 cultivars. Together, these 10 cultivars covered about half of the wheat area in the developing world in 1990. Sonalika[19] alone, one of the oldest of the cultivars, covered more than 10% of the area, probably all in South Asia. The weighted average age of the top 10 cultivars, which is raised significantly by Sonalika and II8156, is 13 years.

The extensive breeding effort that went into developing these leading cultivars is reflected by the large numbers of landraces, generations, and crosses in their pedigrees. Sonalika and II8156, the oldest and probably the most enduringly popular cultivars, have among the shortest and narrowest pedigrees (in number of generations and number of crosses per generation) but less redundancy in use of crosses (proportion of crosses used only once in the pedigree). On average, the pedigrees of the top 10 crosses grown in the developing world contain 44 different landraces, at least 19 generations, and 1,192 parental combinations in their pedigrees, of which about 20% were used only once. By comparison, for all the different crosses grown in the developing world in 1990, the average number of distinct landraces in the pedigree of each cross is 36. The bread wheat cultivars that were the most "successful" in farmers' fields in developing countries in 1990 also represent some of the most complex pedigrees, both in terms of investment by farmers (landraces) and investment by professional wheat breeders (generations and parental combinations).

Yield stability. The *yield stability* of wheat in the developing world is compared over four decades in Table 9. For every region, variation was greater in the decade preceding 1965

Table 8. Characteristics of the top 10 bread wheat cultivars in the developing world in 1990

Cross	Year first released	Area planted, 1990 (million ha)	Percentage of area in developing world, 1990	Maximum number of generations in pedigree	Total number of PCs[b] pedigree (a)	Number of different PCs[b] in pedigree (b)	Percentage of all PCs[b] that are different [(b/a)x100]	Number of different landraces in pedigree	Country that first released cross
Sonalika[a]	1966	6.28	12.61	17	420	90	21	39	India
HD2329	1985	4.07	8.16	22	1,946	153	8	58	India
Veery[a]	1977	3.36	6.75	23	3,169	128	4	49	Mexico
HD2285	1983	2.83	5.67	23	3,295	187	6	59	India
WH147	1977	1.59	3.19	17	295	85	29	48	India
II8156[a]	1965	1.55	3.12	14	117	58	50	37	Pakistan
Gerek 79	1979	1.44	2.89	11	56	31	55	20	Turkey
Klein Chamaco	1978	1.14	2.28	21	1,299	141	11	47	Argentina
Bluebird[a]	1969	1.11	2.23	18	668	91	14	42	Mexico
Lok 1	1981	1.09	2.18	18	650	104	16	39	India

Source: Calculated from CIMMYT Wheat Pedigree Management System and Wheat Impacts Survey.
Note: China excluded from "developing country" category.
[a] Selections from this cross have been released in various countries under different names.
[b] Parental combinations.

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[19] Sonalika, an advanced line from the CIMMYT/Mexican breeding program, was never released in Mexico. It was first released in India, followed by Pakistan and Nepal.

(the year that marks the early phase of the Green Revolution) than in the most recent decade. In regions where the largest proportion of wheat area is planted to modern wheats — South Asia, Mexico/Guatemala, and the Southern Cone of South America — the variation in wheat yields has declined since 1965. In West Asia and North Africa, where modern wheats cover a smaller proportion of area, yield stability has not worsened over the past three decades. Only in the Andean Region and sub-Saharan Africa, two regions with very small wheat areas and with distinctive growing conditions, does the variation in wheat yields appear to have increased since 1965. In both of these regions, however, the overall level of variation is quite low.

As explained previously, because most of the year-to-year variation in aggregate yields is caused by differences in weather, use of irrigation, and pathogens, the factors explaining the largest proportion of variation in aggregate yields are probably associated less with plant stature or genotype than with input supply and pricing policy. The balance of general evidence concerning the relationship between mean yields and yield variance in farmers' fields over time suggests that yield stability has increased even as mean yields have increased, from the 1950s through the 1980s, across the world, in major wheat-producing countries of the developing world, and in India (Anderson and Hazell 1989; Singh and Byerlee 1990; Appendix C). In particular, Singh and Byerlee (1990) showed that technological variables such as the level of adoption of high-yielding varieties and levels of fertilizer use had no effect on differences in wheat yield stability across countries.

Vulnerability to wheat rusts. Table 10 summarizes what is known about the *vulnerability to wheat rusts* across regions of the developing world. Stem rust, which was historically a major worldwide problem, remains so only in East Africa. "Major" implies that crop losses are severe when resistant cultivars are not grown, whereas "minor" means that losses usually occur but are of small magnitude. "Local" means that disease outbreaks occur only in a small part of a region but may be severe. "Rare" implies infrequent occurrence. Leaf rust, although less of a problem historically than stem rust, is still of significance in North Africa. In comparison to stem and leaf rust, no apparent progress has been made in reducing the importance of stripe rust in farmers' fields.

Table 9. Yield stability of all wheats grown from 1955 to 1994 in the developing world

	Sub-Saharan Africa	**North Africa**	**West Asia**	**South Asia**	**Mexico/ Guatemala**	**Andean Region**	**Southern Cone**
	Coefficient of yield variation adjusted for trend (%)						
1955-64	10.8	13.4	8.7	6.5	12.3	9.8	12.9
1965-74	4.3	10.3	8.0	9.1	7.9	2.4	8.1
1975-84	7.1	12.1	4.0	3.0	5.6	5.6	12.2
1985-94	8.8	11.0	7.5	4.0	5.5	4.8	5.0

Source: Constructed from FAO yield data using the Cuddy-Della Valle index (Cuddy and Della Valle 1978).
Note: China is excluded.

Evidence from Breeding Programs

Indicators based on genealogies. The International Spring Wheat Yield Nursery (ISWYN) contains the more advanced breeding materials available to wheat breeding programs in developing countries. The lines in the nursery represent the more successful materials that have been bred internationally, and it is from these lines that national programs can select materials suitable for release to farmers, subject to approval by national release committees. The diversity among the ISWYN entries represents the potential diversity in materials from which future releases to farmers will be selected. Over the past 30 years, the *latent diversity* in the ISWYN germplasm, as measured by the average coefficient of diversity among entries (1 – coefficient of parentage), appears to have decreased slightly within a range that suggests a fairly high level of diversity (Figure 8). The downward trend is statistically significant, though small in magnitude.[20]

The average number of different landraces in the pedigrees of wheat varieties released by developing country programs has increased over time (Figure 9).[21] This finding is important. Although we can expect the frequency of landrace use to increase over time as pedigrees grow longer, it is not necessarily true that the number of *different* landraces will also increase. In a sample of 800 varieties released by national programs in developing countries since the 1960s, those with CIMMYT parents had a higher average number of distinct landraces than those with no CIMMYT parents. In each decade, the average number of landraces per variety increased for all releases, regardless of source of parents (Smale 1995). As we have seen, in the early part of the 20th century, plant breeders in many regions of the world made extensive use of a few landraces from the F.S.U., Europe, and India. Since the late 1970s, however, national programs have released crosses in which an average of one new landrace appears each year.

