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The Green Revolution and Wheat Genetic Diversity: Some Unfounded Assumptions

MELINDA SMALE*
International Maize and Wheat improvement Center, Mexico, D.F.

Summary. — Two propositions have become common assumptions in the development literature: (a) the Green Revolution caused genetic erosion, and (b) the Green Revolution increased genetic vulnerability. With regard to the first proposition, no causal relationship between the Green Revolution and genetic erosion can be established for bread wheat given the difficulties in measuring genetic erosion and of demonstrating causality. The pattern of genetic variation in farmers' wheat fields has undoubtedly changed over the past 100–200 years with increasing cultivation of varieties released by plant breeding programs, but the implications of these changes for the scarcity of useful genetic resources are unclear. With regard to the second proposition, evidence suggests that since the early years of the Green Revolution, the concentration of wheat area in leading cultivars has declined. The semidwarf wheats of the Green Revolution were also less vulnerable to rust diseases than the tall varieties previously released by plant breeding programs as well as traditional varieties. Although rust diseases continue to pose a challenge to wheat scientists, their understanding of the genetic basis of resistance has increased over time. The percentage of area planted to leading wheat cultivars remains a cause for concern, however, and social scientists need to understand better how various policies affect the spatial distribution of cultivars. © 1997 Elsevier Science Ltd

Key words — green revolution, genetic diversity, wheat, genetic erosion, genetic vulnerability, crop disease epidemics

1. INTRODUCTION

Two major propositions about the Green Revolution and genetic resources have become common assumptions in the literature on agricultural development: (a) the Green Revolution caused genetic erosion, and (b) the Green Revolution increased genetic vulnerability. For example, Pretty states that "the introduction of modern varieties and breeds has almost always displaced traditional varieties and breeds" (Pretty, 1995, p. 74). Cooper *et al.* (1992) write that the Green Revolution not only "destroyed" diversity, but "as the new seeds replaced the old traditional varieties and their wild relatives," the future raw material of plant breeding programs was "lost." Further, the genetic uniformity of the "miracle" seeds gave rise to "disastrous crop failures" (p. 5). Like Fowler and Mooney (1990), FAO (1996) claims that cultivars developed by crop breeding programs and multinationals are the major cause of genetic erosion. Shiva states that the food supplies of millions are today "precariously perched" on the "narrow and alien genetic base" of the semidwarf wheats (1991, p. 27). To Shiva (1991), "science and politics were

wedded together in the very inception of the green revolution" (p. 14), which left the Punjab of India "ravaged by violence and ecological scarcity" (p. 12).

In this article, evidence about wheat breeding programs and the bread wheats grown in the developing world is used to examine each of these assumptions and argue that they are not well founded—although they are certainly provocative. The background section that follows clarifies why

these issues have provoked public concern and defines the basic terminology used in the subsequent discussion. Each of the two assumptions is then discussed.

2. BACKGROUND

(a) *The reasons for concern*

Two fundamental social issues merge in the concern for the relationship of the Green Revolution to genetic diversity. One is a growing sense that genetic resources are finite and need to be conserved (Oldfield, 1984; Wilson, 1988). The second is that genetic uniformity will heighten the vulnerability of crops to disease epidemics.

Although it may be true that global genetic resources are in some sense finite, it seems difficult to apply the concept of "finiteness" to wheat genetic resources or those of any other major cultivated crop. For the capacity of cultivated crops to meet the needs of human society, the genetic recombination of groups of genes is more important than the numbers of individual genes we are capable of counting. The basic unit of genetic resources is a gene within the genome.[1] Because scientific technologies can now manipulate genes by moving them from one plant to another, it may appear convenient to think of the most basic unit of genetic resources as a single gene, or DNA sequence. But the expression of any single gene is determined by many other genes, and even noncoding sequences may play an important, although not fully understood, role in inheritance and gene expression. Given the size of the wheat genome and possibilities of incorporating genes from wild relatives or unrelated species through biotechnology and other breeding techniques, genetic combinations do not seem determinate in number. Further, although it is the scarcity of useful genetic combinations that is of social value, we are unable to accurately predict what may be useful in tomorrow's world.

The second social issue is genetic vulnerability to disease. Fear for the potential consequences of replacing farmers' heterogeneous varieties with uniform modern varieties (defined below) was signaled by the research of Frankel and Bennett (1970). The southern leaf blight which swept the US corn crop in 1970 focused public concern on the relationship between genetic uniformity and vulnerability to catastrophic economic losses from diseased crops (NRC, 1972).

