Dimensions of Diversity

In CIMMYT Bread Wheat from 1965 to 2000

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Introduction

The Reasons for Concern in 1970

Nearly 30 years have passed since the scientific community raised the alarm about genetic erosion (National Research Council 1972). A concise scientific definition of "genetic erosion" is difficult to find. The late Jack Harlan used the term in the early 1970s to describe what he viewed as a potentially disastrous narrowing of the germplasm base employed in improving food crops (Harlan 1972). Harlan was one of the first scientists to refer to the crop germplasm base in the same way that economists refer to a natural resource; presumably he borrowed the concept of "erosion" from the environmental sciences.

In cultivated crop species, genetic erosion does not mean that a species is becoming extinct. For crop plants, the term generally describes a dramatic shift in population structure or allele frequencies within a species as a result of any one or combination of natural or human-led processes.

Despite the ambiguity of the term, "genetic erosion" is now synonymous with the displacement of landraces by modern varieties. In 1970, Frankel called for urgent collection expeditions to forestall "the loss of ancient patterns of diversity in the Vavilovian centers," since modern varieties contain "a minimum of genetic variation" and "in many instances . . . have a narrow genetic base" (1970:11). Two years later, Harlan asserted that the "destruction of genetic resources is caused primarily by the very success of modern plant breeding programs" (1972:212). About a decade later, Hawkes concluded that "the breeder, who means well, is destroying by his actions the genetic base for a new generation of varieties" (1983:109).

The alarm raised by these and other specialists alerted the public that diversity in genetic resources was essential to both present and future food supplies. Two types of economic issues motivated the concern. One was related to the pattern of varieties sown by farmers across a crop-producing region and the genetic basis of their resistance to plant disease. When many farmers sow varieties that carry the same genetic mechanism of resistance to a plant disease of economic importance, the crop is vulnerable to an epidemic. Combating epidemics once they occur can be costly to society, both in terms of garnering the resources necessary to control them and the yield losses incurred.

A second economic issue was related to plant breeders' capacity to respond to unforeseen events should they occur, and the loss of potentially valuable alleles in genetic stocks still held on farms. Such alleles can be lost when the seed of varieties or populations that carry them is sown on diminishing areas. Genetic resources are renewed in farmers' fields only as long as farmers continue to sow the seed; storing these resources in collections as back-up seed stocks is but an imperfect substitute for the evolution of crop plants in farmers' fields.

What evidence do we have that genetic erosion has occurred for bread wheat? Brush has argued that the genetic erosion "hypothesis" is "plausible but nowhere documented" (1992:148-149). Assembling conclusive quantitative data on the extent to which genetic erosion has actually occurred and its causes is difficult, given definitional problems and the scale of analysis required (Wood and Lenné 1997:112; Smale 1997). Then what can be said about genetic narrowing in modern plant breeding? To the extent possible, this paper summarizes scientific evidence on the scope of the genetic base in modern bread wheat varieties in the developing world from 1965 to the present, drawing on previously published research and new analyses of experimental and socioeconomic data. The evidence indicates that today, nearly 30 years after the alarm over the loss of crop genetic diversity was first raised, the genetic landscape may not be as treacherous as first predicted, although the current trend towards claiming legal property rights to genetic resources may be a new cause for alarm.

The Hypothesis

Motivated by the assertion that the genetic base of modern varieties tends to narrow as a result of conventional breeding, we adopt the working hypothesis that genetic diversity in CIMMYT and CIMMYT-related spring bread wheat has decreased over time. Stated formally, the test of this hypothesis is:

$$H_o: D \geq 0$$

$$H_a: D < 0,$$

where D is a coefficient on the regression of a diversity index or indicator on the year of variety release. The null hypothesis states that genetic diversity in varieties of CIMMYT-related spring bread wheat has remained constant or has increased over the past 30 years. If the null hypothesis is rejected, the hypothesis that their genetic diversity has narrowed over time is maintained. If the null hypothesis is not rejected, then the data are inconsistent with the maintained hypothesis that genetic diversity has decreased over time (Greene 1997:159).

In the first section of this paper, we identify and describe the ancestry, age, and area distributions of spring bread wheat varieties grown in the developing world in the 1990s. To do so, we apply indices of genealogical, spatial, and temporal diversity to data collected in CIMMYT's 1997 and 1990 global wheat surveys. In the second section, we test the null hypothesis by assessing changes occurring between 1960 and 1990 in the diversity of the progenitors of those wheat varieties. This is accomplished in terms of two "dimensions" of diversity: latent (unobservable) and apparent (observable) diversity. Latent diversity can be viewed through wheat genealogies and measured with molecular markers. Apparent diversity can be gauged from a wheat crop's performance with respect to grain yield, yield stability, input use efficiency, heat and drought tolerance, disease resistance, and other observable factors.

For each dimension of diversity, we present one or more graphs that plot an indicator of diversity against the years in which wheat varieties were released. For latent diversity, the indicator is an index constructed from molecular or coefficient of parentage data; for apparent diversity, the indicator is a measure of performance. These graphs are supported by other analyses, published for the first time here or reproduced from published literature. Data sources and methods are summarized in each subsection. Conclusions and implications for agricultural research policy are discussed in the final section of the paper. For the definition of a CIMMYT-related wheat variety, see "The Definition of a CIMMYT-Related Wheat," page 3.

The Definition of a CIMMYT-related Wheat

Bread wheat, or "common wheat," is the "most valuable single crop in the modern world" (Diamond 1997). Although over half of the world's wheat crop is produced on the large, mechanized farms of industrialized countries, most of the world's wheat farmers live in the developing world. Although winter and facultative habit wheat, and durum wheat, are extensively grown in the developing world, about two-thirds of the total area is sown to spring bread wheat. In the late 1990s, this comprised around 68 million hectares (Heisey, Lantican, and Dubin). There, the popularity of the "green revolution" varieties first attracted the concern of some conservationists in the early 1970s.

By "green revolution" we refer specifically to the development of semidwarf wheat varieties that spread rapidly throughout South Asia during the late 1960s and early 1970s. These varieties contained the *Rht*1 or *Rht*2 genes, two of several dwarfing genes known to exist in the wheat genepool. They were initially introduced into Japanese breeders' materials through Daruma, believed to be a Korean landrace (Dalrymple 1986). A cross descended from Daruma, Norin 10, was introduced into a breeding program at Washington State University (USA) in 1949. The dwarf characteristic from Norin 10 was successfully bred into the first "green revolution" wheat varieties by N.E. Borlaug and colleagues in Mexico.

When grown with optimal quantities of fertilizer and a controlled water supply, these varieties responded to inputs and performed significantly better than the varieties they replaced. Initially, they spread throughout the irrigated zones most favorable to wheat production, replacing the earlier products of plant breeding programs. Later, more widely adapted descendants of these varieties spread gradually into less favorable growing environments, including rainfed areas with a relatively modest production potential, where they are more likely to have replaced landraces.

Many of the semidwarf wheat varieties grown in developing countries today have as ancestors the green revolution wheat varieties described above. This is due in large part to the efforts of the International Maize and Wheat Improvement Center (CIMMYT), which continued the research initiated by Borlaug and his colleagues. Since the establishment of CIMMYT in 1966, the mandate of its wheat program has included the development of spring wheat lines (both durum and bread wheat) for use by breeding programs in the developing world. Nurseries consisting of anywhere from dozens to hundreds of advanced lines are sent routinely by CIMMYT to national agricultural research systems (NARSs) that request them for testing and selection (Fox 1996).

Each nursery contains progeny of various parental combinations and has been designed to overcome one or more factors that constrain yield, such as fungal diseases, high temperature, drought, or soil acidity. From these materials, NARS scientists choose lines demonstrating the best adaptation to local conditions, select from them or cross them to elite local germplasm, and submit the resulting materials to national trials. Superior genotypes are then released as finished varieties. The vast array of spring bread wheat varieties developed in this way and released by NARSs from 1966 to 1997 is referred to in this paper as "CIMMYT-related." They number 1,749 in the 1997 Global Wheat Impacts Survey, which considers only those with recorded ancestry (Heisey, Lantican, and Dubin 1999). However, the actual number of advanced wheat lines produced and distributed by CIMMYT over that same time period is estimated to be more than 30,000 (S. Rajaram, pers. comm.).

Spring Bread Wheat Varieties Grown in the Developing World in the 1990s

To understand the relevance of the genetic erosion hypothesis for wheat production today, it is essential to identify the varieties grown in the wheat fields of developing country farmers. This section presents evidence concerning the ancestry, age, and area distributions of spring bread wheat varieties sown in the developing world today, beginning with a summary of the methods used to obtain and analyze the data. The data are summarized using indicators of spatial and temporal diversity.

Materials and Methods

Sources of data for this section are the CIMMYT Global Wheat Impacts Surveys of 1990 and 1997. In 1990, CIMMYT's Wheat and Economics Programs conducted a survey of wheat research programs in 38 developing countries that produced about 80% of all low-latitude spring wheat. Most of the wheat-producing area in China was excluded from the analysis. The survey elicited information on the output of breeding programs, including the names, pedigrees, and origins of all spring wheat varieties released from 1966 to 1990 and the estimated area sown to individual varieties in 1990. Varieties of spring bread wheat were recorded for 37 of the 38 countries. In some countries, area estimates were based on annual government surveys and seed sales, while in others they were based on special surveys conducted at the regional or country level and on estimates by wheat researchers. The survey data are summarized in Byerlee and Moya (1993).

In 1997, questionnaires were sent to all 41 countries in the developing world that produced 20,000 tons (t) or more of wheat annually (the nations of Central Asia and the Caucasus were not included). Responses were received from 36 countries, representing slightly less than 99% of all wheat production in the developing world. Spring bread wheat areas were reported in 34 of these countries.[1] Again, information was elicited on the names, pedigrees, and origins of individual varieties, as well as the area planted to each. In contrast to the 1990 survey, the 1997 survey attempted to differentiate among semidwarf varieties, tall varieties with pedigrees, landraces, and varieties of unknown ancestry.

[1] Of the 36, Lebanon and Libya reported no spring bread wheat area.

Coverage of China's wheat-producing regions improved in the 1997 survey, although it is less complete for spring wheat than for winter and facultative wheat. Representation across countries also changed slightly between the two surveys (Appendix Table A). The definition of what constitutes a CIMMYT-related variety was also broader in 1997, since it included not only varieties with CIMMYT parents but also varieties with any known CIMMYT ancestry. The set of CIMMYT-related varieties was therefore larger in 1997 than in 1990. Data from the 1997 survey are summarized in Heisey, Lantican, and Dubin (1999).

Other data sources used in this section include CIMMYT's Wheat Pedigree Management System, a part of the International Wheat Information System that contains pedigree information (Skovmand, Fox, and White 1998). In this database, all wheat varieties are identified by cross numbers or landrace identifiers. Identification numbers also distinguish multiple selections (sisters) from the same cross. A computer program was developed to transform pedigree information for a set of varieties with known pedigrees into a matrix of genealogical characteristics such as those summarized later in this paper.

Some tables include data calculated from all spring bread wheat varieties listed in the two survey periods; others include those computed from a sample. This sample is much larger than the sample used in the experiments reported in subsequent sections, but overlaps with it. The sample includes:

1) all CIMMYT-related varieties of spring bread wheat sown on more than 0.25 million hectares in 1990 and 1997 ("major wheat varieties");
2) a systematic random sample drawn from the list of all CIMMYT-related varieties of spring bread wheat sown on less than 0.25 million hectares in 1990 and 1997 ("minor wheat varieties"); and
3) all spring bread wheat varieties sown on more than 1% of the area in the Yaqui Valley of Mexico from 1968 to 1990.

The sample of minor wheats was drawn by stacking the regional lists of all CIMMYT-related varieties of spring bread wheat for which there are identifiers in the Wheat Pedigree Management System, sorting them by descending order of area sown, and drawing 30 cultivars from both time periods.

The Yaqui Valley is a relatively small wheat-producing area in northwestern Mexico where an average of 130,000 hectares (ha) have been planted to wheat each year from 1968 to 1997. The Yaqui Valley is the testing ground of many CIMMYT-related wheats destined for irrigated areas of the developing world that are favorable for producing spring bread wheat. Descriptive information on the varieties in the sample, including a number of varieties grown at one time in the Yaqui Valley, is found in Appendix Tables B to E. Data on varieties grown in the Yaqui Valley are shown in this section.

Spatial Diversity of Spring Bread Wheat in the Developing World, 1990 and 1997

Of the area sown to spring bread wheat in the developing world (including China) in 1997, 96.5% was sown to semidwarf or tall wheat varieties released by breeding programs. The remaining area (an estimated 3.5%) was sown to varieties recognized as landraces or varieties of unknown ancestry. Although the proportion of area under landraces is greater in the case of spring durum wheats and winter/facultative bread wheats, only about 10% of all the wheat area in the developing world in 1997 was sown to landrace populations or varieties of unknown ancestry (Heisey, Lantican, and Dubin 1999).