Table 10. Current and historical importance of leaf, stem, and stripe rusts of wheat in the developing world

	Leaf rust		Stem rust		Stripe rust	
Region	Current	Historical	Current	Historical	Current	Historical
Sub-Saharan Africa						
Eastern	Local	Local	Major	Major	Major	Major
Southern	Local	Local	Local	Major	Rare	Rare
North Africa	Major	Major	Local	Major	Local	Local
West Asia	Local	Local	Local	Major	Major	Major
South Asia	Local	Major	Minor	Major	Local	Local
Mexico/Guatemala	Local	Major	Minor	Major	Minor	Local
Andean Region	Local	Local	Local	Local	Local	Local
Southern Cone	Local	Major	Minor	Major	Local	Local

Source: Adapted from Roelfs, Singh, and Saari (1992).

Note: Major = severe crop losses when resistant cultivars not grown; minor = losses usually occur but are of small magnitude; local = disease outbreaks occur only in a small part of the region, but may be severe; and rare = infrequent occurrence.

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[20] Calculated with a Cox-Stuart one-tailed test. However, missing genealogies in the later years were excluded from the analysis, so measurement errors may affect results.

[21] According to developing country of initial release and year of initial release. Small numbers may explain part of the apparent variation in the 1960s.

Various characteristics of pedigrees suggest a growing *pedigree complexity* in the more successful CIMMYT wheats grown by farmers in developing countries over time (Table 11). The nature of conventional plant breeding is to build on past successes, and the number of generations, total number of parental combinations, and frequency of landrace use can be expected to increase with time. Building on past successes does not necessarily imply utilizing distinctly different materials or landraces, however. Among successful bread wheats grown in developing countries over the past 40 years, the numbers of different parental combinations and different landraces occurring in the pedigrees have increased over time. The Gini coefficients for the genetic contribution of landraces vary over cultivars, but they do not change systematically over time or as the number of landraces in the pedigrees has changed.[22] In none of the pedigrees of the more successful cultivars released from 1950 is the distribution of landraces by genetic contribution highly unequal. Ciano 79 has the most unequal distribution, and Yaqui 50, one of the progenitors of the early Green Revolution wheats, has the most equal distribution among only 12 landraces.

The figures in Table 12 provide a measure of *pedigree complexity* for a sample of 800 lines released by developing countries over the past 30 years. The figures provide an indication of the extent of the scientific effort devoted to varietal development. As expected, the average number of generations and parental combinations in pedigrees increases with each passing decade. While the average number of distinct parental combinations (those counted only the

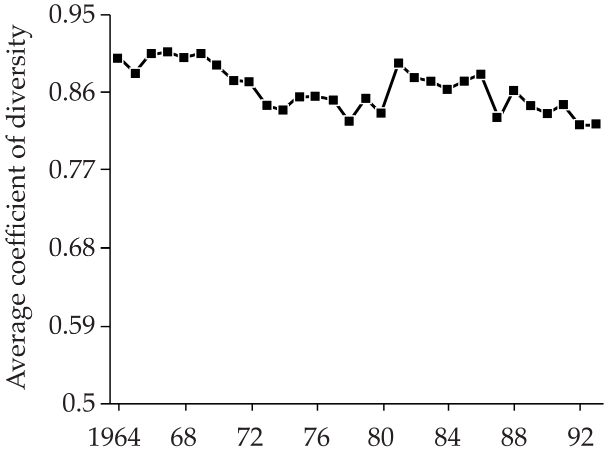

Figure 8. Latent diversity of ISWYN bread wheat entries, 1964-92.
Source: Calculated from International Spring Wheat Yield Nursery; Annual Reports; Nightingale (1995).

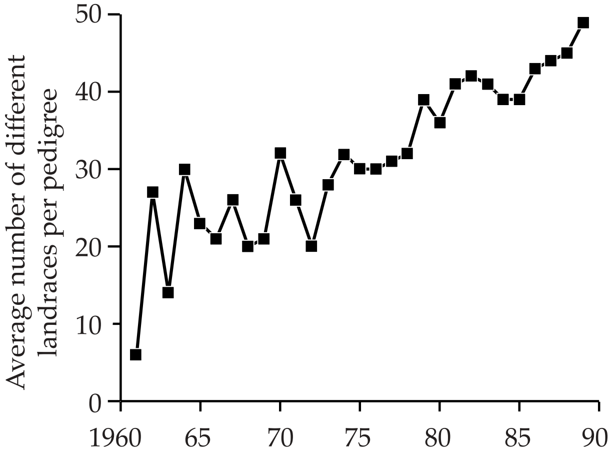

Figure 9. Landraces in pedigrees of wheats released in developing countries, 1961-89.
Source: Calculated from CIMMYT Wheat Impacts Survey and Wheat Pedigree Management System.

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[22] The Mendelian contribution is the expected theoretical contribution of a progenitor to a cross, assuming that each parent contributes genes with an equal probability. The Gini coefficient, usually used to measure income inequality, is used here to measure inequality of landrace contribution. To calculate the Gini coefficient, a Gini curve must be drawn. For example, suppose a cultivar is made up of contributions from 30 landraces. These landraces can be arranged in order of increasing theoretical Mendelian contribution to that cultivar, and a curve plotted that indicates cumulative theoretical Mendelian contribution from the addition of successive landraces. The first point on the curve would be 0, the second point the theoretical contribution from the first landrace, the third point the cumulative contribution from the first and second landraces, and so on. The ratio of the area under the curve to the area under the triangle that would result if all theoretical Mendelian contributions were equal is the Gini coefficient. A Gini coefficient of 1, therefore, would indicate complete equality of theoretical contributions from all landraces; a Gini coefficient that approaches 0 would indicate that one or a few landraces are heavily weighted in the cultivar in question.

first time they are used) also increases over time, the number of parental combinations that have been used before increases more rapidly, so that the percentage of reused parental combinations rises over time. The pattern is the same for all materials regardless of whether they have CIMMYT parents. The size of the pedigrees increases with CIMMYT parents in each decade, although the redundancy is also greater in materials with CIMMYT parents.[23] One implication of these figures may be that as national programs release less CIMMYT material directly or use fewer CIMMYT materials as immediate parents of new releases, a growing proportion of national program releases may contain pedigrees with distinct components.

Table 11. Pedigree complexity of leading CIMMYT bread wheat varieties grown in developing countries, 1950-92

Cultivar/cross	Year first released	Number of generations in pedigree	Number of different parental combinations in pedigree	Number of different landraces in pedigree	Gini coefficient for landrace contribution
Yaqui 50	1950	8	20	12	0.87
Penjamo	1962	13	40	26	0.64
Sonora	1964	15	55	31	0.56
Inia	1966	17	71	34	0.56
Tobari	1966	16	61	35	0.50
II8156	1966	14	57	35	0.60
Bluebird	1971	18	92	39	0.67
Tanori F 71	1971	18	84	36	0.58
Jupateco F	1973	19	96	40	0.83
Pavon F	1976	20	124	45	0.64
Nacozari F	1976	21	105	45	0.62
Ciano T	1979	21	160	62	0.39
Veery (Seri M8)	1982	23	127	47	0.68

Source: Calculated from CIMMYT Wheat Pedigree Management System; Skovmand and Fox (personal communication).