In fact, the loss of 15% of the US corn crop to leaf blight in 1970 was "not catastrophic" in epidemiological terms (NRC, 1972, p. 7). Future catastrophic losses—if they occur at all—would be more likely to occur in developing nations, whose infrastructure and budgetary constraints make responding to disease outbreaks slow or inefficient. Further, concern for disease is hardly recent; the diseases of crop plants are as old as the crops themselves. The genetic basis of resistance to disease has long been a concern of most wheat breeding programs. Disease prevention through genetic resistance is generally believed to be a more effective means for reducing the probability and extent of an epidemic than chemical treatment.

(b) *Some definitions of terms*

In this article, *modern* is used to refer to all products of plant breeding programs, including both tall and semidwarf varieties. The term *traditional* refers to varieties that are the products of farmer selection. We define a *landrace* as a cultivated form of a crop species, which has evolved over generations of selection by farmers. As used in this paper, the terms landrace and traditional variety are synonymous. The *Green Revolution* in wheat refers specifically to the development and diffusion of semidwarf wheat varieties in the developing world which began in South Asia during the 1960s. These semidwarf varieties contain the $Rht1$ or $Rht2$ genes, two of numerous dwarfing genes 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 US breeding program at Washington State University in 1949, and the dwarf characteristic from Norin 10 was successfully incorporated in the Green Revolution wheats by N. Borlaug in Mexico. The semidwarf wheats currently developed by the International Maize and Wheat Improvement Center (CIMMYT) and many national breeding programs in developing countries are descendants of the wheats developed and released in the early phases of the Green Revolution, but their pedigrees also contain many distinctive ancestors and landraces from other sources.

According to IPGRI (1991), the diversity in the genetic base of a population of crop plants is related to the number of possible responses to selection pressures. The diversity of responses to selection pressures is likely to be related to the potential value of that diversity in production. In applied genetics, *genetic diversity* is a complex statistical concept referring to the variance among alleles[2] at individual gene loci, among several loci, between individuals within populations and between populations (Brown et al., 1990). The relationship between precise quantitative measures and what can be casually observed in farmers' fields, and between these

measures and what could be potentially observed, is indeed complex.

3. THE GREEN REVOLUTION AND GENETIC EROSION IN WHEAT

In the case of bread wheats, there are two basic reasons why the assertion that the Green Revolution caused genetic erosion cannot be proved or disproved. The first reason is the difficulty in assembling the necessary scientific evidence that genetic erosion has occurred on such a large geographical scale. An estimated 90% of the world's wheat area (an average of about 220 million harvested hectares per year, 1993–95) is planted to bread wheat. About 70% of the bread wheat area in the developing world is planted to semidwarf varieties, with 20% in traditional varieties and the remaining 10% in tall varieties previously released by scientific plant breeding programs.[3] In general, little is known about the actual rate of genetic erosion of crops and their wild relatives (Ceccarelli et al., 1992). The second problem is asserting that the Green Revolution caused genetic erosion when so many factors (unrelated to the seed itself) affect the pattern of varieties grown by farmers in any given geographical area. These two reasons are explored in greater detail below.

(a) Problems of definition and measurement

(i) What is genetic erosion?

IPGRI (1991) defines genetic erosion very broadly as the loss of genetic material (genes, genotypes) from individuals or plant populations. A genotype refers to the genetic constitution of a plant or group of plants. We cannot confirm through visual observation of plants whether genetic erosion has or is occurring, because genotypes interact in complex ways with the environment in which they are planted. Plant populations that appear different may in fact carry the same genes, and populations that appear the same may carry different genes.

In principle, molecular analysis can be used as a tool to detect genetic erosion by identifying differences in certain alleles in a sample of plant populations. With molecular data, it is now feasible to show whether erosion has occurred at specific loci in specific populations in a particular geographic area. Even if analysis indicates that genetic erosion has occurred in several alleles in a given geographical area, results may not hold for a larger area because the alleles of interest may be present in high frequencies in an adjacent region. Hence, a finding that one population has been replaced by another that carries a different allele at a given gene locus is not evidence that an allele has been "lost."

(ii) When did genetic erosion occur?

The time period since the beginning of the Green Revolution is negligible compared to the time that has lapsed since farmers began cultivating bread wheat. In the broadest sense, the narrowing of the genetic base in wheat began over 9,000 years ago when earlier wheat forms were domesticated. As with any cultivated plant, the human selection pressures that accompanied domestication were in one sense narrowing. Farmers selected among the full range of plant types those that produced more seed and whose grain threshed more easily but shattered less.