As shown in Table 1, 89% of all spring bread wheats grown in the developing world (excluding China) in 1997 and 75% of all those grown in 1990 were CIMMYT related. The percentage in 1997 drops to 78% when China is included (Heisey, Lantican, and Dubin 1999). Differences between 1990 and 1997 reflect in part the broader definition of CIMMYT-related varieties used in the later survey.

These data confirm that the genetic diversity of the bread wheat—and, in particular, the spring bread wheat—grown in the developing world today was shaped more by the activities of professional plant breeding than those of the farmers who originally domesticated and selected wheat populations. Most of the area sown to wheat landraces is found in sub-regions of West Asia, North Africa, and Sub-Saharan Africa (Ethiopia and Sudan). These geographical areas contain the primary and secondary centers of origin and diversity for wheat, to the best of scientific knowledge.[2]

In 1997, the count of named varieties of spring bread wheat grown in the developing world was 382, compared to 310 in 1990 (Table 1). Both counts are understated for at least two reasons. First, only varieties that occupy a recognizable area and whose names are known are counted. In both time periods, the most widely grown variety was a CIMMYT-related varietiy. In terms of total area planted, the dominance of the most popular wheat variety in 1997 was clearly less than that of the most popular variety in 1990. However, the 6 million hectares sown to Sonalika in 1990 were distributed across a number of countries, whereas the 4 million hectares planted to HD-2329 and to Inqalab in 1997 were concentrated in single countries (India and Pakistan, respectively). The 1997 survey occurred at a time when the area planted to HD-2329 was declining, while the area planted to Inqalab was rising.

2 The locus of origin and diversity for wheat has been disputed (Vavilov 1926, 1951; Zohary 1970; Zhukovsky 1975; Harlan and Zohary 1966; Harlan 1971). Zohary (1970) called it "confused" and Harlan (1992) characterized it as "diffuse."

Table 1. Area shares, numbers of varieties, and variety dominance, by parentage, for spring bread wheat varieties grown in the developing world, 1990 and 1997

Year and parentage	Area (m ha)	Percent of spring bread wheat area	Number of named varieties[a]	Dominant variety	
				Name	Area (m ha)
1990					
CIMMYT-related wheats	34.3	75	246	Sonalika	6.28
All spring bread wheats	45.5	100	310	Sonalika	6.28
1997					
CIMMYT-related wheats[b]	49.1	89	341	HD-2329	4.25
				Inqalab	4.22
All spring bread wheats	55.0	100	382	HD-2329	4.25
				Inqalab	4.22

Source: Calculated from 1990 and 1997 CIMMYT Wheat Impacts Survey data. Survey data prepared in 1990 by Byerlee and Moya, and in 1997 by Heisey, Lantican, and Dubin.

Note: Though survey coverage in China was better in 1997 than 1990, 20% of the spring bread wheat area was reported sown to semidwarf varieties whose names were not identified. For this reason, data from China were excluded from this analysis in 1997 as well as 1990.

a The estimated number of varieties is based only on named varieties, excluding not only landraces but other unknown semidwarf and tall varieties. Landraces are probably underestimated, in particular for the West Asia/North Africa region.

b The 1997 survey definition includes not only parents, but more distant ancestry.

Summaries by region (Appendix Tables F and G) suggest that the numbers of CIMMYT-related and other varieties of spring bread wheat have been maintained or have increased between 1990 and 1997, except in Mesoamerica. The decline in the Mesoamerican region reflects primarily the shift from bread to durum wheat in northwestern Mexico, since this sub-region represents a large proportion of Mesoamerican spring bread wheat area. Farmers have shifted to durum wheat in response to favorable price and credit incentives associated with production for the durum export market (Aquino 1999). Durum wheats currently grown in northwestern Mexico also yield more than bread wheats and have better resistance to Karnal bunt.

The leading spring bread wheat in each region, with the exception of Sub-Saharan Africa in 1990, is the leading CIMMYT-related variety. The highest number of varieties was recorded in South Asia and the West Asia/ North Africa regions. The highest percentage of CIMMYT-related varieties, according to the broader definition used in 1997, is found in Mesoamerica (in Mexico, principally in the Yaqui Valley), the Andean Region, and South Asia. In each region of the developing world excluding China, however, over 80% of the area in spring bread wheats in 1997 was sown to CIMMYT-related varieties.

In Table 2, ecological indices of spatial diversity are used to summarize in a compact way the area distribution of varieties across a wheat-producing region. Magurran (1988) classified indices of the spatial diversity of species in terms of three concepts: 1) richness, or the number of species encountered in a given sampling effort; 2) abundance, or the distribution of individuals associated with each of the species; and 3) equality of abundance, or evenness. We have adapted these indices by substituting variety area shares for frequencies of individual plant species (see Appendix Table H).

A count of species reported or collected in an area, although usually the simplest index to implement, assumes that all species at a site contribute equally to its biodiversity. Since this is often not the case, frequency counts of individuals within a species provide more information. The Margalef richness index adjusts the numbers of species sampled in a reference area by the logarithm of the total number of individuals sampled, summed over species. The higher the Margalef index, the richer the diversity of the population.

Indices of abundance detect whether or not certain species dominate others. The Berger-Parker index expresses the relative abundance of the dominant species. The index is computed as the inverse of the numbers of individuals of that species relative to the total number of individuals sampled across species. The Berger-Parker index thus measures inverse dominance,

Table 2. Spatial diversity indices, by type of parentage, for spring bread wheat varieties grown in the developing world, 1990 and 1997

Year and parentage	Richness (Margalef)	Dominance^{-1} (Berger-Parker)	Evenness (Shannon)
1990			
Varieties from CIMMYT cross	10.3	4.5	3.5
Varieties with CIMMYT parents	4.4	8.7	3.5
All spring bread wheats	17.5	9.9	4.3
1997			
Varieties from CIMMYT cross	12.3	12.7	4.3
Varieties with CIMMYT parents or ancestors[a]	8.0	7.4	3.3
All spring bread wheats	24.8	12.9	4.5

Source: Calculated from 1990 and 1997 CIMMYT Wheat Impacts Survey data. Databases prepared in 1990 by Byerlee and Moya and in 1997 by Heisey, Lantican, and Dubin.

Note: The 1997 survey definition includes not only parents, but more distant ancestry. China was not included in either year because of limited information on spring bread wheats.

so that the more dominant the most abundant species, the lower the index.

The third category, which combines the richness of species with a measure of their relative abundance, includes the widely used Shannon index. "Evenness," or "equitability," refers to the degree of equality in the abundance of the individuals, or the relative uniformity of their distribution across species. When all species in a sample are equally abundant, evenness reaches a maximum. The Shannon index has been called a "nonparametric index" because it accounts for the distribution of species without making assumptions about the shape of those underlying distributions. The Shannon index was originally used in information theory, but it has been commonly employed to evaluate species diversity in ecological communities.

For the spring bread wheat grown by farmers in developing countries, indices of spatial diversity suggest a greater global richness and less dominance in 1997 compared to 1990, with similar evenness in the two years (Table 2). However, since country coverage was not identical in the two survey years, differences between the numbers cannot be tested statistically and may be an artifact of the survey design. In some cases, the magnitude of the difference is large enough to suggest that it is meaningful. As shown in Table 1 and confirmed here in the Berger-Parker index, the global dominance of the most popular variety selected from a CIMMYT cross is much less in 1997 than in 1990.

Differences among regions and between time periods are not particularly visible in terms of the evenness in the distribution of varieties across wheat-producing areas (Appendix Tables I and J). Including South Africa in the survey coverage of Sub-Saharan Africa seems to be associated with greater richness but similar dominance, in all categories of ancestry. A drop in richness and evenness among CIMMYT-related spring bread wheats in Mesoamerica is evident between 1990 and 1997, even though the definition of parentage was broader in 1997.

The figures reported above provide two snapshots in a seven-year period. No time-series data on varieties grown by farmers over large areas of the developing world have been assembled to permit analysis at the same level of detail. From historical data, we know that the number of varieties released from the Veery cross in developed countries by 1990 was at least twice that of varieties released from the Mexipak cross. At the same time, the area planted to all Veery varieties in that year was only about one-fifth of the area once sown to Mexipak (Byerlee and Moya 1993).

Of all the varieties released during the early green revolution period in the 1960s, the highest number were selections from the Mexipak (1965) and Sonalika (1967) crosses. The Veery cross (1977), which widened the spring bread wheat gene pool through the 1B/1R translocation from rye, was the leading cross among varieties released during the 1980s. Although the Veery cross is still the cross that generated the greatest proportion of varieties grown in the developing world during the 1990s,[3] varieties selected from Kauz (1985) and Attila (1990), the major crosses of the CIMMYT spring bread wheat program in the 1990s, are becoming more popular in farmers' fields.

Data from the Yaqui Valley enable us to see variation in spatial diversity indices over 30 years for this small, but historically important,

[3] The Veery cross has been selected many times and released under different variety names by national programs. Sister lines may be diverse, however, with respect to certain important alleles such as those conferring resistance to biotic pests. More detail about varieties released from the Veery cross can be found in Skovmand et al. (1997).

testing ground for CIMMYT wheats (Figure 1). Peaks (lower dominance) and troughs (greater dominance) are most evident in the Berger-Parker index. In general, variation in spatial diversity is jointly determined by a number of economic, agroecological, and technical factors (Smale et al. 1999). Behind the peaks and troughs in spatial diversity indices lie the cyclical patterns representing the rise and decline in popularity of individual varieties. The troughs in spatial diversity occur at three points in time: 1) with the dominance of Jupateco, immediately before the leaf rust epidemic of 1977-78; 2) with the dominance of CIANO in the early 1980s; and 3) with the dominance of Opata in the late 1980s. The highest peak occurs at about the time that durum wheats begin to replace spring bread wheats in the Yaqui Valley. The lowest levels in all spatial diversity indices occur at both extremes of the time period—in 1969 and in 1997—with the dominance of Rayon.

Temporal Diversity of Spring Bread Wheat in the Developing World, 1990 and 1997

Temporal diversity, which Duvick (1984) has called "genetic diversity in time," refers to the turnover in farmers' fields of varieties developed through plant breeding programs. An important means of controlling pathogen evolution and maintaining yield, variety turnover in modern wheat in some sense substitutes for the spatial diversity characteristic of heterogeneous populations of wheat landraces (Apple 1977; Plucknett and Smith 1986). Temporal diversity, like spatial diversity, is jointly determined by a number of economic, agroecological, and technical factors (Heisey and Brennan 1991). The area-weighted average age (Brennan and Byerlee 1991) has the advantage of combining information about variety diffusion (in the form of area shares) with variety age, and it is used here as an indicator of temporal diversity.

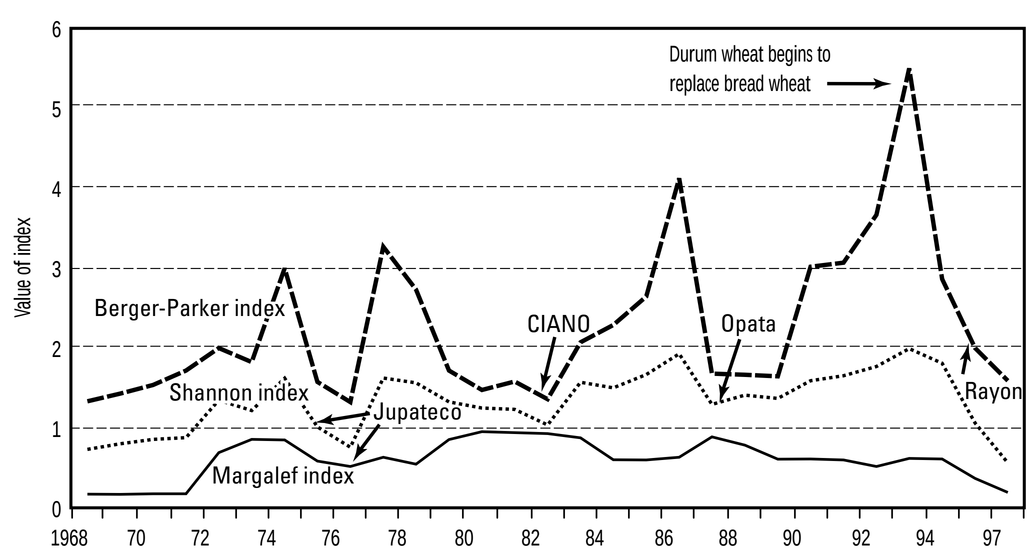

Figure 1. Spatial diversity indices for spring bread wheat varieties grown from 1968 to 1997 in the Yaqui Valley of Mexico.

For the developing world as a whole, the average age of varieties changed very little between 1990 and 1997, even though more tall and thus generally older varieties may have been identified in the later survey year (Table 3). For any category of ancestry, in either year, whether weighted by area or not, the average age of all varieties of spring bread wheat grown by farmers was 9-11 years. The percentage of CIMMYT-related varieties older than the average seems to have decreased slightly between 1990 and 1997.