Table 12. Pedigree complexity by source of parent lines, wheat varieties released by developing countries, 1960-90

	1960-69 No. of CIMMYT parents			1970-79 No. of CIMMYT parents			1980-90 No. of CIMMYT parents		
Pedigree characteristic	0	1	2	0	1	2	0	1	2
Numbers of observations	38	9	29	82	83	129	77	105	243
	Average over pedigrees								
Number of generations	9	18	16	10	18	19	15	20	22
Total number of parental combintations	140	491	214	166	516	739	829	883	2,084
Different parental combintations	20	67	58	25	73	85	67	92	1,964
Parental combintations reused	120	424	156	141	443	654	763	761	1,964
Percentage of reused parental combinations in all varieties	26	68	64	27	68	80	53	77	90

Source: Calculated from CIMMYT Wheat Pedigree Management System and CIMMYT Wheat Impacts Survey.

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[23] In assembling the data, it has not been possible to disaggregate by source of grandparents, and the figures therefore underestimate the contribution of CIMMYT materials in the ancestry of the lines. Lines that are recorded as having no CIMMYT parents may nevertheless contain a CIMMYT ancestor. *Parents* are the lines in the most recent cross.

Yield stability. Advances in yield stability have been made since the early semidwarf wheats of the Green Revolution were released. Figure 10, from Pfeiffer and Braun (1989), shows that the best CIMMYT advanced line in 1989 yielded more under all moisture regimes, at low or high nitrogen levels, and under weedy or weed-free conditions than the older cultivars Yaqui 50 (1950) and Nainari (1960). Econometric analysis of trial data provides evidence that since the 1950s, successive CIMMYT wheat releases have shown increasing yield stability, higher mean yields, or both (Traxler et al. 1995). Ortiz-Monasterio et al. (1996) have shown that since 1950, the nitrogen-use efficiency of spring bread wheat germplasm developed by CIMMYT and its predecessor organizations has increased (Figure 11).

Vulnerability to wheat rusts. The wheat rusts are not modern diseases; the Romans sacrificed red dogs to the god of grain, in the hope that he would prefer meat to the wheat crop and would not release the red rust of wheat (Large 1962). Resistance to rusts was an early goal in scientific plant breeding. In the early years of the 20th century, Farrer in Australia introduced some wheat forms from the Asian subcontinent to breed varieties capable of escaping rust disease by maturing early (Lupton 1987). A few of Farrer's wheats, such as Florence, contained some genetic resistance to stem rust (Macindoe and Brown 1968). Genetic resistance to stem and leaf rust in Australia was first achieved in the 1930s, when wheat breeders crossed Steinwedel with *T. timopheevi* and, later, *khapli*. The French plant breeder Scribaux introduced early maturity and some genetic resistance to rust from an Italian landrace in one of the earliest government-sponsored plant breeding institutes, established in 1921 in France. During the rust epidemic that began in 1916 in North America, the vulnerability of Marquis led to the introduction of genetic resistance in the bread wheats through crosses with the durum wheat Iumillo and Yaroslav emmer.

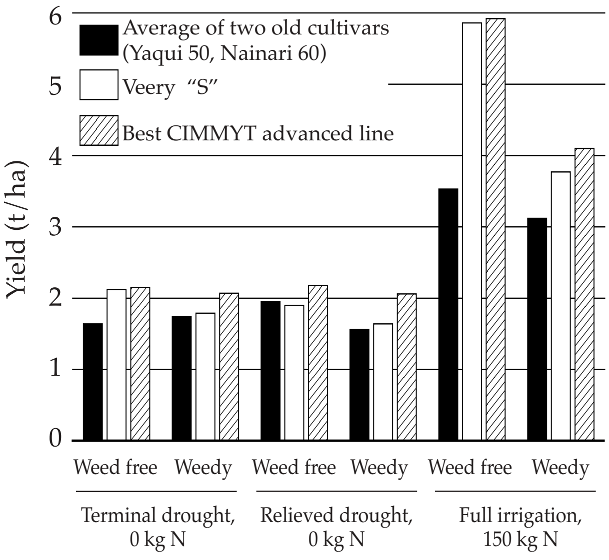

Figure 10. Input efficiency of old and New CIMMYT varieties under differing production conditions.
Source: Pfeiffer and Braun (1989).

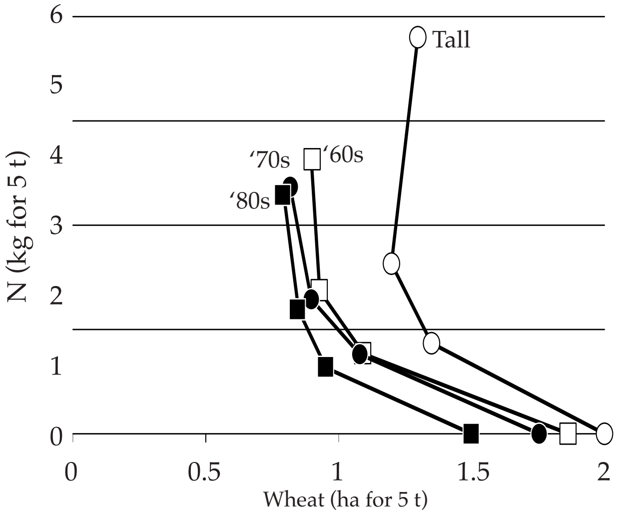

Figure 11. Kg of N required to grow 5 tons of wheat. From right to left, the labels and cultivars are: *Tall*, two cultivars of 1950 and 1960; *'60s*, three of 1962-66; *'70s*, three of 1971-79; and *'80s*, two of 1981 and 1985. Cultivars not labelled *tall* are semidwarfs.
Source: Calculated by Waggoner (1994) from data in Ortiz-Monasterio et al. (1996).

In the Asian subcontinent, the first stem rust epidemic was recorded in 1786 (Nagarajan and Joshi 1985). Concern over the magnitude of losses from rust was expressed in government documents from 1839, well before scientific plant breeding began. According to government records, Indian landraces, which were planted on millions of contiguous hectares, were notably susceptible to rust. Average annual losses were estimated at 10% of the value of the crop (Howard and Howard 1909; Nagarajan and Joshi 1985). Before farmers in the Asian subcontinent began growing tall modern cultivars in the 1920s and 1930s, the wheat price was significantly correlated with the incidence of weather favorable for rust epidemics (Howard and Howard 1909). One of the attractions of the semidwarf cultivars released in the 1960s was that they were less vulnerable to rust than the older, taller, later maturing, modern cultivars (Pal 1966; ICAR 1978).

The semidwarf wheats inherited the results of more than 20 years of research in Mexico on improving resistance to the major rust diseases (Byerlee 1994). From 1967 to 1981, in 50 locations in over 30 countries, CIMMYT tested local, improved tall, and semidwarf spring wheats for resistance to stem, leaf, and stripe rust. The average coefficient of infection (ACI), an index ranging from 0 (no disease) to 100 (maximum infection), is shown in Figure 12 for each cultivar type. The semidwarf cultivars' resistance to leaf and stem rust was clearly superior to the resistance of modern tall varieties and local farmers' varieties. Data on stripe rust indicate that semidwarf wheats were on average less susceptible to the rusts than farmers' selections, but slightly more susceptible than modern tall varieties.

Of the six screening nurseries that CIMMYT annually distributes to cooperators in wheat-growing countries around the world, the nursery with the longest history is the International Bread Wheat Screening Nursery (IBWSN), initiated in 1967. The nursery contains 200-400 new, elite, advanced lines from the Bread Wheat Breeding Program. Data on disease resistance in the IBWSN since 1967 are shown in Figure 13. The percentage of advanced bread wheat lines with an ACI of less than 10 for stem, leaf, and stripe rust has an upward trend from 1967 through 1992 (updated from van Ginkel and Rajaram 1993).