Porceddu et al. (1988) argue that at least two major stages of genetic narrowing have occurred in wheat in modern times. The first took place in the 19th century when plant breeders responded to the demand for new plant types as farming systems emerged that were based on livestock production, organic manures, and the intensive use of land and labor. Changes in cultivation methods favored those genotypes which diverted large amounts of photosynthates to the ear and grain. The second stage identified by Porceddu et al. occurred in the 20th century, when genes were introduced to produce major changes in plant type. Use of the dwarfing genes $Rht1$ and $Rht2$, for example, conferred a positive genotype-by-environment interaction in which yield increases proved greater given a certain combination of soil moisture, soil fertility, and weed control.

Not all agree, however, about what constitutes narrowing of the genetic base of wheat. In contrast to Porceddu et al., Hawkes (1983) cites the introduction of $Rht1$ and $Rht2$ genes into Western breeding lines (through the crossing of the Japanese line Norin 10) as an example of how diversity has been broadened by scientific plant breeders. Norin 10 carried the $Rht1$ and $Rht2$ genes from the landrace Daruma.

As this example seems to suggest, today's breakthrough in achieving genetic diversity is tomorrow's potential source of narrowing precisely because the breakthrough often produces wheat cultivars that many farmers adopt. Similarly, the 1B1R translocation[4] widened the gene pool of bread wheats and provided resistance to certain stresses, but it also contributed to the popularity in farmers' fields of the resulting Veery cross and its descendants (Villareal et al., 1991).

In any case, there seems to be no clear consensus about the breadth of the genetic base of bread wheat or how it has changed over time. Bread wheat is found only in cultivated form, which implies that it has been relatively isolated from other species and the potential for genetic variation may be minor compared with that found in some of wheat's wild progenitors and

other relatives. According to some scientists, the utilization of bread wheat landraces maintained in collections offers only limited possibilities for diversification within the genepool constituted after domestication (Jaaska, 1993). On the other hand, the lengthy history of cultivation of wheat and the early dispersion of wheat forms from the Near East throughout Europe, Asia, and North Africa imply considerable local adaptation. Continued farmer selection and modern plant breeding have extended wheat cultivation into new and different areas, creating diversity in one sense and narrowing it in another. Statements about the relative breadth of the genetic base of wheat over time seem more a matter of scientific intuition than of scientifically proven fact.

(iii) *Can genetic erosion be measured by numbers of varieties?*

The most common indicator that is used for genetic erosion is the change in the number of varieties grown in farmers' fields, but the relationship between allele frequencies or gene combinations and individual varieties is not direct. The concept of "genetic drift" seems to describe more precisely than the term "genetic erosion" the potential effect of a decline in spatial diversity of varieties on genetic resources. "Genetic drift," which is clearly defined in the quantitative genetics literature (Falconer, 1981), implies that when plant populations decline in size below a certain threshold level, the random fluctuations of allele frequencies may lead to the fixation or extinction of particular alleles that may be of great future value to farmers and consumers.

Another complication results from the fact that it is not easy to distinguish varieties in a way that is meaningful for genetics. First, farmers classify varieties differently than professional plant breeders. For example, a wheat farmer may identify the plant population in a field as a variety, but a wheat breeder may identify several distinct lines in that same plant population. Second, products of wheat breeding

programs are also hard to distinguish accurately in secondary data. In wheat breeding programs, the most precise identification of a line is provided by the cross and selection information. The same cross, or the same selection from the same cross, may be released with different names in various countries, although all represent one variety. The opposite is also true: two varieties resulting from two different crosses and selections may carry similar sets of genes due to common ancestry.

There are also terminology problems arising from differences in the conventions for reporting numbers of cultivars and area planted to cultivars, by type, in published sources. Previous releases from breeding programs may be lumped together with landraces under the heading of "traditional" or "local" varieties, while only semidwarf varieties are recorded as "modern" or "introduced."

(b) *Evidence on numbers of varieties*

(i) *Changes over time*

Given these strong caveats regarding data interpretation, what evidence do we have for the changes in numbers of bread wheat cultivars before and since the early Green Revolution? In 1990, the top five bread wheat crosses covered an estimated 36% of the wheat area planted to cultivars produced by plant breeding programs. Among developing country regions, West Asia had a relatively low concentration of area among leading crosses, and also a greater proportion of area in traditional varieties of bread wheat (Smale *et al.*, 1996).