Among regions, in 1990, the highest turnover rates were found in Mesoamerica and the Southern Cone, and the lowest were found in the Andean Region and South Asia. The oldest varieties derived from CIMMYT crosses were grown in South Asia. West Asia/North Africa had the oldest variety (Florence Aurore, originally released in Australia in the 1920s. The oldest variety from a CIMMYT cross was Mexipak, released in the mid-1960s. In 1997, the highest rates of variety turnover were found in the Southern Cone, and Mesoamerica is now one of the least temporally diverse regions. In both 1990 and 1997, the oldest varieties were found in West Asia/North Africa (Appendix Tables K and L).

Figure 2 shows that the area-weighted age of bread wheats planted in the Yaqui Valley rose as farmers switched from bread wheats to durum wheats and as they planted more of the bread wheat area to Rayon, released in 1989 (in other words, the temporal diversity of wheat varieties in the Yaqui Valley declined). Rayon has the best bread making quality of all varieties grown in the Yaqui Valley, and since the North American Free Trade Agreement, it has been a good competitor with Canadian and US bread wheats.

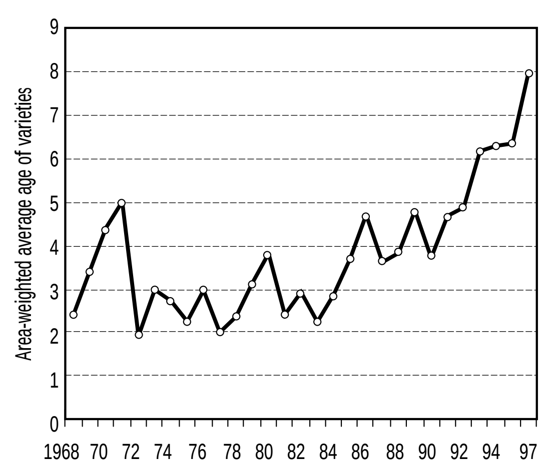

Figure 2. Temporal diversity of spring bread wheat varieties grown from 1968 to 1997 in the Yaqui Valley of Mexico.

Table 3. Temporal diversity of spring bread wheat varieties grown in the developing world, 1990 and 1997

Year and parentage	Average age in 1990	Area-weighted average	Maximum age	Percent older than maximum	Name of oldest variety
1990					
Varieties from CIMMYT cross	8.6	14.2	25	46	Mexipak
Varieties with CIMMYT parents	10.1	9.8	21	56	Taian
All spring bread wheats	9.9	11.7	58	40	Florence Aurore
1997					
Varieties from CIMMYT cross	9.7	10.9	32	37	T 4
Varieties with CIMMYT parents	10.1	11.1	29	42	Sugamuxi 68
All spring bread wheats	11.1	12.1	65	39	Florence Aurore

Source: Calculated from 1990 and 1997 CIMMYT Wheat Impacts Survey data. Survey data prepared in 1990 by Byerlee and Moya, and in 1997 by Heisey, Lantican, and Dubin.
Note: Includes tall and semidwarf varieties released by plant breeding programs. Age defined as years from date of variety release in country. China excluded because of limited information on spring bread wheats.

Genealogical Diversity of Spring Bread Wheat in the Developing World, 1990 and 1997

The coefficient of parentage (COP) provides a theoretical estimate of the genetic relationship between two cultivars based on genealogical information. The COP estimates the probability that a random allele taken from a random locus in one variety is identical, by descent, to a random allele taken from the same locus in another variety (Falconer 1981; see also Kempthorne 1969; Malecot 1948; Wright 1922). Calculated with detailed pedigrees and Mendelian rules of inheritance, the pairwise COP has been employed in the crop science literature as a measure of similarity between two modern varieties due to inheritance (for some applications in wheat, see Cox, Murphy, and Rodgers 1986; Mercado, Souza, and Kephart 1996; Murphy, Cox, and Rodgers 1986; Souza, Fox, and Skovmand 1998; Souza et al. 1994; van Beuningen and Busch 1997). Cox, Murphy, and Rogers (1986) developed assumptions and algorithms to account for the effects of re-selection in wheat. The advantages and disadvantages of the method are discussed in detail in the sources cited earlier.

The matrix of pairwise COPs for a set of modern varieties has been used to construct indices of latent genetic diversity (Souza et al. 1994) or genetic distance (Skovmand and DeLacy 1999). The average coefficient of diversity, or one minus the average coefficient of parentage, summarizes the genealogical diversity in a set of varieties grown by farmers. When weighted by area shares, the difference between the average COP and the area-weighted average COP expresses the effects of the socioeconomic and policy variables determining variety diffusion, as is the case with the spatial and temporal diversity indices employed above. Both average and area-weighted average COPs range between 0 and 1, where 0 is the COP between two unrelated varieties and 1 is the COP between a variety and itself.

Table 4 shows the average, area-weighted average, and range of pairwise COPs among all spring bread wheats sown on more than 0.25 million hectares in 1990 and 1997, as well as for varieties sown on less land in each year. The level of diversity due to inheritance appears high at this scale of analysis, since all average COPs are far below the level commonly used for sisters from the same cross (0.5625).[4] The average and area-weighted averages are almost

Table 4. Coefficients of parentage and pedigree characteristics for spring bread wheat varieties grown in the developing world, 1990 and 1997

	All varieties grown on more than 0.25 m ha		Sample of varieties grown on less than 0.25 m ha	
	1990	1997	1990	1997
Coefficient of parentage				
Average	0.229	0.211 [a]	0.255	0.252 [a]
Area-weighted	0.175	0.172	0.194	0.201
Minimum	0.019	0.028	0.042	0.042
Maximum[b]	0.563	0.563	0.563	1
Pedigree characteristics				
Average total number of parental combinations per pedigree	960	1,932	1,326	1,906
Average percent of parental combinations used once in pedigree	16	10	15	13
Average number of different landrace ancestors per pedigree	45	50	44	48

[a] Distributions of pairwise coefficients of diversity are different for major and minor varieties, at 1% level of statistical significance, with Wilcoxon test.
[b] Maximum in 1990 is 0.563, the COP for selections from the same cross.

identical for each size class between the two time periods, and the differences between size classes in each period are not statistically significant. Nonparametric tests show that the frequency distributions of the pairwise COPs are not significantly different among the major varieties grown in either of the two years. In both 1990 and 1997, however, frequency distributions differ statistically between major and minor varieties.

The hypothesis that the average COP among varieties increases with their popularity was tested across all area size classes ranging from several hundred hectares to 4.2 million hectares (Figure 3). Since averages are sensitive to the size of the matrix, area classes are irregular in definition to ensure that each matrix includes the same number of varieties (20). Regression analysis reveals no systematic relationship between the midpoint of an area class and its average COP. This result may be explained by the fact that minor varieties include once popular varieties on their way out of production, newly released materials, and varieties whose optimal area sown is limited by farmer demand or seed supply. Sister varieties selected from the Veery cross, for example, are found in each area class.

The relative "genealogical complexity" (Evenson and Gollin 1997) of major and minor varieties of spring bread wheat grown in the developing world in 1990 and 1997 is also indicated in Table 4. As mentioned previously, the set of major varieties includes all those sown on more than 0.25 million hectares, and the set of minor varieties represents those grown on less than that area. Since pedigrees grow longer over time as a result of breeding, the average total number of parental combinations in pedigrees of major and minor varieties was higher in 1997 than in 1990. There are no statistically significant differences between the average percentage of parental combinations used once or the average number of distinct landrace ancestors per pedigree for major and minor wheats in either survey year or between survey years. Minor varieties in 1990 seem to have more parental combinations than the major varieties grown in that year, even though they were on average younger (Appendix Tables B and D).

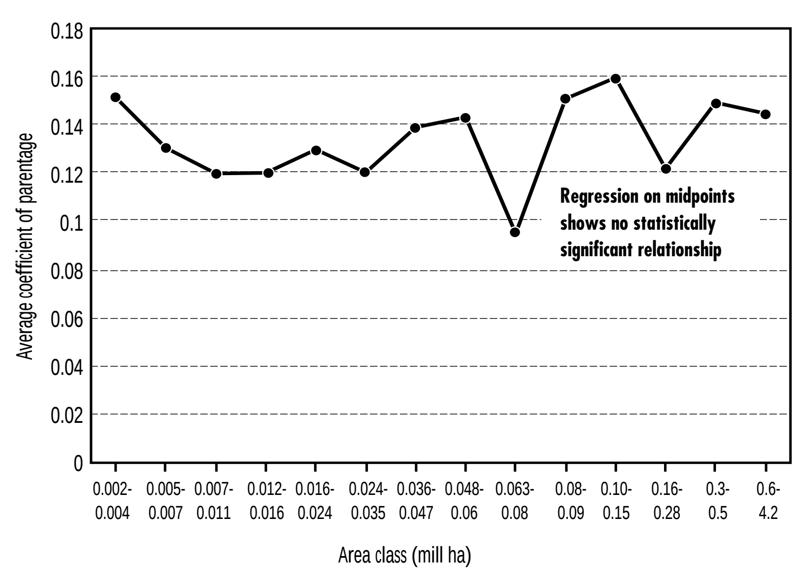

Figure 3.Average coefficient of parentage of spring bread wheat varieties grown in the developing world in 1997, by area class.

Source: Calculated using 1997 Global Wheat Impacts Survey data, summarized in Heisey, Lantican, and Dubin (1999), and CIMMYT Wheat Pedigree Management System. Note that classes are defined to assure COP matrices of equal size. About 300 varieties for which datailed pedigree information is known are included.

4 0.563=0.75*0.75, where 0.75 is the COP between a variety and a selection from a variety (Souza et al. 1994).

Dimensions of Diversity in CIMMYT Bread Wheat over Time

To say that most spring bread wheat varieties grown in the developing world today are related to CIMMYT wheats does not imply that they are genetically uniform, or that uniformity has been increasing among them over time. The previous section of this paper reviewed evidence on spatial, temporal, and genealogical diversity among spring bread wheat varieties grown in farmers' fields in the developing world during the 1990s. Here, data from genealogies, historical trials, and controlled experiments are used to test the null hypothesis that genetic diversity in varieties of CIMMYT-related spring bread wheat has remained constant or increased over the past 30 years against the maintained hypothesis of genetic narrowing.

This section is divided into two major parts. The first part presents evidence on indices of latent diversity by year of variety release based on new genealogical or molecular analysis. The second part assembles new and published evidence on apparent diversity, also by year of release. "Apparent diversity" refers to the performance of experimental lines or varieties of wheat across environments and management regimes.[5]

[5] In the case of a cross, the date used is the year that the line no longer segregated.

Indicators of Latent Diversity

Genealogy

As suggested by the information on bread wheat genealogies presented previously, "CIMMYT-related" implies there is a diversity of materials in the genetic background of varieties because 1) wheat breeders at CIMMYT continuously introgress germplasm from other sources into the lines they develop, and 2) CIMMYT-related wheat includes varieties derived from crosses with local materials made by national breeding programs in the developing world.

Skovmand and DeLacy (1999) analyzed the distance among COPs for a set of 25 CIMMYT-related bread wheat varieties released over the past four decades (Figure 4). The pattern over time shows a rate of increase in diversity that increases over successive releases, with a marked expansion in genealogies from 1950 to 1967 and a flattening during the 1990s. A narrowing of the genetic base owing to the recycling of the sample parents would result in a negative slope, reflecting a diminishing distance among ancestors.

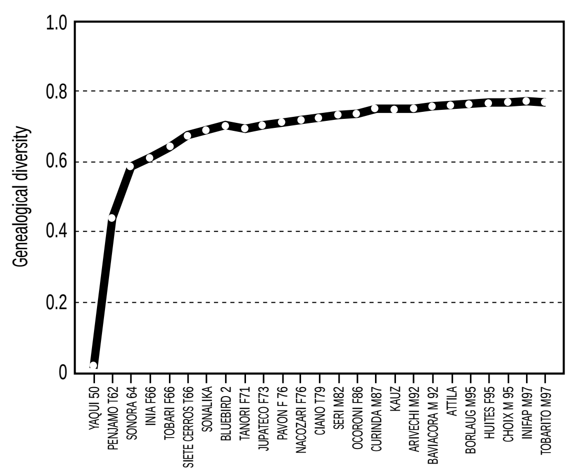

Figure 4. Genealogical diversity in CIMMYT-related wheat varieties over the past 40 years.

Source: Adapted from Skovmand and DeLacy (1999).

Note: Genealogical distance is calculated as the average pairwise coefficient of diversity between successive wheat varieties and Yaqui 50. The coefficient of diversity is 1–the coefficient of parentage. The coefficient of parentage expresses the similarity between two wheat varieties due to common ancestry.

Over the past 30 years, the germplasm used in the bread wheat program at CIMMYT has come from breeding programs throughout the world, and parents of CIMMYT wheats have included varieties with pedigrees as well as named landraces. Table 5 shows a positive, statistically significant trend in the number of different landrace ancestors of all major wheats grown in the Yaqui Valley from 1962 to 1989, which include many of the major parents used by the CIMMYT breeding program during that period. With the use of wide crossing to introduce genes (and entire genomes in the case of synthetic hexaploid wheat) from related species (Mujeeb-Kazi and Hettel 1995; Mujeeb-Kazi, Rosas, and Roldan 1996), materials currently in the crossing blocks of the CIMMYT bread wheat program, like the first ancestors of bread wheat, have germplasm from wild grasses.