CIMMYT's wheat breeding policy has been to utilize sources of germplasm that are as diverse as possible for rust resistance. The various sources of rust resistance in CIMMYT materials have widespread geographic origins, including the Southern Cone of South America; the Andean Region of South America; Mexico/Guatemala; the U.S. and Canada; the eastern highlands of Africa; North Africa; the Iberian Peninsula; the Middle East; the Nile Valley; Europe;

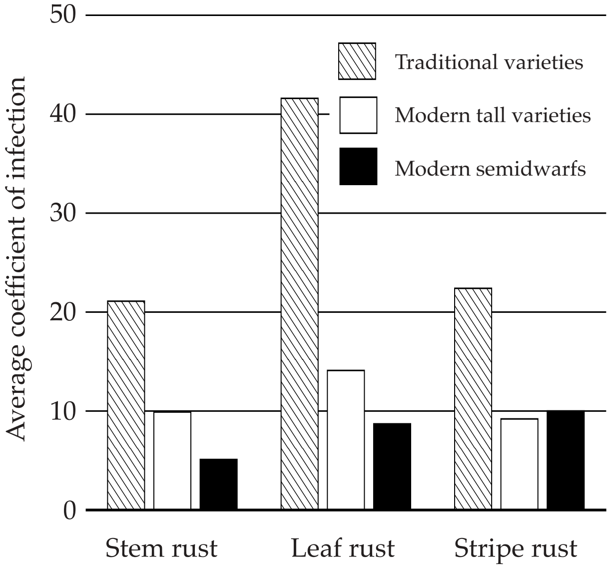

Figure 12. Rust resistance by wheat type, 50 locations in 30 countries, 1980.
Source: Rajaram, Singh, and Torres (1988).

Australia; and New Zealand. Disease "hot spot" locations (noted for maximum variability of a pathogen and/or severity of a disease) are selected for inclusion in the international multilocation testing system.

Wheat breeders have recognized for some time that developing monogenic resistance in such diseases as the wheat rusts contributes to a "boom-bust" cycle of resistance and vulnerability because the pathogen is able to mutate rapidly and form new strains. Breeding for monogenic resistance, which is also known as race-specific or qualitative resistance, is still practiced by many wheat breeders because it is relatively cheap and simple — the presence of the resistance gene is generally easily verified in the seedling as well as in the adult plant. However, in the long term this strategy leads to a continual, expensive search for such genes (Singh and Rajaram 1995).

Achieving resistance that endures through time is clearly a preferable objective. Increasingly, scientists are breeding for polygenic resistance by accumulating diverse, multiple genes from new sources and genes controlling different mechanisms of resistance within single varieties. Diversity among genes that confer race-specific resistance does not assure resistance, however, since most of these genes are no longer effective. Durable resistance in wheat results from the additive interactions of a few unnamed, "slow-rusting" (Caldwell 1968) genes, each of which has a minor visible impact, but which together confer nonspecific resistance (van der Plank 1963). The selection methodology used in the CIMMYT breeding program is based on the accumulation of genes with nonspecific resistance (van Ginkel and Rajaram 1993).

Most of the major varieties in the world today, and almost all of CIMMYT's bread wheat germplasm, contain resistance genes for stem and leaf rust that are currently understood to be durable (Singh and Rajaram 1991; Singh 1993; van Ginkel and Rajaram 1993). The source for stem rust resistance employed by breeders in the late 1940s was the cultivar known as FKN (Frontana/Kenya 58/Newthatch). The resistance of Newthatch, a Canadian bread wheat, traces back through Hope to Yaroslav emmer, the original donor of the gene *Sr*2. *Sr*2 is expressed as partial resistance, and in combination with other resistance genes, the *Sr*2 complex has been commercially exposed to the stem rust fungus on tens of millions of hectares for more than 40 years without succumbing. FKN also carries the source of resistance to leaf rust through Frontana, whose

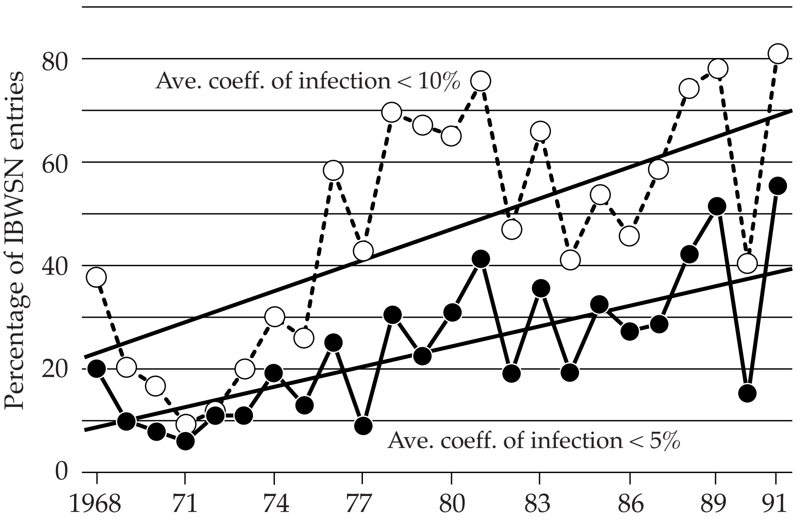

Figure 13. Resistance of advanced lines in IBWSN to leaf rust.
Source: Updated from van Ginkel and Rajaram (1993).

origin was discussed earlier. Currently, leaf rust resistance is based primarily on *Lr*34 and several additional slow rusting genes, which are unknown.

Tables 13 and 14 illustrate the challenge of breeding for durable, polygenic resistance to the wheat rusts. As shown by the column describing resistance at the seedling stage, none of the single, named genes confers resistance among the cultivars listed for Mexico and South Asia. Where cultivars remain resistant, their resistance is partial and is conferred by more than one known gene, each of which has a minor additive effect, as well as unknown genes in the genetic background of the cultivars. A comparison of types of resistance for several of the lines also illustrates what little is now known about the basis of their resistance. Among the varieties listed in Table 8, WH147, Sonalika, Lok1, and WL711 all carry the known leaf rust resistance gene *Lr*13 and are susceptible at the seedling and adult plant stage. HUW234 also carries that gene but retains moderate resistance — perhaps because of unknown, background resistance. Similarly, all of the known resistance genes in Pavon 76 have been overcome, but the cultivar continues to show moderate resistance across extensive areas in

Table 13. Named genes for leaf rust resistance and current adult plant resistance of some bread wheat cultivars grown in Mexico