While these percentages appear high, it is important to recognize that the concentration of wheat area among modern cultivars is probably less today than in earlier decades of this century for major wheat-producing nations of the world. Early in this century, new products from plant breeding programs dominated the wheat fields of European countries, Australia, India, and the United States. For
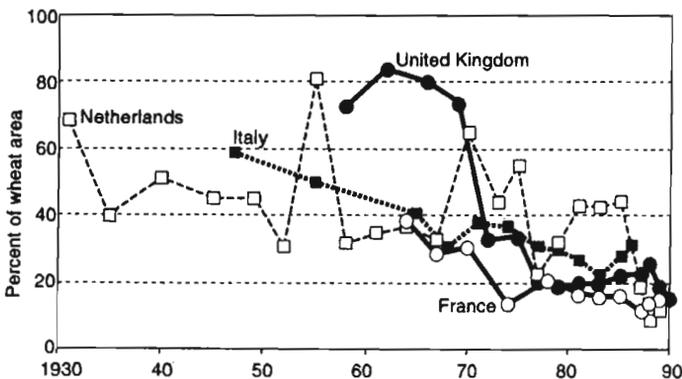

Figure 1. *Area of dominant wheat cultivar, Europe, 1930–90. Calculated from Lupton (1992).*

example, in Australia, Federation (released in 1901) occupied most of the wheat area from 1910 to at least 1925 (Macindoe and Brown, 1968). The variety Gentil Rosso, derived from an Italian landrace, was cultivated over a large part of Northern and Central Italy, where it represented over 60% of the wheat crop in the early 1920s (de Cillis, 1927). Wilhelmina, an early Dutch release, and subsequently its descendant, Juliana, covered much of the area in the Netherlands for decades at the beginning of this century (Lupton, 1987).

Since then, the percentage of wheat area planted to the dominant cultivar has declined in Italy (durum wheat), as well as in France, the United Kingdom, the Netherlands, Hungary, and Yugoslavia (winter wheats) (Figure 1). Bagnara et al. (1996) report that the number of varieties grown in Italy is higher now than several decades ago, with many of these varieties suited to their own agroecological "niche". The pattern of concentration in area is less clear for Sweden, Norway, Czechoslovakia, Poland, Spain, and Germany, but in none of these countries does the percentage distribution among leading cultivars appear more concentrated over time (Lupton, 1992). Downward trends are also found in the United States from the 1920s (Dalrymple, 1988).

Since the beginning of the Green Revolution the concentration of planted area among leading bread wheats has also changed in the developing world. At least twice as many cultivars based on the Veery cross were released in developing countries starting in the 1980s, compared to the number of cultivars derived from the II8156 (Mexipak) cross and released in the mid-1960s. The area planted to all of these cultivars in 1990 however, was only about one-fifth the area once sown to the II8156 cultivars alone (Byerlee and Moya, 1993). Estimates suggest that the area planted to a single cultivar was high in the Indian Punjab in the late 1950s prior to the Green Revolution: a cultivar called C591 covered most of

the irrigated area and some of the rainfed area (Figure 2). In the high potential wheat production zones, semidwarf wheats generally replaced the tall cultivars that had been released by the Indian national breeding program from the early 1900s (such as C591), rather than traditional varieties (see also evidence cited in Wood and Lenné, 1996). Since the late 1960s, the percentage of area under leading cultivars has fluctuated, but if any long-term trend is observable since 1947, it has not been upward.

(ii) *Semidwarf varieties and the "loss" of landraces*

Many factors other than seed itself have affected and continue to affect the spatial distribution of wheat cultivars in farmers' fields. One obvious factor is the development of the commercial seed industry. The early phases of commercialization in agriculture played a large role in reducing the relative number of traditional varieties grown in farmers' fields during this century. In France, for example, protective legislation restricted the number of varieties that French seed merchants could sell to farmers (Lupton, 1987). Agricultural mechanization, such as more complex and precise seeding and harvesting machinery, requires more uniform phenotypes to work properly. Larger areas grown to uniform phenotypes are linked to economies of scale in machinery use (i.e., the per-unit cost of machinery delines as area on which is it used increases). Industrial processing also demands uniform grain quality. Today, the breadth of wheat varieties available to farmers in both developed and developing countries is clearly influenced by seed industry development and the impact of government regulations on public and private sector breeding efforts.