In turn, CIMMYT-related wheats released by national programs in developing countries have a larger number of different landraces in their pedigrees than those that are not CIMMYT-related. One hundred fifty-one wheats with known pedigrees and no known relationship to CIMMYT in their ancestry were released by developing country wheat programs (including China) from 1965 to 1990. For those 151 wheats, the average number of distinct landrace ancestors per pedigree is 19, compared to 45 for the 999 CIMMYT-related releases with known pedigrees.

The international exchange of breeding materials increases the likelihood of introducing landraces new to the genetic background of the materials crossed. For the more than 1,000 spring bread wheat varieties released in the developing world from 1966 to 1996, the number of unique landraces per pedigree has increased significantly by an average of one landrace each year (Figure 5). Had breeders been unable to introduce materials with distinct ancestry into their programs and had the same ancestors recurred, the slope of the line would be constant.

As Witcombe (1999) has pointed out, such tabulations misstate the absolute number of landraces in the genetic backgrounds of varieties, though the trend indicates positive changes in relative numbers over time. Landraces and modern varieties are counted on a different metric, since landraces have no known pedigree but are often mixtures or the result of hybridization among several farmers' varieties. Furthermore, in the typical wheat breeding program, landraces enter the genetic background at the base of the pedigrees of advanced materials that breeders cross, not as immediate parents (Rejesus, Smale, and van Ginkel 1996), and their genetic contributions lessen as the pedigree lengthens. Rather than illustrating genetic diversity, Figure 5 essentially depicts a modern breeding process in which many materials with different genetic backgrounds are assembled in the crossing blocks.

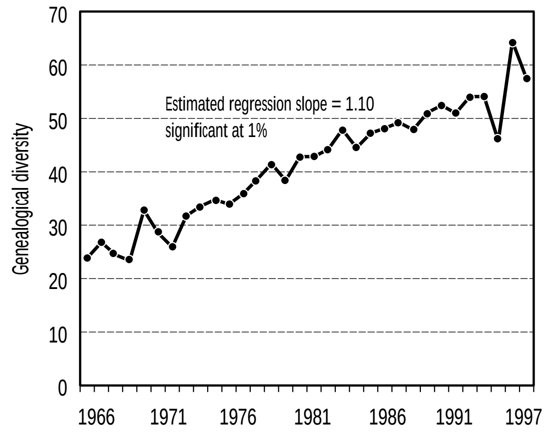

Figure 5. Landrace ancestors of spring bread wheat varieties released by developing countries, 1966-97.

Note:Calculations based on CIMMYT 1997 Global Wheat Impacts Survey data prepared by Heisey, Lantican, and Dubin and pedigree information in CIMMYT Wheat Pedigree Management System. Data were available for 1,162 (included here) of the 1,749 spring bread wheats recorded (in the survey data) as released during these years. Coverage is less complete for China and for wheats released in the last few years.

Table 5. Pedigree characteristics of bread wheat varieties grown from 1968 to 1996 in the Yaqui Valley of Mexico[a]

Variety	Release year	Years grown on >1% of total area	Total no. of parental combinations in pedigree	Total no. of ancestors in pedigree	No. of different landrace ancestors[b]
Penjamo	1962	3	68	69	28
INIA	1966	9	399	399	36
Siete Cerros	1966	8	117	118	37
Super X	1966	3	117	118	37
Nuri	1970	7	661	657	42
Potam	1970	4	102	103	24
Saric	1970	4	661	657	42
Yecora	1970	4	664	662	42
Cajeme	1971	2	661	657	42
Tanori	1971	5	915	909	38
Vicam	1971	5	498	496	39
Jupateco	1973	4	887	880	42
Torim	1973	9	887	880	42
Anahuac	1975	4	887	880	42
Cocoraque	1975	1	887	880	42
Zaragoza	1975	6	393	358	42
Nacozari	1976	6	850	819	47
Pavon	1976	7	1,668	1,629	47
Pima	1976	7	596	585	45
Tesapaco	1976	4	668	661	41
Hermosillo	1977	4	3,010	2,846	49
CIANO	1979	12	325	326	36
Imuris	1979	7	2,339	2,253	66
Tesia	1979	4	2,666	2,519	47
Genaro	1981	8	2,684	2,435	49
Glennson	1981	6	2,684	2,435	49
Sonoita	1981	8	1,776	1,729	44
Tonichi	1981	11	872	857	43
Ures	1981	9	2,684	2,435	49
Seri	1982	6	2,684	2,435	49
Opata	1985	10	1,677	1,606	47
Cucurpe	1986	9	1,688	1,601	61
Oasis	1986	9	1,927	1,854	43
Papago	1986	8	3,803	3,563	68
Bacanora	1988	5	3,970	3,506	52
Cumpas	1988	4	3,863	3,418	55
Rayon	1989	3	5,768	4,839	55
Tepoca	1989	3	3,051	2,871	67

[a] Includes only varieties covering more than 1% of total wheat area.
[b] Time trend significant at 1%.

Genetic distance

Molecular analysis was used for statistically testing the maintained hypothesis that the diversity of marker alleles in CIMMYT wheats has declined over time. Based on their popularity in the developing world and/or their importance in CIMMYT's bread wheat crossing program, 27 varieties were selected for molecular analysis (Table M). DNA of the 27 lines was extracted and molecular fingerprinting using SSR (simple sequence repeat) and AFLP (amplified fragment length polymorphism) analyses conducted according to the standard practices in CIMMYT's Applied Biotechnology Center (Hoisington et al. 1999). Data were analyzed using the program NTSYS pc 1.7 (Applied Biostatistics, Inc., New York) to calculate simple matching coefficients of similarity for all pairs of individuals in the study.

First, the coefficients were analyzed using principal components analysis (Figure 6). When data from each individual line are plotted onto axes that represent the three first principal components, the pattern of genetic relationships between all lines in the study emerges. Lines tend to cluster together based on pedigree and year of release, which is to be expected, because lines released within a short time of one another tend to have similar pedigrees. Lines can be grouped based on year of release so that there is a similar number of lines in each group. Circles around each group make it possible to see that older lines form smaller, denser clusters than compared to lines released more recently, which form very dispersed clusters. These results indicate that there is more diversity present in more recently released groups of lines, suggesting a trend of increasing genetic diversity in CIMMYT wheats over time.

Next, genetic distance (1–similarity) was regressed on two-year increments in release years, beginning with 2 and ending with 26 years (Figure 7). A significant ($P<0.05$) positive correlation between the difference in release years and genetic distance was found. The greater the difference in release year, the greater the genetic distance between any pair of wheat lines. The estimated regression slope indicates an average increment in genetic distance of 0.09% per unit increment in year of release. Over the 28-year period, genetic distance increased by an estimated 2.3%.

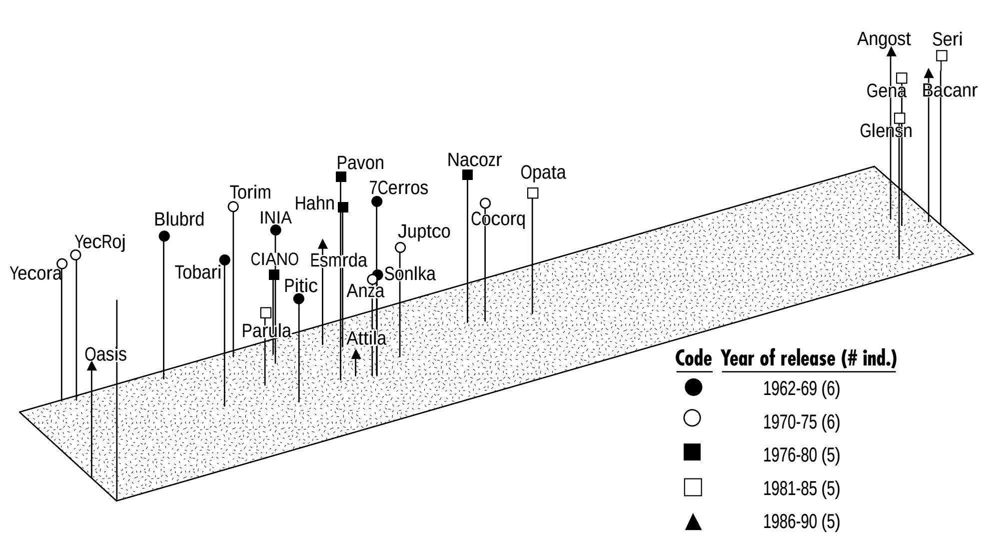

Figure 6. Principal components analysis of 27 CIMMYT spring bread wheat lines released from 1962 to 1990.

Source: CIMMYT Applied Biotechnology Laboratory.

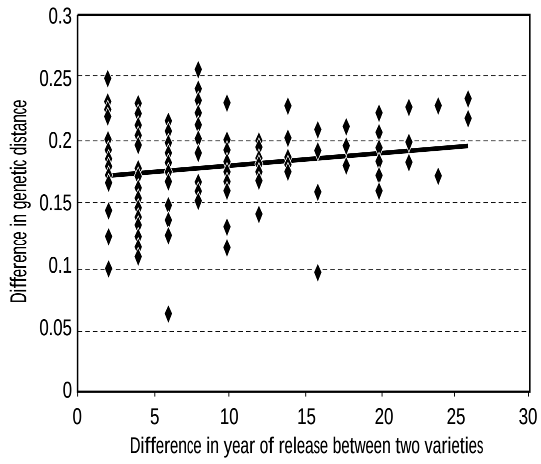

Figure 7. Regression of difference in genetic distance and year of release for 27 CIMMYT spring bread wheat lines released from 1962 to 1990.

Source: CIMMYT Applied Biotechnology Laboratory.

The findings of the molecular analysis are consistent with Skovmand and DeLacy's (1999) genealogical analysis and the molecular and genealogical studies of Almanza-Pinzon (2000). Breeders have selected for uniformity of certain agronomic traits in which diversity would be detrimental for crop performance and for farmers, such as day length sensitivity and late maturity. At the same time, they have selected for genetic diversity when it is desirable, such as in resistance to disease. They have also selected for yield stability, heat tolerance, and other traits governing performance across environments. The relationships between traits that influence crop performance and genetic diversity are described next.

Indicators of Apparent Diversity

Much of the concern for genetic uniformity arises from its hypothesized relationship with performance. While there is an assumption that more diversity is "good," a direct relationship between increased diversity levels and performance has yet to be demonstrated conclusively. The positive role of genetic diversity in reducing crop vulnerability through enhancing the longevity of resistance to certain biotrophic pathogens is fairly well accepted. In general, however, the contributions of genetic diversity to crop performance are likely to be complex, influenced by environmental factors, and difficult to represent in molecular terms, though the use of genomics to investigate this issue holds promise (R. Cooke; D. Hoisington; R.A. Fischer, pers. comm.).

The relationship between diversity and crop performance may also be more difficult to establish in wheat because it is a predominantly inbred crop. Since bread wheat has chromosome pairs from three different ancient contributors (the A, B, and D genomes), diversity could mean different alleles fixed in each genome at homeologous loci. Diversity could also mean that many genes at different locations in bread wheat affect the same function. For each variety (excluding hybrids) of an open-pollinated species such as maize, measurable genetic diversity is possible for given loci, since alleles vary from plant to plant. This type of diversity may under some conditions lead to quicker response to environmental change and some temporal stability. The options in breeding for genetic diversity in an inbred crop like wheat are to 1) develop lines with the proper combination of fixed alleles that provide reasonably good performance across environments and time, or 2) produce a number of lines, each of which is specific for a particular environment. Breeders often employ a combination of these two options (R.A. Fischer; D. Hoisington, pers. comm.).

This section summarizes scientific evidence of changes in the performance of CIMMYT bread wheats over the past 30 years. No attempt is made to establish a direct relationship between changes in performance and changes in genetic diversity. For each "dimension" (i.e., for each trait that influences wheat performance), a regression parameter was used to assess or test whether performance has improved over time, other factors held constant. As mentioned previously, performance across environments and management regimes is referred to as "apparent diversity."

Replicated trials for a set of major CIMMYT varieties released over a 30-year period provided the opportunity to examine changes over time in yield potential, yield stability, nitrogen use efficiency, and resistance to leaf rust. If findings were drawn from published analyses of data from these trials, the methods used in the original work are reported. Other data on heat and drought tolerance are assembled for the first time in this paper. Varieties included in the historical trials and data assembled for this paper overlap with, but are not identical to, those employed in the molecular and genealogical studies reported above (Appendix Tables M and N).

Yield potential and yield stability

Byerlee and Moya (1993) and Rejesus, Heisey, and Smale (1999) surveyed the published literature on global progress in wheat yield potential and reported for the most part positive trends. In the latest analysis of progress in yield potential of CIMMYT bread wheats, Sayre, Rajaram, and Fischer (1997) estimated an average annual linear increase of 67 kg/ha/yr, representing a 0.88% rate of progress per year from 1960 to 1990 (Figure 8). This rate of progress, they argue, is similar to that reported in earlier studies summarized by Byerlee and Moya (1993) and in two other studies conducted in the Yaqui Valley (Fischer and Wall 1976; Waddington et al. 1986). Their study was based on six years of data with three to four replications in each year, using eight outstanding varieties from the historical trials (Appendix Table N). Varieties received optimal agronomic management and were protected from disease and lodging.