		Current resistance	
Cultivar	**Named *Lr* gene(s)**	**Seedling**	**Adult plant**
Opata 85	*Lr*10, *Lr*34	S	MR-MS
Salamanca 75	*Lr*13, *Lr*34	S	MR-MS
Ures 81	*Lr*13, *Lr*26	S	MR-MS
Esmeralda 86	*Lr*10, *Lr*14a, *Lr*34	S	R
Oasis 86	*Lr*13, *Lr*19	S	S
Ciano 79	*Lr*16	S	R
Papago 86	*Lr*16	S	R
Anahuac 75	*Lr*13, *Lr*17, *Lr*27+*Lr*31	S	S
Ocoroni 86	*Lr*27+*Lr*31, *Lr*34	S	R
Cucurpe 86	*Lr*10, *Lr*34	S	MR-MS
Delicias 81	*Lr*13, *Lr*17, *Lr*27+*Lr*31	S	S
Pavon 76	*Lr*1, *Lr*10, *Lr*13	S	MR
Jauhara 77	*Lr*10, *Lr*14a, *Lr*34	S	MR-MS
Sonoita 81	*Lr*1, *Lr*13, *Lr*34	S	R-MR
Tonichi 81	*Lr*1, *Lr*13, *Lr*27+*Lr*31, *Lr*34	S	R-MR
Mexico 82	*Lr*23	S	MS
Cumpas 88	*Lr*13, *Lr*26, *Lr*34	S	R-MR
Cleopatra 74	*Lr*1	S	MR-MS
Bacanora 88	*Lr*26, *Lr*34	S	MR
Angostura 88	*Lr*13, *Lr*2,*Lr*26,+	S	MR-MS
Galvez 87	*Lr*3, *Lr*10, *Lr*13	S	MR-MS
Tepoca 89	*Lr*16	S	MR-MS
Tesia 79	*Lr*3bg, *Lr*10, *Lr*34	S	MR
Rayon 89	*Lr*13, *Lr*34	S	R-MR

Source: R. Singh, updated from Singh and Rajaram (1991) and Singh (1993).

Note: Current resistance is based on the prevailing pathotypes during the 1994-95 growing season in Mexico. All cultivars were R or MR at the time of release. R (resistant) indicates that the cultivar possesses good resistance; MR (moderately resistant) indicates adequate resistance; MR-MS (moderately resistant to moderately susceptible) indicates that although resistance is usually adequate, in some years it could be inadequate; MS (moderately susceptible) indicates inadequate resistance; and S indicates susceptibility to disease.

Pakistan. The incorporation of new single genes in a cultivar, even when they are alien resistance genes, does not solve the resistance problem. Examples include *Lr*26 (present in the 1B/1R translocation) and *Lr*19 (from *Agropyron* spp.). In each case, new pathotypes evolved shortly after the cultivar's release.

Adding New Dimensions to Genetic Variability in Bread Wheats through Wide Crosses and Biotechnology

Wide crosses can provide new sources of higher yield potential and resistance to disease and numerous abiotic stresses. Over the past 15 years, CIMMYT researchers have used wide crosses with the *Triticum* and *Aegilops* grass species to improve bread wheat (see Mujeeb-Kazi and Hettel 1995). The most significant aspect of this work is the identification and incorporation into breeding lines of sources of variability that are not normally accessible in conventional crop breeding.

Table 14. Named genes for leaf rust resistance and current adult plant resistance of some bread wheat cultivars grown in South Asia

		Current resistance	
Cultivar	**Named *Lr* gene(s)**	**Seedling**	**Adult plant**
Sonalika	*Lr*13	S	S
HD2329	*Lr*10, *Lr*13	S	MR-MS
HD2285	*Lr*13, *Lr*23	S	MS
PAK81	*Lr*23, *Lr*26	S	MR-MS
WH147	*Lr*13	S	S
Mexipak	Unknown	S	MS
Lok 1	*Lr*13	S	S
UP262	*Lr*13, *Lr*23	S	MR
WL711	*Lr*13	S	S
HUW234	*Lr*13	S	MR-MS
Lyallpur 73	*Lr*1, *Lr*13, *Lr*34	S	MR
C306	*Lr*34	S	MR
Kanchan	*Lr*13, *Lr*23	S	MR-MS
Pavon 76	*Lr*1, *Lr*10, *Lr*13	S	MR
Pari 73	*Lr*1, *Lr*13	S	S
HD2009	*Lr*10, *Lr*13, *Lr34*	S	MR

Source: R. Singh, updated from Singh and Rajaram (1991) and Singh (1993).

Note: Current resistance is based on the prevailing pathotypes during the 1994-95 growing season in Mexico. R (resistant) indicates that the cultivar possesses good resistance; MR (moderately resistant) indicates adequate resistance; MR-MS (moderately resistant to moderately susceptible) indicates that although resistance is usually adequate, in some years it could be inadequate; MS (moderately susceptible) indicates inadequate resistance; and S indicates susceptibility to disease.

Of the approximately 325 perennial and annual grasses within the Triticeae tribe, relatively few have been hybridized with wheat. CIMMYT's recent successful hybridizations among wheat species have provided a stock of new germplasm for breeding programs. This new germplasm is complemented by a growing number of synthetic bread wheats, developed through crosses between durum wheat and a number of diploid grass species, and other hybrid combinations produced by crossing wheat with various perennial species in the Triticeae. One of the major recent innovations of CIMMYT's wide cross laboratory has been the development of a method for creating a synthetic bread wheat, which can be directly used in crossing programs, by reenacting the initial hexaploid cross of an early form of durum wheat with *T. tauschii*. The products of these crosses can be crossed directly with advanced bread wheat lines. In this way, previously untapped sources of disease resistance and genetic variability can be joined with known sources of yield and disease resistance to enhance the range of known beneficial traits and the diversity in the genetic background of the bread wheat. The synthetic hexaploids possess many other characteristics, which are being evaluated by national and international breeding programs.

Two major prerequisites for continued success in wide cross breeding programs are the capacity for long-term investment with delayed payback periods and international collaboration among specialists and institutions which do not respond to competing interest groups. Both prerequisites are more likely to be met by international rather than national institutions.

Molecular biology also promises to enhance the genetic variation in wheat that can be made available to farmers through plant breeding. The development of a detailed understanding of the wheat genome will help molecular biologists to trace useful chromosome segments with greater accuracy as well as expand the range of genetic variability in a number of ways. For example, a better understanding of the wheat genome has facilitated work on wide crosses. Molecular markers can be used to test for the presence of alleles conferring resistance to disease. Germplasm banks can increase their efficiency through DNA "fingerprinting," which can verify that the banks do not hold duplicate accessions. Isozyme analyses can be used to measure the extent of gene flows between introductions and local populations, which has implications for the design of conservation projects. Other techniques, such as genetic transformation, may radically expand the genetic bases of crop plants.

Conclusions

Genetic diversity is difficult to measure because it has many dimensions, and diversity is difficult to discuss because the biological and social scientists who study it may not share a common technical language, although they share common goals. Even within a single disciplinary approach, researchers may use various indicators to measure the same aspect of genetic diversity, without necessarily generating consistent results. If we do not understand the meaning of genetic diversity and the limitations of our measurement techniques, however, methods for valuing diversity and assessing policy tradeoffs will have no scientific basis. Without a scientific basis, economic analysis of genetic diversity issues will have at best little utility and at worst dangerous consequences.

Historically, many of the genes necessary for achieving disease resistance and other important attributes have been introduced into bread wheats through crosses with other relatives in primary and secondary gene pools. Currently, wide crosses with wild grasses are a major avenue for incorporating new genetic diversity into bread wheats. As human and animal populations continue to expand, the marginal lands where these wild relatives thrive will urgently need protection. Transformation techniques that use genes extracted from other crops and organisms could also expand genetic boundaries. Because the genetic narrowing of cultivated bread wheats began long ago, it is not clear how much breeding programs might benefit from the contributions of bread wheat landraces grown in the few remaining microcenters of on-farm diversity. Pedigree analysis helps identify gaps in types or sources of landraces used in developing modern wheat cultivars, but successful recombination of landraces with modern wheat varieties is not assured.