Sayre and his colleagues also found that the effects on yield of variety by year interactions were significant but not correlated with year of release. Deviations from the regression line tended to decrease with yield progress. Six-year means were very stable for irrigated conditions in northwestern Mexico and, by inference, in other temperate, low-latitude, irrigated environments. Yield stability was pronounced for Oasis 86 and Bacanora 88, the latest varieties included in the study.

Data on nine varieties from this same trial, with three years of three replications each, were used in an earlier study by Traxler et al. (1995) to investigate changes in both yield potential and yield stability (Appendix Table N). They employed an econometric method (Just and Pope 1979) commonly utilized by agricultural economists to examine the relationship of nitrogen use and variety development to the mean and variance of yield. Their results suggest that mean yield potential increased steadily between 1950 and 1980, and leveled off in

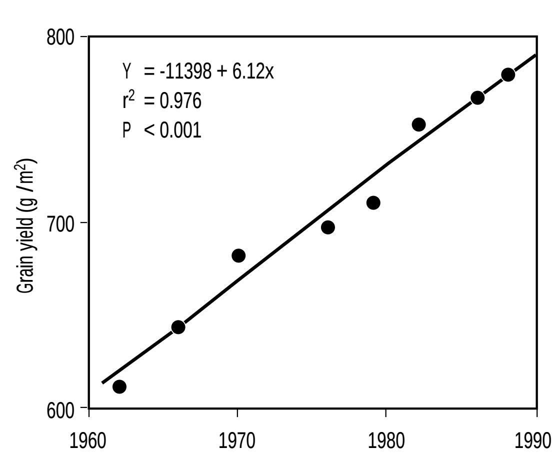

Figure 8. Yield progress in CIMMYT wheats, 1960-90.

Source: Sayre, Rajaram, and Fischer (1997).

the 1980s. The variance peaked about 1970 and then decreased. Traxler and his colleagues concluded that "the analysis indicates steady progress in producing 'better' varieties; successive releases have improved either stability, mean yield, or both" (p. 6).

More than ten years ago, Pfeiffer and Braun (1989) presented an analysis based on data from the First to the Fifteenth International Spring Wheat Yield Nurseries (ISWYNs), distributed by CIMMYT from 1965 to 1980 and grown in sites representative of major wheat-growing environments in the developing world. The ISWYN is a standardized international yield nursery consisting of three replications of 49 spring bread varieties and advanced lines, plus one local check. Pfeiffer and Braun subdivided the genotypes according to their ancestry[6] and analyzed their stability using several types of statistical models.

A comparison of the yield performance of the groups indicated the superiority of CIMMYT-bred varieties released directly by national crop improvement programs, despite changes over time in the composition of the nurseries. Yield potential was positively associated with CIMMYT ancestry (p. 161). The most stable of the groups they analyzed included genotypes with initial crosses made by CIMMYT, and at least one further selection made by national programs (p. 164). In other words, the ancestral diversity that is enhanced by the selection and crossing activities of national programs was reflected in greater stability. Neither materials of exclusively local development nor CIMMYT crosses released as varieties were as stable. Pfeiffer and Braun found a significant positive relationship between mean yield and yield stability in 9 of the 15 ISWYNS (p. 166).

Yield stability of individual varieties as analyzed in trial data is related to, but does not necessarily imply, stability in crop yields across production environments and countries. In 1989, Anderson and Hazell provided a comprehensive overview of analyses of variability in world cereal production. Hazell (1989) concluded that the overwhelming sources of rising variability in cereal production over 1960-82 were increases in yield variance and simultaneous loss of offsetting variations. Contemporaneous covariance in crop yields was more likely to have resulted from synchronization of water, fertilizer, and other purchased inputs over large areas than from greater sensitivity of new seed types and genetic changes.

Hazell (1989) reported that the coefficient of variation of world cereal production around trend rose by 21% between the 1960s and the 1970s. Production variability did not increase for all crops—in particular, it declined by 11.5% for wheat between the two decades (p. 16). Later analyses confirmed this result for subsequent decades and different geographical scales (Singh and Byerlee 1990; Smale 1998). Nor did crop yield instability appear to increase with the diffusion of modern varieties in the cradle areas of crop domestication and genetic diversity for wheat (Brush 1992).

Input use efficiency

When Pfeiffer and Braun (1989) subdivided the materials in their study by environments, the most important CIMMYT cross made in the 1980s (Veery) was higher yielding across all environments than both the best locally developed variety and Siete Cerros, the most popular semidwarf wheat of the early green

[6] CIMMYT-bred wheat released directly by national crop improvement programs; crosses made by CIMMYT with at least one further selection by a national program; locally developed varieties with CIMMYT ancestry; locally developed cultivars without CIMMYT ancestry.

revolution period. The authors also found that responsiveness to better growing conditions was positively related to CIMMYT ancestry, as was mean yield. When production conditions were poor, yields were low for all varieties, and the differences between the varieties of CIMMYT origin and locally developed varieties were small. When conditions improved, the CIMMYT wheats tended to yield considerably more than local varieties. Pfeiffer and Braun therefore concluded that semidwarf wheats of CIMMYT origin were both "input efficient and input responsive" (p. 164). Based on experimental results comparing Yaqui 50 and Nainari 60 (tall wheats) to Veery and 12 other CIMMYT advanced lines, they also found that the later materials produced yields under water stress, zero input, weed-free, and weedy conditions that were at least as high or higher than those given by the tall varieties.

Recent work by Ortiz-Monasterio et al. (1997) investigated in detail the issue of nitrogen use efficiency. A common misconception is that first semidwarf wheat varieties did not perform well in the absence of nitrogen fertilizer (Simmonds 1979) and that farmers would be better off growing their older, tall wheat varieties if no fertilizer were available.

Trial data do not support this assertion. Ortiz-Monasterio et al. (1997) showed that CIMMYT's semidwarf spring wheats produce higher yields than older, tall wheats under both high and low nitrogen fertility conditions in the Yaqui Valley of Mexico (varieties included shown in Appendix Table N). Researchers in other countries have also shown that semidwarf wheat varieties either yield the same or more than tall wheats under low nitrogen fertility conditions (Jain et al. 1975; Wall et al. 1984; Entz and Fowler 1989; Austin et al. 1993). Semidwarf wheat varieties do not require more nitrogen than the old tall wheats; in fact, they often need less to produce the same yield (Figure 9).

This popular misconception may have evolved because semidwarf wheats have a better response to nitrogen and, therefore, the economically optimum rate of fertilizer application is higher. According to Moll et al. (1982), the nitrogen use efficiency (grain yield/ N supplied) of a plant can be divided into two components. The first component is uptake efficiency (plant total N/N supplied), which is the ability of the plant to extract nitrogen from the soil. The second is utilization efficiency (grain yield/plant total N), which measures the capacity of the plant to convert the nitrogen it has absorbed into grain yield. One of the conditions for breeding nitrogen use efficient wheats is the presence of genetic diversity for that trait. Genetic variability for nitrogen use efficiency in wheat has been reported (Dhugga and Waines 1989; van Sanford and MacKown 1986; Ortiz-Monasterio et al. 1997).

Furthermore, it has been shown that by breeding under medium to high nitrogen fertility conditions, the performance of CIMMYT's spring wheat cultivars under both high and low nitrogen fertility improved consistently from 1950 to 1985. In semidwarf

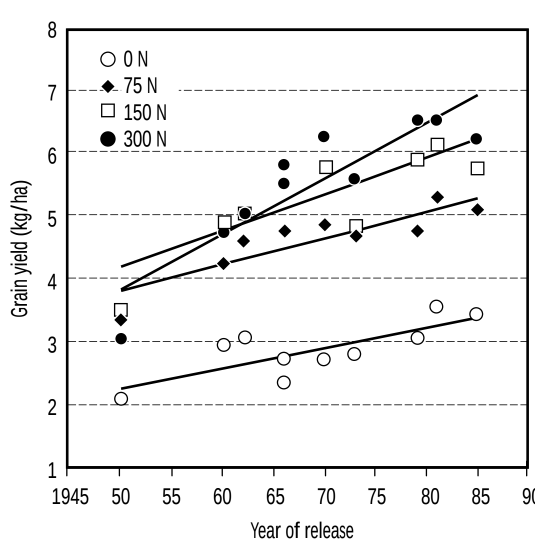

Figure 9. Mean genetic progress of 10 spring bread wheat varieties across three years at four levels of applied N.

Source: Ortiz-Monasterio et al. (1997).

wheat this increase in grain yield has been associated with gains in both components described above. At medium to high levels of nitrogen fertility, uptake and utilization efficiency have improved; at low levels of nitrogen fertility, only uptake efficiency has increased (Ortiz-Monasterio et al. 1997).

This finding suggests that the level of nitrogen in the soil plays a very important role in the genetic expression of uptake and utilization efficiency in wheat. At low soil nitrogen levels there is a better expression of uptake, whereas at high levels utilization is better expressed. In theory the nitrogen level in the soil can be manipulated, together with the genetic diversity of the crop, as a tool for breeding wheats with enhanced uptake and/or utilization efficiency (Ortiz-Monasterio et al. 1997).

This theory was put to the test by van Ginkel et al. (2000), who recently completed an eight-year study in which two wheats with good nitrogen uptake efficiency were crossed with two having good nitrogen use efficiency. High and low nitrogen levels were alternately applied to successive generations from those crosses. In one treatment, the alternation began with a high nitrogen rate applied to the F2 generation; in another, it began with low nitrogen levels applied to the F2. The treatment in which the alternation began with high nitrogen levels produced lines that yielded better than all the rest, including lines bred using CIMMYT's standard practice of applying intermediate to high nitrogen levels throughout the breeding process. Since they combine good nitrogen uptake with good nitrogen use efficiency, these high yielding lines could improve yields and yield stability in both high and low nitrogen environments.

Genetic resistance to disease

Sayre et al. (1998) demonstrated that while the grain yield potential of CIMMYT-derived cultivars has increased significantly over the past 30 years, progress in protecting this yield potential through the incorporation of genes that confer slow rusting resistance has been more dramatic. They used the historical trial data set described previously (Appendix Table N) and established leaf rust epidemics by inoculating spreader rows planted next to plots of cultivars that were not protected by fungicide. The average annual progress in grain yield over the four trials planted on normal dates was estimated to be 0.52% in protected plots and 2.07% in unprotected plots (Figure 10).

Genetic resistance, rather than use of fungicides, remains the principal means of controlling the rust diseases of wheat—especially in the wheat-producing areas of the developing world. During the past 25 years, CIMMYT's bread wheat program has emphasized selection for nonspecific

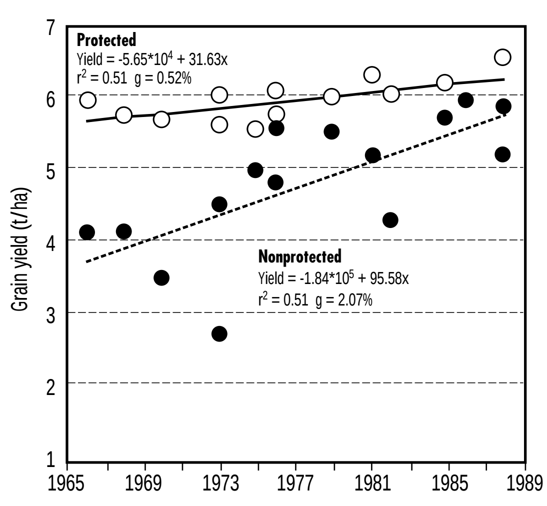

Figure 10. Relationship between year of release of spring bread wheat varieties and their grain yields under fungicide-protected and nonprotected conditions for normal plantings (g = annual genetic progress).

Source: Sayre et al. (1998).

resistances, as defined theoretically by Vanderplank (1963) and applied to leaf rust resistance by Caldwell (1968).

Genes conferring race-specific resistance tend to produce a resistant reaction in the host plant, but their effects are overcome in a relatively short period of time by pathogen mutations. In contrast, genes conferring race-nonspecific resistance to leaf rust in wheat have partial and additive effects. Although the host's response to infection is essentially one of susceptibility, the rate of disease progress within the plant is slowed (resulting in "slow rusting"). Geneticists and pathologists at CIMMYT now believe that adequate levels of nonspecific resistance can limit disease losses to insignificant levels under farmers' conditions. In addition, race-nonspecific resistance is more likely to endure for many cropping seasons than race-specific resistance. Using the data summarized in Sayre et al. (1998), Smale et al. (1998) found that the economic benefits of breeding for nonspecific resistant to leaf rust in bread wheats are probably substantial.

While leaf rust resistance gene *Lr*34 is important for slow rusting and known to be present in several wheats included in the Sayre et al. (1998) study, other genes involved in durable resistance (Johnson 1988) also appear to be present in a number of them (Rajaram, Singh, and van Ginkel 1997). One such gene, *Lr*46, was recently identified in the variety Pavon F76 (Singh, Mujeeb-Kazi, and Huerta-Espino 1998). Rajaram, Singh, and Torres (1988) identified at least 12 different slow rusting genes for leaf rust resistance in a set of 10 varieties, with 2 or 3 genes usually present in combination. In addition to these, Singh and Rajaram (1991) identified a total of 13 named race-specific genes in varieties derived from CIMMYT germplasm that were released in Mexico. Another 10 named race-specific genes have been detected in CIMMYT germplasm. Taken together, these findings suggest that both a large number of gene combinations and a wide range of reactions to rust disease are present in the materials sent through international nurseries to national breeding programs.

Heat tolerance

Over 7 million hectares of wheat grown in approximately 50 countries are subjected to continual heat stress in environments with mean daily temperatures greater than 17.5°C in the coolest month of the year (Fischer and Byerlee 1991). At least as great an area may experience heat stress at the end of the growth cycle, as occurs in the Punjab of India. During an international consultancy, national wheat program leaders identified improving heat tolerance of wheat as being a major research priority (CIMMYT 1995).

As part of a collaboration between national wheat programs and CIMMYT to identify improved breeding strategies for heat stressed environments, a representative set of wheat varieties were grown in 16 warm environments around the world (Reynolds et al. 1998). Varieties were selected based on their yield or broad adaptation, or because they had been developed for warmer regions (Reynolds et al. 1994). Ten were either CIMMYT lines or had CIMMYT ancestry. Regression analysis of their average yield performance across all 16 environments on year of release demonstrates that yield potential of varieties in warm environments has improved by approximately 40% between 1965 and 1985 (Figure 11).

More recent varieties have higher crop biomass and increased photosynthetic rate (Reynolds et al. 1994), indicating that they are physiologically better adapted to higher temperatures, in addition to being well adapted in terms of their phenological development. Though the physiological basis of improved heat tolerance is complex and not completely understood, one of the most interesting traits associated with it is the ability of varieties to maintain cooler leaves through increased evapotranspiration rates at critical times of day when the heat load is highest (Amani et al. 1996). The identification of physiological traits associated with heat tolerance provides a basis for screening germplasm collections for new sources of genetic diversity (Hede et al. 2000; Vilhelmsen et al. 2001) that could be used to broaden the genetic base of wheat cultivars developed for heat stressed environments.

Drought tolerance

The CIMMYT bread wheat program began targeting germplasm for dry environments in 1990, with the introduction of the Semi-Arid Wheat Yield Trial (SAWYT). Prior to the deployment of this nursery, the Elite Spring Wheat Yield Trial (ESWYT), containing advanced material developed under optimal, irrigated conditions, was distributed and sown in wheat growing environments around the world. Figure 12 shows the mean performance of the five highest yielding lines, compared to the best locally adapted cultivar, averaged across environments. These data represent 200 environments or individual replicated trials sown between 1990 and 1997 in many different locations globally. Environments were separated into low yielding (less than 2.5 t/ha) and medium yielding (2.5–4.5 t/ha) areas. The yield trends suggest that yields have improved significantly under low to intermediate yielding conditions following the introduction of the targeted SAWYT nurseries.

The positive trend in medium yielding areas suggests that breeding for adaptation to stress tolerance has not reduced yield potential. This is an important observation as CIMMYT aims to provide farmers in the drier areas with cultivars that will produce high, stable yields under a range of conditions. When the environment is favorable, as it is in some years, these cultivars will respond to available moisture and fertilizer, and the production realized during these years can be an important contribution to farmer income.

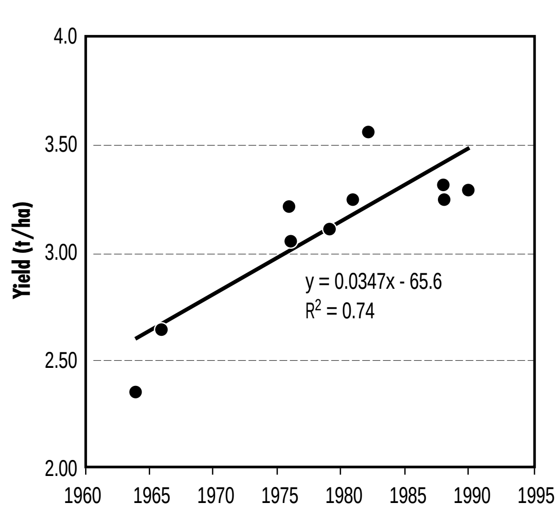

Figure 11. Average yield of historical CIMMYT spring bread wheat lines in 16 hot environments, 1990-92.

Source: Reynolds et al. (1998).

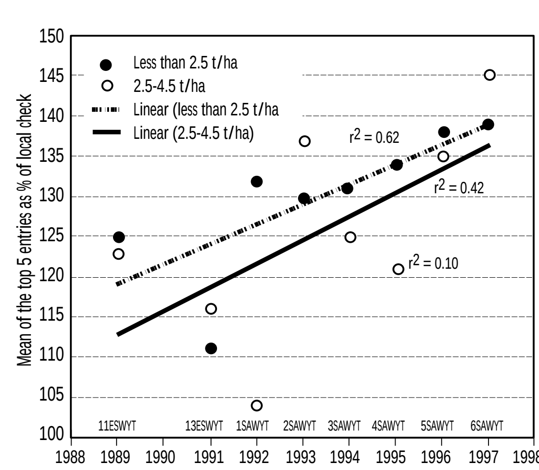

Figure 12. Trends in yield of spring bread wheat lines over time in low and medium yielding environments.

Conclusions

In one respect the predictions of Harlan and Hawkes were correct: the products of modern plant breeding, for spring bread wheat in particular, have today largely replaced "ancient patterns of diversity." Data presented in the first section of this paper reveal conclusively that the patterns of genetic variation in the bread wheats grown in the developing world in 2000 are shaped more by the genetics of scientific plant breeding than by the farmers who historically grew and selected them. Modern and traditional patterns of variation coexist, but on vastly different scales. Only an estimated 3.5% of the spring bread area in the developing world in 1997 was sown to landraces. Though the area they occupy is minor on a global scale, small niches with great genetic variation in landrace populations can be found.

Between the last two CIMMYT Global Wheat Impacts Surveys, the dominance of the leading variety has declined in terms of total area but not in terms of its relative importance in any single country. The richness of spring bread wheat varieties (their numbers, standardized by area planted) appears to have been maintained or increased globally and in each region, with the exception of Mesoamerica. There, in part because of the economic changes that have encouraged farmers to shift from bread wheat to durum wheat in northwestern Mexico, the richness and evenness (relative abundance) of spring bread wheat have declined, while the dominance of the leading variety and average age of varieties have increased.

The genetic similarity due to ancestry is much the same for major and minor wheat varieties between the two survey periods, but it differs between major and minor varieties in each time period. No systematic relationship can be established, however, between popularity (area planted) and genetic similarity due to ancestry (average coefficient of parentage).

Nearly 90% of the scientifically bred spring bread wheats in the developing world (excluding China) are CIMMYT-related wheats, meaning that they are CIMMYT crosses or selections from CIMMYT crosses released as varieties, or they have proximate or more distant CIMMYT ancestors in their pedigrees. CIMMYT-relatedness does not imply genetic uniformity. CIMMYT-related varieties constitute a vast array of germplasm developed by genetically recombining diverse materials from all over the wheat-growing world. Genealogical analyses show:

- a significant positive trend in the number of different landrace ancestors in the genetic background of all spring bread wheat varieties grown in the Yaqui Valley since 1962;
- a significant positive trend in the number of distinct landrace ancestors in the pedigrees of more than 1,000 spring bread wheat varieties released by national agricultural research systems in the developing world since 1966; and

- a significantly higher number of different landrace ancestors in released varieties that are CIMMYT related versus those with no known CIMMYT ancestry.

The number of landraces in a pedigree does not, in and of itself, constitute diversity, since the genetic contribution of landraces is likely to be small. In modern breeding programs, landraces are usually distant rather than proximate ancestors. Rather, increasing numbers of different landraces in pedigrees demonstrate conclusively that germplasm of diverse genetic background is continually brought into the crossing blocks of CIMMYT and national program collaborators through an international system. It also reveals the broad scope of the international germplasm exchange that has produced the varieties now grown in the wheat fields of the developing world.

The evidence assembled in the second section of this paper makes a strong case that both the genetic diversity of CIMMYT wheats and their performance have improved over the past three decades. Genealogical and molecular analyses indicate enhanced genetic diversity. Wheat yield potential has increased, yield stability of individual bread wheat varieties has improved over time, and the variability of wheat production around the trend has generally declined at the country, regional, and global levels. In each decade leading CIMMYT varieties have required smaller and smaller amounts of land and lower rates of nitrogen application to produce the same yield levels. Although advances in yield potential have continued, advances in yield maintenance through genetic resistance to disease have been greater. Gains have been achieved in tolerance to heat and drought. Finally, since CIMMYT-related varieties are at least as diverse as CIMMYT lines (because they are the result of crosses between CIMMYT lines and national program materials), the genetic diversity in CIMMYT lines represents the lower bound for the diversity of the wheat germplasm currently available in national programs.

On the basis of these results, it is not possible to reject the null hypothesis that the genetic diversity of CIMMYT-related bread wheats has increased during 30 years of crossing and selection. The data are not consistent with the hypothesis that the genetic base of CIMMYT germplasm has tended to narrow over time. Hence, while ancient patterns of genetic diversity have largely been replaced on a global scale by the patterns of diversity formed by modern crop breeding programs, these have not shown a tendency to narrow during the time period in which they can be observed.[7]

7 This conclusion in no way contradicts the notion that society may be willing to pay to conserve some of the remaining on-site genetic diversity present in wild relatives and landraces of wheat.

The Reasons for Concern in 2000

Although some argue that new genetic variation can be generated without the addition of new ancestral material (Rasmusson and Phillips 1997), our consensus view is the contrary. We believe that improvements in crop performance and genetic diversity are accomplished through the open exchange of large numbers of diverse materials among the wheat breeding programs of the developing world, most of which are publicly funded programs. This open exchange of germplasm is jeopardized by the trend in industrialized countries toward claiming genetic materials as private property. Access to alleles and components of biotechnology, as well as to the genetic backgrounds into which traits may be transferred, is a controversial issue, and trade negotiations and noisy legal battles are being waged over the exclusive rights to genetic resources in various forms.

Molecular marker-assisted selection and genetic transformation offer great promise to expand the genetic base of varieties, but advances in these techniques are accomplished increasingly by scientists working for privately owned corporations. The research of these corporations is of necessity oriented primarily toward large-scale commercial farmers who have access to good information and operate within markets that function well.

Not all developing countries meet the minimum conditions required to support a successful private seed industry (for wheat or for other crops). Nor can advanced molecular techniques be employed without access to genetic resources and in the absence of a strong conventional breeding program with well-equipped laboratories. The relative strength or capacity of wheat breeding programs in the developing world is not easy to assess (Maredia and Byerlee 1999), but the size and client base of many of programs may not always justify the investments required to obtain and use state-of-the-art technology. Genes or alleles have no value until they are inserted in adapted genetic backgrounds that can grow in a range of environments; without functioning seed systems, improved varieties cannot raise yields in farmer's fields.

Our view is that the "genetics of disaster" in the year 2000 are different from those envisaged by Harlan in the early 1970s. At least in the case of wheat, massive collection efforts and investments in germplasm storage have resulted in the ex situ maintenance of a substantial portion of the variation in the wheat genus that was once present in farmers' fields. Furthermore, though landraces represent but a minor percentage of global wheat area, they continue to evolve in the hands of farmers over extensive tracts stretching across northern Africa and Asia from Turkey to Tibet. Even in advanced economies in the Mediterranean region, pockets of ancient wheat forms and landraces persist.

Among CIMMYT-related spring bread wheats, our evidence is not consistent with the hypothesis of genetic narrowing in modern plant breeding. New diversity continues to be generated in breeding programs through crossing and recombination. We conclude that while the *destruction* of genetic resources Harlan predicted may not have occurred, the *restructuring* of rights to those resources, if mishandled, may unnecessarily encumber wheat improvement—with unfavorable consequences for both the developing and developed world. This is the more pressing agricultural research policy issue in 2000.

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Appendix Tables

Table A. Countries included in the CIMMYT Global Wheat Impacts Surveys, 1990 and 1997, by region

Sub-Saharan Africa	West Asia	North Africa	South Asia	Mesoamerica	Andean Region	Southern Cone of South America
1990						
Burundi	Afghanistan	Algeria	Bangladesh	Mexico	Peru	Argentina
Ethiopia	Iran	Egypt	India	Guatemala	Bolivia	Brazil
Kenya	Jordan	Libya	Nepal		Colombia	Chile
Nigeria	Lebanon	Morocco	Pakistan		Ecuador	Paraguay
Sudan	Saudi Arabia	Tunisia	Myanmar			Uruguay
Tanzania	Syria					
Zambia	Turkey					
Zimbabwe	Yemen					
1997						
Ethiopia	Afghanistan	Algeria	Bangladesh	Mexico	Peru	Argentina
Kenya	Iran	Egypt	India	Guatemala	Bolivia	Brazil
Nigeria	Jordan	Morocco	Nepal		Colombia	Chile
S. Africa	Syria	Tunisia	Pakistan		Ecuador	Paraguay
Sudan	Turkey					Uruguay
Tanzania	Yemen					
Zambia						
Zimbabwe						

Note: China has been excluded in both years. Although the survey coverage in China was better in 1997 than in 1990, many of the spring bread wheat varieties (as compared to winter and facultative varieties) were not identified by name and could not be used in the calculations for this paper. In 1997, no spring bread wheats were reported for Lebanon and area data were not available for Libya.