Even so, it is important to remember that although most bread wheats grown today are modern cultivars, modern plant breeding itself can generate new patterns of genetic variation. Over this century, pedigrees have necessarily become longer as breeders have built on past research successes. Pedigrees have also become wider. Germplasm has circulated even more than in previous centuries, and rather than merely using the same landraces and crosses in different combinations, breeders have been able to bring materials with distinct pedigrees into their breeding programs. The number of different landraces in pedigrees has steadily increased over the past 30 years at least, and the geographical origins of the landraces have broadened. Various characteristics of wheat pedigrees suggest that the pedigree complexity of the more successful cultivars planted in the developing world has grown over time. Large numbers of different landraces, generations, and parental combinations are now contained in the pedigrees of those cultivars. Wide cross techniques and genetic transformation may further expand the genetic bases which can be used by wheat breeders.

Yield stability, both in terms of the performance of individual lines and in terms of regional yields, on farms, appears to have increased in the past few decades. One aspect of genetic diversity that has direct economic value in terms of yield savings — the diversity that confers resistance to the wheat rusts — has also increased over time. Genetic diversity matters for disease resistance only in the genes that confer resistance, although since pathogens constantly mutate, not all can be known about the genes that may eventually be relevant in breeding for resistance. Many of today’s plant breeders, and particularly CIMMYT’s, attempt to improve the durability of rust resistance by accumulating genes that confer partial but longer-lasting resistance. But the geographical distribution of cultivars and national policies toward disease control are also major determinants of the rate at which wheat disease evolves and spreads.

In the developing world, bread wheats are far more important than durum wheats in terms of cultivated area. The proportion of area sown to modern (tall and semidwarf) varieties is greater for bread wheat than for durum wheat; in fact, the more important a region is in terms of area sown to bread wheat, the less diverse it is in numbers of different crosses grown per million hectares. Spatial diversity, measured as the percentage of area sown to leading modern cultivars, is lowest in West Asia and highest in Mexico/Guatemala. The number of crosses per million hectares is very low in South Asia, one of the largest bread wheat producing regions in the developing world, and the area planted to a few cultivars is very large, for example, in India’s major wheat-producing state, Punjab.

Temporal diversity is highest in Mexico/Guatemala (primarily because of Mexico) and lowest in North Africa, a region where bread wheats are less important than durum wheats, but temporal diversity is also fairly low in South Asia, a major bread wheat producer. However, temporal diversity is fairly high for many developing countries compared to some of the major industrialized producers, such as Canada.

Latent diversity, as calculated from pedigree analysis, is fairly high across the developing world, and it does not appear lower than in the major industrialized, wheat-producing countries of Australia, Canada, or the U.S. When the data are weighted by the percentage distribution of area planted to crosses, they show even more clearly that average diversity decreases for all the regions in the developing world but that it decreases by a smaller magnitude than for Canada, for example. The socieconomic factors that affect adoption can strongly influence latent diversity in farmers' fields, a point that emerges quite clearly in the section on India in Appendix C. Genealogical distance measures, calculated from cluster analysis of pairwise coefficients of diversity among the cultivars grown in each region, demonstrate the comparative diversity among the top 10 bread wheats grown in West Asia and the marked similarity of leading bread wheats grown in Mexico/Guatemala and Canada. Again, South Asia ranks fairly low among the developing world regions for latent diversity indicators.

Several questions emerge from this review of the indicators of genetic diversity. Is it cause for concern that certain "blocks" of ancestors are common to the major wheat varieties grown in the developing world today? Does it matter that the major wheats grown internationally have a relatively high similarity of parentage, owing to their common CIMMYT ancestry, if — because of international collaboration — the genetic base of CIMMYT bread wheats is so much broader than anything available within most national boundaries? What if molecular analysis shows that the largest genetic contributors among landraces in the pedigrees of today's major wheats share the same DNA sequences because of earlier germplasm flows, even though the names and national origin of the major wheats are known as distinct?

Still other questions related to genetic diversity, not raised in this paper, remain to be answered. A major question is what *in situ* or *ex situ* conservation might contribute to genetic variability in the bread wheats. What is known about the probability of finding useful genes for known and unknown diseases among current bread wheat landrace accessions or in the few remaining pockets of microdiversity in bread wheat? Would successes be more likely and costs lower if the genetic variability in wild relatives were exploited? Models for valuing the conservation of diversity require information on the probabilities of discovering genes that are of use for particular breeding objectives, as well as a measurement of genetic variation that has empirical meaning but also a scientific basis, such as that found among accessions at gene loci known to confer disease resistance.

Finally, although this paper has examined the relationship between scientific wheat breeding and genetic diversity, it is important to emphasize that numerous factors play a larger role than scientific plant breeding in shaping the pattern of genetic variation in farmers' fields in the developing world today. These factors are related to the adoption and diffusion of new varieties, such as pricing policies for seed and associated inputs, and to the structure of seed multiplication and distribution systems. These relationships are shown by the downward trends in area sown to leading cultivars and the increasing temporal diversity in many industrialized countries during the 20th century as their seed systems evolved. They are also apparent in the large difference between the average similarity of parentage of wheat releases and the weighted similarity of parentage of wheats grown in farmers' fields for the Indian Punjab. Yet it is clear that maximizing spatial diversity in farmers' fields can have costs in terms of short-term yield losses, not only for a nation, but for individual farmers. These trade-offs will need to be investigated both empirically and theoretically. Resolving these issues will be challenging, but ultimately we hope to learn how agricultural research can enhance genetic diversity in wheat, particularly the diversity that may be valuable to future generations of farmers in developing countries.

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Appendix A

Data Sources

This paper draws heavily on data from the CIMMYT Global Wheat Impacts Survey and the Wheat Pedigree Management System. In 1990, CIMMYT's Wheat and Economics Programs conducted an intensive survey of research impacts in all wheat-producing countries of the developing world (excepting most of China). Wheat scientists in 38 countries provided data on wheat releases, adoption of wheat varieties, and overall levels of scientific investment in wheat research. The survey data have been analyzed extensively and results reported by Byerlee and Moya (1993).

Here, the data on varietal distributions by area have been combined with detailed pedigree information compiled in CIMMYT's Wheat Pedigree Management System.[1] In this database, all wheat varieties are identified by cross numbers or landrace identifiers. Multiple selections (sisters) from the same cross are also distinguished by identification numbers. Cultivars are traced back to their parental landraces or to lines of unknown pedigree. A computer program was developed to transform the pedigree information for a set of cultivars into a matrix of genealogical characteristics such as those presented in this report.

Sources of secondary data are listed in the references.

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[1] The Wheat Pedigree Management System is a component of CIMMYT's International Wheat Information System, which also includes data from international trials, national trials, germplasm collections, industrial quality and pathology laboratories, and molecular studies. Details on the system are found in Fox and Skovmand (1996).