Table B. Spring bread wheat varieties planted on more than 0.25 million hectares in the developing world, 1990

Country	Name	Release year	Age in 1997	Area (ha)
India	Sonalika	1967	23	4,591,000
India	HD-2329	1985	5	4,068,000
India	HD-2285	1983	7	2,828,000
Pakistan	Pak-81	1981	9	2,472,000
Pakistan	WH147	1977	13	1,589,000
Pakistan	Mexipak	1965	25	1,192,000
Argentina	Klein Chamaco	1978	12	1,136,000
India	Lok-1	1981	9	1,088,000
Pakistan	UP-262	1977	13	996,000
India	UP-2003	1980	10	965,000
India	WL-711	1978	12	884,000
Argentina	Marcos Juárez INTA	1971	19	859,000
Brazil	Anahuac	1978	12	695,000
Saudi Arabia	Yecora Rojo	1980	10	675,000
India	HD-2189	1979	11	600,000
India	HUW-234	1984	6	483,000
Brazil	BR-23	1988	2	475,000
India	Yezin Wheat-3	1980	10	389,000
Pakistan	Lyallpur-73	1973	17	353,000
Bangladesh	Kanchan	1983	7	327,000
Pakistan	Pavon-F76	1978	12	320,000
Egypt	Sakha-69	1980	10	304,000
Pakistan	Pari-73	1973	17	297,000
Pakistan	HD-2009	1973	17	287,000
Turkey	Cumhuriyet-75	1975	15	257,000
Iran	Bayat	1976	14	252,000
Pakistan	Faisalabad-83	1983	7	252,000
Average			12	1,060,000

Note: Yecora Rojo and Pari-73 are varieties selected from the same cross.

Table C. Spring bread wheat varieties planted on more than 0.25 million hectares in the developing world, 1997

Country	Name	Release year	Age in 1997	Area (ha)
India	HD-2329	1985	12	4,247,000
Pakistan	Inqalab-91	1991	6	4,219,000
India	HUW-234	1984	13	3,387,000
India	Lok-1	1981	16	2,094,000
Argentina	Prointa Federal	1989	8	1,398,000
Iran	Maroon	1991	6	1,342,000
Argentina	Klein Cacique	1991	6	1,313,000
India	WH-147	1977	20	1,288,000
India	UP-262	1977	20	1,261,000
India	HD-2285	1983	14	1,137,000
India	Sonalika	1966	31	1,073,000
Argentina	Granero INTA	1987	10	744,000
India	PBW-343	1995	2	714,000
Iran	Falat	1991	6	707,000
India	WH-542	1992	5	651,000
Bangladesh	Kanchan	1983	14	613,000
India	HD-2189	1979	18	609,000
India	Sonali	1992	5	527,000
Morocco	Achtar	1988	9	512,000
Turkey	Gonen	1986	11	491,000
India	HUW-206	1985	12	479,000
Egypt	Sakha-69	1980	17	471,000
India	WH-283	1984	13	414,000
South Africa	Palmiet	1983	14	397,000
Argentina	Prointa Quintal	1992	5	375,000
Algeria	Hidhab	1985	12	370,000
Morocco	Marchouch	1984	13	365,000
Morocco	Tilila	1990	7	365,000
Argentina	Klein Dragon	1993	4	357,000
Pakistan	Chakwal-86	1986	11	310,000
Argentina	Prointa Imperial	1992	5	266,000
Average			11	1,048,000

Note: Falat, Tilila, and HUW-206 are varieties selected from the same cross.

Table D. Sample of spring bread wheat varieties planted on less than 0.25 million hectares in the developing world, 1990

Country	Name	Release year	Age in 1990	Area (ha)
India	Raj-1482	1982	8	178,000
Argentina	Las Rosas INTA	1983	7	159,000
Pakistan	Faisalabad-85	1985	5	130,000
Iran	Chenab	1976	14	98,000
Algeria	Anza	1978	12	91,000
Chile	Nobo INIA	1986	4	86,000
Pakistan	Nuri	1975	15	61,000
Brazil	BR-14	1985	5	57,000
Burma	Mexipak	1968	22	37,000
Peru	Gavilan	1982	8	36,000
Yemen Arab Republic	Sonalika	1978	12	35,000
Uruguay	B.Ombu	1984	6	33,000
Libya	Anza	1975	15	29,000
Uruguay	B.Napuca	1987	3	22,000
Egypt	Sakha-61	1980	10	22,000
Iran	Moghan-1	1974	16	18,000
Kenya	Kenya Nungu	1975	15	18,000
Tanzania	Tausi	987	3	9,000
Pakistan	Zargoon-79	1979	11	8,000
Iran	Biston	1980	10	6,000
Bolivia	Saguayo-79	1979	11	4,000
Brazil	BR 11-Guarani	1984	6	4,000
Zambia	Loerie II	1987	3	3,000
Nigeria	Samwhit-7	1990	0	2,000
Burma	Yezin Wheat-1	1980	10	2,000
Guatemala	Icta Patsun-84	1984	6	2,000
Zimbabwe	Torim-F73	1978	12	1,000
Zambia	Coucal	1988	2	<1,000
Bolivia	Jaral-F66	1971	19	<1,000
Bolivia	Totora-80	1980	10	<1,000
Average			9	38,000

Note: Tausi, Loerie II, and Nobo INIA are varieties selected from the same cross, as are Moghan-1 and Anza and as are Gavilan and Totora-80.

Table E. Sample of spring bread wheat varieties planted on less than 0.25 million hectares in the developing world, 1997

Country	Name	Release year	Age in 1997	Area (ha)
Argentina	Prointa Oasis	1989	8	194,000
Syria	Cham-6	1991	6	149,000
India	HP-1209	1979	18	88,000
Pakistan	Pavon	1978	19	84,000
Nepal	AnnaPurna-1	1988	9	71,000
South Africa	SST-822	1993	4	69,000
Argentina	Prointa Puntal	1994	3	61,000
Turkey	Marmara-86	1986	11	48,000
India	Cpan-3004	1992	5	41,000
Brazil	IAPAR-28	1988	9	35,000
Egypt	Sakha-61	1980	17	25,000
Bolivia	Chane Ciat	1986	11	24,000
Kenya	K.Paka	1974	23	24,000
Kenya	Mbuni	1987	10	14,000
Egypt	Giza-160	1982	15	10,000
Kenya	Pasa	1989	8	8,000
Pakistan	Faisalabad-85	1985	12	8,000
Uruguay	Buck Guarani	1993	4	7,000
India	WH-416	1990	7	6,000
Yemen	Ahgaf	1983	14	5,000
Kenya	Mbega	1993	4	3,000
Zimbabwe	Nata	1989	8	2,000
Algeria	Mexicano-1481	1979	18	1,000
Tanzania	Mbuni	1975	22	1,000
Colombia	Tota-63	1963	34	1,000
Brazil	Embrapa-21	1993	4	<1,000
Iran	Alborz	1978	19	<1,000
Tanzania	Kozi	1976	21	<1,000
Average			12	35,000

Note: Mbuni appears twice because it is grown in two countries. Nata, Annapurna, IAPAR -28, and Chane CIAT are all varieties selected from the same cross.

Table F. Area shares, numbers of varieties, and variety dominance, by region and parentage, for spring bread wheat varieties grown in the developing world, 1990

Region and parentage	Area (m ha)	Percent of area	Number of varieties	Dominant variety	
				Name	Area (m ha)
Sub-Saharan Africa					
All spring bread wheats	0.721	100	47	Enkoy	0.120
CIMMYT-related wheats	0.426	59	36	Condor	0.110
West Asia-North Africa					
All spring bread wheats	5.84	100	59	Yecora Rojo	0.674
CIMMYT-related wheats	4.24	73	46	Yecora Rojo	0.674
South Asia					
All spring bread wheats	29.2	100	70	Sonalika	6.280
CIMMYT-related wheats	20.9	72	57	Sonalika	6.280
Mesoamerica					
All spring bread wheats	0.880	100	42	Opata	0.211
CIMMYT-related wheats	0.873	99	40	Opata	0.211
Andean Region					
All spring bread wheats	0.173	100	27	Gavilan	0.036
CIMMYT-related wheats	0.111	64	20	Gavilan	0.036
Southern Cone					
All spring bread wheats	8.63	100	65	Klein Chamaco	1.140
CIMMYT-related wheats	7.77	90	47	Marcos Juarez INTA	0.859

Source: Calculated from 1990 CIMMYT Wheat Impacts Survey data by Byerlee and Moya.
Note: China was not included because of limited coverage.

Table G. Area shares, numbers of varieties, and variety dominance, by region and parentage, for spring bread wheat varieties grown in the developing world, 1997

Region and parentage	Area (m ha)	Percent of area	Number of varieties	Dominant variety Name	Dominant variety Area (m ha)
Sub-Saharan Africa					
All spring bread wheats	2.150	100	82	Palmiet	0.397
CIMMYT-related wheats	1.856	86	73	Palmiet	0.397
West Asia-North Africa					
All spring bread wheats	9.100	100	87	Maroon	1.340
CIMMYT-related wheats	7.400	82	75	Maroon	1.340
South Asia					
All spring bread wheats	35.000	100	103	HD 2329	4.250
				Inqalab	4.220
CIMMYT-related wheats	31.600	91	80	HD 2329	4.250
				Inqalab	4.220
Mesoamerica					
All spring bread wheats	0.463	100	17	Saturno	0.161
CIMMYT-related wheats	0.454	99	16	Saturno	0.161
Andean Region					
All spring bread wheats	0.275	100	28	Gavilan	0.052
CIMMYT-related wheats	0.254	92	25	Gavilan	0.052
Southern Cone					
All spring bread wheats	8.020	100	66	Prointa Federal	1.400
CIMMYT-related wheats	6.470	81	53	Prointa Federal	1.400

Source: Calculated from 1997 CIMMYT Wheat Impacts Survey data. Survey data prepared in 1997 by Heisey, Lantican, and Dubin.

Note: The 1997 survey definition included not only parents, but more distant ancestry. Of the total area in spring bread wheats with CIMMYT ancestry in 1997, an estimated 4.5% of spring bread wheat area in India and 20% of spring bread wheat area in China were planted to semidwarf varieties whose names were not identified. The number of varieties in India is therefore understated. China has been excluded from the analysis.

Table H. Definition of spatial diversity indices used in this paper

Index	Concept	Mathematical construction[a]	Explanation	Adaptation in this paper
Margalef	Richness	$D=(S-1)/\ln N$ $D \geq 0$	number of species S recorded, corrected for the total number of individuals N summed over species	S=number of wheat varieties grown in a season N= total hectares of wheat in that season
Berger-Parker	Dominance	$D=1/(N_{max}/N)$ $D \geq 1$	the less dominant the most abundant species, the higher the index value	inverse of maximum area share occupied by any single wheat variety
Shannon[a]	Richness and evenness	$D=-\Sigma_i p_i \ln p_i$ $D \geq 0$	p_i is proportion, or relative abundance, of a species	p_i is area share occupied by i-th variety

[a] Magurran (1988) reported that in species diversity models, the value of the Shannon index usually falls between 1.5 and 3.5, rarely surpassing 4.5. The maximum of the Shannon index is ln S (when all species are equally abundant).

Table I. Spatial diversity indices, by region and parentage, for spring bread wheat varieties grown in the developing world, 1990

Region and parentage	Richness (Margalef)	Dominance^{-1} (Berger-Parker)	Evenness (Shannon)
Sub-Saharan Africa			
All spring bread wheats	3.41	6.01	2.98
Varieties with CIMMYT parents	0.80	2.62	1.82
Varieties from CIMMYT cross	2.03	5.96	2.57
West Asia-North Africa			
All spring bread wheats	3.72	8.66	3.53
Varieties with CIMMYT parents	0.93	4.11	2.15
Varieties from CIMMYT cross	2.97	4.51	2.83
South Asia			
All spring bread wheats	4.01	6.36	3.17
Varieties with CIMMYT parents	1.26	4.95	2.60
Varieties from CIMMYT cross	3.92	2.83	2.28
Mesoamerica			
All spring bread wheats	2.99	4.20	2.65
Varieties with CIMMYT parents	0.40	2.85	1.51
Varieties from CIMMYT cross	2.49	4.05	2.52
Andean Region			
All spring bread wheats	2.16	4.78	2.55
Varieties with CIMMYT parents	0.32	2.08	1.19
Varieties from CIMMYT cross	1.31	2.69	1.73
Southern Cone			
All spring bread wheats	4.01	7.60	3.37
Varieties with CIMMYT parents	1.11	3.79	2.35
Varieties from CIMMYT cross	1.86	4.03	2.47

Source: Calculated from 1990 CIMMYT Wheat Impacts Survey data prepared by Byerlee and Moya.
Note: China was not included because of limited coverage. See text and Appendix Table H for definitions of indices.

Table J. Spatial diversity indices, by region and parentage, for spring bread wheat varieties grown in the developing world, 1997

Region and parentage	Richness (Margalef)	Dominance^{-1} (Berger-Parker)	Evenness (Shannon)
Sub-Saharan Africa			
All spring bread wheats	5.62	5.41	3.18
Varieties with CIMMYT parents and ancestors	2.22	2.99	2.11
Varieties from CIMMYT cross	3.06	3.25	2.44
West Asia-North Africa			
All spring bread wheats	5.40	6.12	3.38
Varieties with CIMMYT parents and ancestors	1.35	2.09	1.67
Varieties from CIMMYT cross	3.52	6.50	3.10
South Asia			
All spring bread wheats	5.92	7.68	3.43
Varieties with CIMMYT parents and ancestors	1.66	5.31	2.55
Varieties from CIMMYT cross	3.21	7.36	3.29
Mesoamerica			
All spring bread wheats	1.23	4.13	2.05
Varieties with CIMMYT parents and ancestors	0.25	1.50	0.68
Varieties from CIMMYT cross	0.88	3.14	1.76
Andean Region			
All spring bread wheats	2.24	5.02	2.73
Varieties with CIMMYT parents and ancestors	0.69	1.71	1.36
Varieties from CIMMYT cross	1.30	4.40	2.45
Southern Cone			
All spring bread wheats	4.08	5.72	2.95
Varieties with CIMMYT parents and ancestors	1.43	1.83	1.59
Varieties from CIMMYT cross	1.97	2.91	2.36

Source: Calculated from 1997 CIMMYT Wheat Impacts Survey data. Survey data prepared in 1997 by Heisey, Lantican, and Dubin.

Note: The 1997 survey definition included not only parents, but more distant ancestry. China was not included because of limited information on spring bread wheats. See text and Appendix Table H for definitions of indices.

Table K. Temporal diversity, by region and parentage, of spring bread wheat varieties grown in the developing world, 1990

Region and parentage	Average age in 1990	Area-weighted average	Maximum age	Percent older than maximum	Name of oldest variety
Sub-Saharan Africa					
All spring bread wheats	10.1	11.4	25	47	Samwhit
Varieties with CIMMYT parents	13.4	12.2	21	64	Taian
Varieties from CIMMYT cross	7.1	8.2	20	32	Kweche
West Asia-North Africa					
All spring bread wheats	12.1	10.2	58	30	Florence Aurore
Varieties with CIMMYT parents	10.4	9.0	16	57	Karaj, Arvand
Varieties from CIMMYT cross	11.2	10.6	25	50	Mexipak
South Asia					
All spring bread wheats	12.2	12.8	56	49	C-591
Varieties with CIMMYT parents	11.3	11.1	20	40	Chenab
Varieties from CIMMYT cross	11.7	16.3	25	31	Mexipak
Mesoamerica					
All spring bread wheats	6.4	8.0	16	43	Cleopatra-74
Varieties with CIMMYT parents[a]	9.4	9.4	16	60	Cleopatra-74
Varieties from CIMMYT cross	6.0	7.9	15	40	Anahuac-F75
Andean Region					
All spring bread wheats	12.2	13.7	27	33	Tota, Bonza, Crespo
Varieties with CIMMYT parents[b]	11.3	12.6	17	50	Huanca
Varieties from CIMMYT cross	7.6	7.1	19	33	Jaral
Southern Cone					
All spring bread wheats	6.7	9.2	23	34	BH-1146
Varieties with CIMMYT parents	6.7	7.6	16	11	Naofen
Varieties from CIMMYT cross	6.8	11.6	19	31	Marcos Juárez INTA

Source: Calculated from 1990 CIMMYT Wheat Impacts Survey data. Survey data prepared in 1990 by Byerlee and Moya.

Note: Includes tall and semidwarf varieties released by plant breeding programs. Age defined as years from date of variety release in country. China not included because of limited coverage.

[a] Includes only five varieties.

[b] Includes only four varieties.

Table L. Temporal diversity, by region and parentage, of spring bread wheat varieties grown in the developing world, 1997

Region and parentage	Average age in 1997	Area-weighted average	Maximum age	Percent older than maximum	Name of oldest variety
Sub-Saharan Africa					
All spring bread wheats	13.0	12.1	57	43	Verbeterde Kenia
Varieties with CIMMYT parents or ancestors	12.4	13.5	26	53	Samwhit-4
Varieties from CIMMYT cross	10.5	11.4	27	29	INIA
West Asia-North Africa					
All spring bread wheats	11.9	10.9	65	35	Florence Aurore
Varieties with CIMMYT parents or ancestors	8.3	9.3	24	46	Nasma
Varieties from CIMMYT cross	11.4	11.2	27	37	Kalyansona
South Asia					
All spring bread wheats	11.3	11.4	35	46	N-59
Varieties with CIMMYT parents or ancestors	10.1	11.8	20	49	WH-147
Varieties from CIMMYT cross	10.2	12.0	30	43	Sonalika
Mesoamerica					
All spring bread wheats	12.7	11.8	23	40	Zacatecas-74
Varieties with CIMMYT parents or ancestors[a]	14.8	10.8	20	50	Chivito-77
Varieties from CIMMYT cross	10.4	12.4	23	33	Zacatecas-74
Andean Region					
All spring bread wheats	13.3	11.7	34	48	Crespo-63
Varieties with CIMMYT parents or ancestors	16.6	20.5	29	38	Sugamuxi-68
Varieties from CIMMYT cross	7.0	9.5	17	24	Totora IBTA-80
Southern Cone					
All spring bread wheats	7.3	7.3	19	26	Anahuac-75
Varieties with CIMMYT parents or ancestors	5.7	5.6	13	33	Cordillera-4
Varieties from CIMMYT cross	8.2	8.2	19	45	Anahuac-75

Source: Calculated from 1997 CIMMYT Wheat Impacts Survey data by Heisey, Lantican, and Dubin.

Note: The 1997 survey definition includes not only parents, but more distant ancestry. China is not included because of limited information on spring bread wheats. Includes tall and semidwarf varieties released by plant breeding programs. Age defined as years from date of variety release in country.

[a] Only four varieties.

Table M. Summary of spring bread wheat varieties included in the molecular analysis

Variety	CID	SID	Year of release	Cultivated variety or sister from same cross[a]			Area in 1990 (ha)	Area in 1997 (ha)	Description
				Year	Country	Name			
Pitic	6674	7	1962						Major early variety and parent
INIA	7124	41	1966	1970	Tanzania	Kweche	2,177	707	Major early parent
			1970		South Africa	INIA	—	26,112	12 varieties released from cross by 1990
Tobari	6348	9	1966						Early parent
Siete Cerros	6831	33	1966	10 varieties or sisters grown in 9 countries in 1990			1,553,567	223,493	The first widely popular semidwarf wheat
				5 varieties or sisters grown in 4 countries in 1997					20 varieties released from cross by 1990
									Still appears as minor wheat in 1997
Sonalika	6977	3	1967	7 varieties or sisters grown in 7 countries in 1990			6,284,362	1,223,863	Major semidwarf wheat in 1970s
				5 varieties or sisters grown in 5 countries in 1997					Most widely grown cross in 1990
									Still popular in Asian subcontinent in 1997
Bluebird	6980	0	1969	6 varieties or sisters grown in 4 countries in 1990			203,499	113,256	Important parent in 1970s
				Variety still grown in Egypt in 1997					One of top ten crosses in 1990
									23 varieties released from cross by 1990
Yecora	6980	7	1970	1974	Pakistan	Yecora 70	205,947	—	Selection from Bluebird major parent
									Major semidwarf wheat in 1970s
Yecora Rojo	6980	32	1975	1977	Libya	Yecora Rojo	29,066	—	Selection from Bluebird
				1980	Saudi Arabia	Yecora Rojo	674,566	—	
Anza	6733	19	1973	1974	Iran	Moghan	18,435	—	Important parent 1970s-80s
				1978	Algeria	Anza	90,827	108,993	
			1975	Libya	Anza	29,067	—		
Torim	7316	5	1973	1978	Zimbabwe	Torim	1,292	—	Popular in Mexico and a parent
Jupateco-F73	7538	4	1973	1973	Mexico	Sister of Cocoraque			Dominant in Yaqui Valley for short period
Cocoraque	7538	9	1975	1981	Brazil	Cocoraque	25,427	—	Variety and sisters popular in Mexico
				1975	Mexico	Anahuac	29,899	—	and Southern Cone of Latin America;
				1978	Brazil	Anahuac	695,408	12,448	important parent
				1987	Paraguay	Anahuac	47,140	—	
Nacozari	7401	9	1976	1977	Mexico	Jahuara-M 77	4,983	—	Important parent in 1970s
				1976	Mexico	Nacozari	5,980	—	
				1982	Bolivia	P.A.I. Comomosi	3,911	5,324	
				1981	Pakistan	Sind-81	22,883	—	
				1983	Pakistan	Tandojam-83	45,766	83,788	
				1980	Tunisia	Tanit-80	22,500	—	
Pavon	7624	163	1976	1982	Peru	El Gavilan	36,226	52,030	Popular variety
				1978	Pakistan	Pavon	320,362	83,788	14 varieties released from cross by 1990
				1976	Mexico	Pavon	12,159	26,030	Important parent
				1990	Nigeria	Samwhit 6	5,000	7,748	
				1980	Bolivia	Totora 80	196	20,676	
				1987	Tanzania	Azimio 87	—	1,769	
				1983	Yemen	Marib 1	—	5,454	
CIANO-79	7027		1979	1979	Mexico	CIANO-79	4,4849	—	Popular variety in Mexico
				1985	Brazil	Br12-Aruana	246	—	and important parent
Esmeralda	7506	77	1986	1987	Argentina	Granero INTA	—	744,314	Variety and sisters popular
				1989	Brazil	Br-23 Cuara	—	3,958	in Mexico and Southern Cone
				1986	Mexico	Esmeralda	109,632	—	of Latin America; important parent
Hahn	7877		1980	1987	Tanzania	Juhudi	16,329	106	Important parent in 1980s
Parula	50800	0	1981	—	—	—	—	—	Important parent 1980s-90s
Genaro	7691	18	1981	3 Veery wheats:			3,361,536	3,088,572	One of top ten crosses in 1990 and 1997
Glennson	7691	359	1981	27 varieties or sisters grown in 20 countries (1997)					43 varieties released from cross in 1990
Seri-82	7691	50	1982	24 varieties or sisters grown in 16 countries (1990)					Major parent
Oasis	7593	5	1986	1986	Mexico	Oasis	44,949	—	Important parent in 1990s
Opata	7741	7	1985	1989	Bolivia	Agua Dulce CIAT	379	26,051	Popular in Mexico
				1985	Mexico	Opata	209,298	—	and important parent in 1990s
				1988	Brazil	IAPAR 29-Cacatu	—	49,619	
Angostura	7866	493	1988	1988	Mexico	—	—	997	Important parent
Bacanora	7896	254	1988	1988	Mexico	Bacanora	1,993	—	Popular variety and
				1993	India	WH-542	—	739,598	important parent in 1990s
				1995	Iran	Atrak	—	192,421	
Attila	8890	0	1990		India	PBW-343	—	713,557	Currently a popular wheat and
									important parent

[a] Data sources for cultivated varieties: CIMMYT Wheat Impacts Surveys (1990, 1997). Calculations include only varieties grown in those years. Data from these surveys are summarized in Byerlee and Moya (1993) and Heisey, Lantican, and Dubin (1999). Only countries in the developing world are included.

Table N. Spring bread wheat varieties evaluated in the analysis of historical trial data

Sayre et al. (1997)	Traxler et al. (1995)	Ortiz-Monasterio et al. (1997)	Sayre et al. (1998)
Pitic-62	Yaqui-50	Yaqui-50	Siete Cerros-66
Siete Cerros-665	Nainari-60	Nainari-60	Sonalika-68
Yecora-70	Pitic-62	Pitic-62	Yecora-70
Nacozari-76	Siete Cerros-66	Siete Cerros-66	Jupateco-73
CIANO-79	Yecora-70	INIA-66	Torim-73
Seri-82	Jupateco-73	Yecora-70	Cocoraque-75
Opata-85	CIANO-79	Jupateco-73	Nacozari-76
Oasis-86	Genaro-81	CIANO-79	Pavon-76
Bacanora-88	Opata-85	Genaro-81	CIANO-79
Attila-90		Opata-85	Genaro-81
Baviacora-92			Seri-82
Weaver-91			Opata-85
			Oasis-86
			Angostura-88
			Bacanora 88

Note: In Sayre et al. (1997), emphasis was placed on the first nine varieties, with Opata-86 included from the third year of study onwards. In Traxler et al. (1995), INIA-66 was not included in the analysis to avoid two sets of variety observations for 1966.