Appendix B

Regions of the Developing World

Table B1. Countries included in regions of the developing world

Region and countries
Sub-Saharan Africa
Burundi, Ethiopia, Kenya, Nigeria, Sudan, Tanzania, Zambia, Zimbabwe
West Asia
Afghanistan, Iran, Iraq, Jordan, Lebanon, Saudi Arabia, Syria, Turkey, Yemen
North Africa
Algeria, Egypt, Libya, Morocco, Tunisia
South Asia
Bangladesh, India, Myanmar, Nepal, Pakistan
Mexico/Guatemala
Andean Region
Bolivia, Colombia, Ecuador, Peru
Southern Cone of South America
Argentina, Brazil, Chile, Paraguay, Uruguay

Appendix C

Indicators of Genetic Diversity for Wheat in the United States and India over 90 Years

Indicators of Diversity in the United States

Varietal improvement in U.S. wheats can be divided into three stages (Dalrymple 1988). The first stage, which began with European settlement of the U.S., consisted of introductions from foreign countries. A second, in which pure-line selections were made from introduced varieties, followed. In the late 1800s, the third stage, consisting of crossing as well as selection, began.

For the U.S. spring wheat pool alone, a total of 124 ancestors can be traced to 32 countries on five continents. The area that contributed the most germplasm to the U.S., as measured by theoretical Mendelian contributions through pedigrees, appears to have been the territory of the F.S.U. (van Beuningen 1993). Until the 1930s, virtually all wheat produced in the U.S. was harvested from either introductions or cultivars derived by direct selection from introductions (Cox 1991). Data from Reitz (1979) show that from 1919 to 1974, the percentage of U.S. wheat area occupied by foreign introductions and selections from introductions gradually decreased from a peak exceeding 80% in the mid-1930s to less than 10% in the mid-1970s (Figure C1). The percentage of area planted to the leading five wheat cultivars has declined over time (Dalrymple 1988).

The primary ancestors of North American spring wheats were Fife — believed to have originated in Galicia (see Clark et al. 1922, cited in van Beuningen 1993) — and selections from Fife. One of the selections from Fife, Red Fife, was crossed with Hard Red Calcutta (from India; see later) to produce Marquis in 1892 (Morrison 1960). Through Marquis, these two landraces became the principal components of the hard red spring wheat foundation germplasm in North America (Cox 1991). Crosses of Marquis with Yaroslav emmer (from southern Russia) and Iumillo (from Spain) introduced resistance to stem rust and other diseases into U.S. wheats. Turkey wheat, together with other selections from the Crimea and southern Russia, became the progenitors of the winter wheats developed at the Kansas Agricultural Experiment Station at the turn of the 20th century (Flora 1988; Quisinberry and Reitz 1974). Despite the dominance of these materials in the pedigrees of early breeding materials, evidence from molecular research by Cox (1991) indicates that many of the original introductions were genetically variable landraces.

The early, tall introductions had little effect on yield but carried other desirable qualities. A major upward shift in yield trends began in the U.S. in about 1940 as a result of short plant stature and increasing fertilizer use. The Norin 10-Brevor (U.S.) cross, made at Washington State University in 1949, was used by the Washington State breeding program and by Borlaug in the wheat breeding program of CIMMYT's predecessor organization. The dwarfing genes carried by Daruma (Korea) through Norin 10 (Japanese cross from the

1930s) had no effect on commercial wheat yields in the U.S. until the 1960s, through the variety Gaines (Dalrymple 1988). Coefficients of variation in national wheat yields calculated for one-decade intervals from 1900 to 1990 indicate no change in yield stability over time in U.S. national wheat yields.

Average coefficients of parentage for 311 hard red spring wheat cultivars released in the U.S. from before 1900 to 1991 are also shown in Figure C1. For the two decades from 1900 to 1920, the pedigree information indicates no relatedness among the ancestors of cultivars (Mercado Paredes 1994). Relatedness seems to increase from 1920 to 1940, when it reaches its highest point. From 1940, genetic diversity appears to have increased. Cox, Murphy, and Rodgers (1986) calculated the mean relationship among all cultivars grown in a given year, the mean relationship among primary (i.e., leading) cultivars, and the mean relationship among primary cultivars weighted by area grown. For all three measures, Cox and coauthors found that similarity of parentage increased in soft red winter wheats from 1919 through the mid-1970s but dropped to a very low level in the 1980s. The similarity of parentage in hard winter wheats, which is always higher than for soft winter wheats because of the dominance of germplasm from Turkey, has decreased over time (Figure C1). Important genetic contributions to the U.S. wheat ancestral pool over the past 60 years include new wheat parents from every continent, many of them from species other than the bread wheats, such as durum wheat, rye, or wild relatives of wheat (Cox 1991).

Combined, the data in Figure C1 suggest that as the area planted to scientifically bred wheat crosses has increased in the U.S., the diversity of parentage has increased as well, and the stability of national yields has remained constant. (Variation in national yields, it should be remembered, reflects differences in environment, climate, and changes in management practices and the use of related inputs, more than differences among genotypes.)

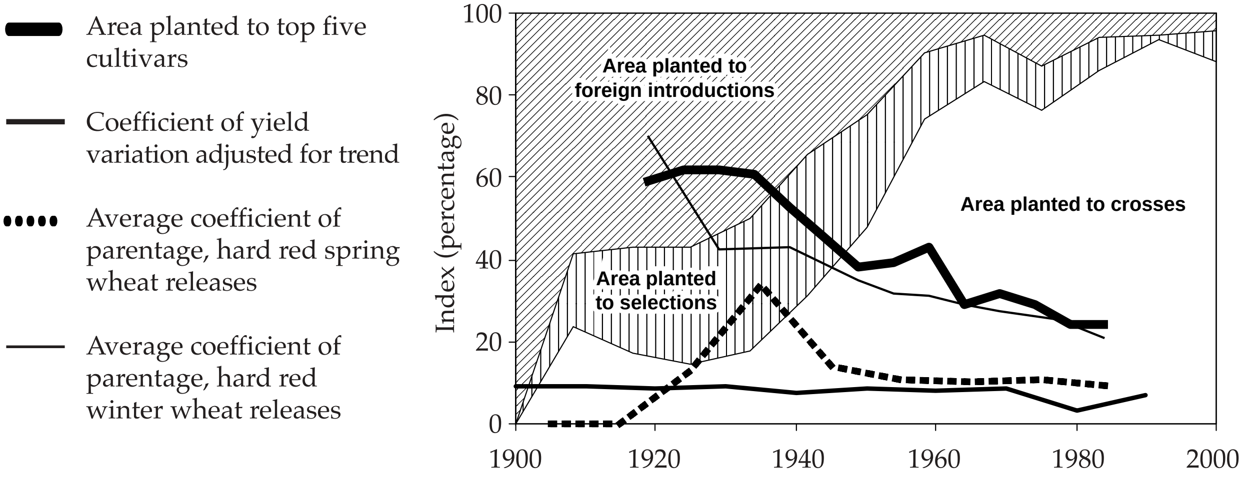

Figure C1. Measures of diversity in U.S. wheats over 90 years.
Source: Cox, Murphy, and Rodgers (1986); Dalrymple (1988); Mercado Paredes (1994); and Reitz (1979).

Indicators of Diversity in India

The Asian subcontinent has been an important historical source of genetic diversity in wheats. Today India is one of the major wheat-producing nations among developing, low-income countries, given the size of the area sown to wheat and the importance of wheat calories in the diet. Prior to the commencement of wheat improvement in India, the wheat crop consisted of a mixture of different varieties. The mixtures, known as "sorts," were classified on the basis of grain characters, such as red or amber color, or hard or soft grain, rather than botanical characters. Farmers often grew botanically distinct varieties in their fields as long as the varieties' grain characters were similar (Pal 1966). The wheats cultivated in India and Pakistan consisted and still consist not only of bread wheat, but also of durum and dicoccum (dicoccum is emmer, commonly known as *khapli*, and has both cultivated and wild forms).

Early foreign introductions into India's breeding lines included Australian No. 27 (1905-06), Bena, and Federation (by 1910) from Australia (Jain 1994). The first selections and crosses in India and Pakistan were made in the early part of this century (Jain 1994). The history of wheat breeding in India between 1905 and 1962 has been classified into three phases (ICAR 1978). In the first phase, pure lines were selected from local mixtures. Some of these were known for excellent grain type and quality. In the second phase, breeders attempted to combine different characters in one cultivar through hybridization. In the third phase, breeders wished to develop disease-resistant cultivars. In none of these phases were significant yield gains achieved. Almost all of the wheats bred during this 60-year period were tall and weak-strawed and hence not suitable for intensive agriculture. According to Khan (1987), the early emphasis of the Pakistani (then also Indian) breeding program was on the use of local varieties in hybridization because of a concern for maintaining grain quality. As a consequence, the number of lines in use was low, they were often closely related, and the progeny derived from the crosses often fell into the same yield group. After 1962, breeders realized the importance of strong-strawed wheats and began to develop varieties resistant to lodging. Some Italian wheats with these characteristics were identified (e.g., Funo), but they were susceptible to the rusts (ICAR 1978). The semidwarf materials were more resistant to lodging and to rusts.

Point estimates of the area sown to improved tall wheat cultivars for all of India suggest that by the beginning of the Green Revolution in the mid-1960s, much of the irrigated area and some of the rainfed wheat area were already planted to scientifically bred crosses or selections (Dalrymple 1986; Pray 1983). Much of the area planted to improved tall varieties was then rapidly covered by the semidwarf varieties introduced in the 1960s, and the percentage of area sown to local varieties decreased further (Figure C2). Semidwarf varieties have expanded more rapidly across irrigated zones compared to rainfed zones, but even in the rainfed zones semidwarf wheats occupy about 40% of the wheat area (Byerlee 1992).

At the same time that the area planted to semidwarf varieties increased, however, yield stability improved for the nation as a whole (FAO) and for Punjab State in particular (Singh and Byerlee 1990), for reasons largely unrelated to plant stature or genotype. Coefficients of parentage calculated from a sample of the wheat lines released by the national program from 1910 to 1990 do indicate a slight upward trend in the similarity of parentage, although the overall level of diversity remains fairly high (and higher than for U.S. releases).

In the major wheat-producing zones of India and Pakistan, available estimates indicate that the area planted to leading wheat cultivars has been high since at least 1945 (Figure C2). Improved wheats diffused slowly until the mid-1930s, when C591 was introduced and replaced local and other improved varieties (Pray 1983). More than 50% of the irrigated area and about 31% of the unirrigated area in the Punjab of India was planted to C591 in 1945 (Sukhatme 1945). By 1955, NP52 covered approximately 80% of the wheat area in Bihar, and C591 occupied nearly the same percentage of area in the Punjab of India (Pal 1966). C591 represented 70-100% of seed sales to small-, medium-, and large-scale farmers in some irrigated districts of Pakistan in 1959 (Government of Pakistan 1966). After the introduction of the first semidwarf varieties, the area sown to leading wheat varieties decreased at first and gradually rose as the semidwarf cultivars became more popular. Following a peak in the early 1970s, however, the trend is generally downward, with more cultivars occupying smaller percentages of the wheat area (Punjab Agricultural University, unpublished data; CIMMYT 1995). In 1990, Sonalika continued to occupy 20% of the bread wheat area throughout India, and the top five cultivars covered 60%.

Figure C2 also illustrates the relationship between the diversity in the wheats released by the breeding program (the average coefficient of parentage) and the diversity in the subset of releases that farmers grow (the weighted average coefficient of parentage). The difference between the average and weighted average coefficient of parentage provides a crude measure of the effect of adoption and diffusion patterns on latent diversity. Farmers' choices of which wheat cultivars to grow reflect their more than their own objectives. Such choices also reflect the constraints imposed upon farmers by the seed distribution system and the policy variables that influence the extent and pattern of cultivar adoption, such as input and

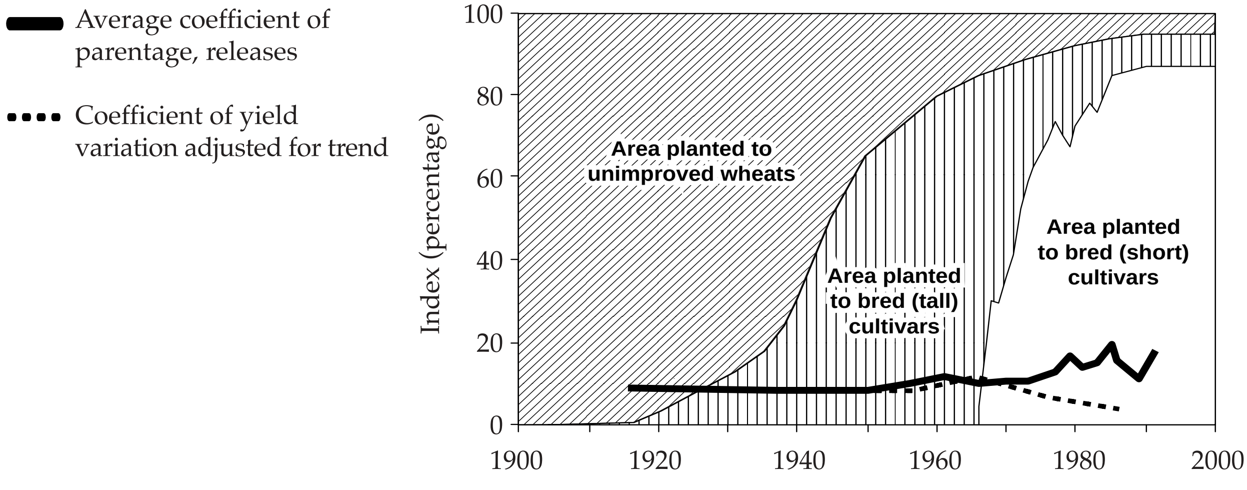

Figure C2. Measures of diversity in Indian wheats over 90 years.
Source: CIMMYT Wheat Pedigree Management System; Dalrymple (1986); FAO, Agrostat/PC; Jain (1994); Pal (1986); Singh and Byerlee (1990); Sukhatme (1945); and Howard and Howard (1909).

output pricing, the proportion of released cultivars for which seed is actually multiplied and distributed, and the regional allocation of seed supplies. As is apparent here, the large area sown to leading cultivars in the Indian Punjab shifts the similarity of parentage in the cultivated wheats upward considerably. The implication of this result is that some of the major determinants of latent diversity of cultivars grown in farmers' fields are the policy variables related to the adoption rather than to the development and release of cultivars.

Available evidence from India indicates that as semidwarfs have replaced the improved tall cultivars, both national and regional yield stability have improved, losses from the rusts have decreased, and the area sown to leading cultivars, though still high, has decreased. The similarity of parentage among wheat releases appears to have shifted upwards only slightly at the national level and to have decreased over time among the top five cultivars planted in India's Punjab (Smale 1995). Even so, the fact that so much area in such an important wheat-producing state is sown to the five leading cultivars means that, when weighted by percentage of area, average similarity of parentage among cultivars in farmers' fields is cause for concern.

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