As suggested by the arguments above and expressed more succinctly by Wood and Lenné, to relate the spread of semidwarf varieties to the loss of traditional varieties "goes beyond our knowledge of the facts of genetic erosion" (1997, p. 112). The term
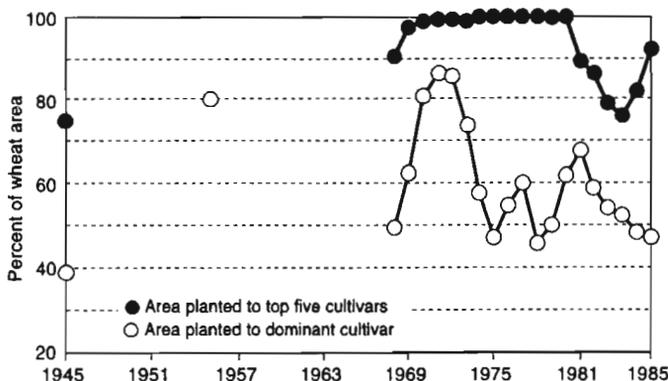

Figure 2. *Spatial diversity in the Indian Punjab. Calculated from unpublished data, Punjab Agricultural University; Sukhatme (1945); Pal (1966).*

Table 1. *Type of parent materials used in crossing, by breeding goal, wheat programs in developing countries, 1994*

Parent material*	Percentage of crosses, by goal				
	Yield	Biotic resistance	Abiotic resistance	Quality	All
Wild relatives and landraces	4.7	15.4	22.1	20.9	14.4
Advanced materials	69.0	54.6	51.2	55.1	59.2
CIMMYT International Nurseries	23.2	26.6	22.3	20.4	23.0
Others	3.1	3.4	4.4	3.6	3.4
Total	100	100	100	100	100

*Advanced materials includes released varieties and advanced lines from respondent's program or other national programs. Other category includes materials with other, subnational programs in the respondent's nation, or materials from other international nurseries.
Source: calculated from CIMMYT survey data. Includes responses from 70 wheat breeders.

"loss" is also problematic, since many of the traditional varieties that are no longer cultivated are stored in germplasm banks or in the genealogies of modern cultivars. The following paragraphs discuss how wheat breeders use landraces and present some genealogical evidence for bread wheats grown in the developing world.

Landraces are infrequently the direct parents of the modern wheats grown by farmers. New germplasm brought into a wheat breeder's program consists mostly of advanced lines with long pedigrees. Many have similar genealogical backgrounds to lines previously used by the breeder. Some have landrace ancestors that are not found in materials previously used by the breeder. Very few are landraces that have never been used before in wheat breeding. Gerek 79, a major Turkish bread wheat (but not a semidwarf) and one of the top 10 wheat varieties grown in the developing world in 1990, is an exception: one of Gerek's immediate parents is a selection from a Turkish landrace, and one of its grandparents is a selection from a varietal mixture. The mixture contains lines selected from crosses between Mentana, a major Italian variety, and two other Turkish landraces.

One measure of the use of materials by breeders is their presence in crossing blocks. Crossing blocks are the nurseries containing the parental stocks for breeders' crossing programs. Among wheat breeding programs in developing countries, wild relatives and landraces are entered less frequently in crossing blocks than other germplasm materials. Breeders do use these materials (in roughly 14% of all crosses), particularly when they make crosses to enhance resistance to biotic stresses, tolerance to abiotic stresses, or quality (Table 1). Results reported in Rejesus *et al.* (1996) suggest that the turnover of wild relatives and landraces in wheat breeders' crossing blocks is also lower than for other types of germplasm.

Turnover of landraces in crossing blocks and the representation of landraces among active parental stocks probably reflects closely the way in which landraces are used and breeders' perceptions of expected returns from their investment. To determine which landraces "combine" well with modern germplasm and transmit the trait(s) of interest requires several breeding cycles and many crosses. Verifying that a desirable trait has been transferred to and is stable in the progeny requires further testing. Transferring desirable genes without also transferring deleterious genes represents a further challenge. As Harlan has stated, the plant breeder "wants the genes not the linkages" (Harlan, 1992, p. 154).

None of this implies, however, that landraces not found in crossing blocks or used as the immediate parents of modern varieties have been "lost." Increasing the utilization of landrace collections would certainly increase the current economic rate of return to genebank accessions. But the genetic backgrounds of modern varieties are rich in landraces that have been bred into their pedigrees over the course of breeding generations from the beginning of plant breeding programs at the turn of this century. In a sample of 800 wheats released by breeding programs in developing countries over the past 30 years, the average number of different landraces per pedigree has continued to increase (Figure 3). Although we can expect the frequency of landrace use to increase over time as pedigrees grow longer, it is not necessarily true that the number of different landraces also increases.

International exchange of breeding materials increases the likelihood that landraces new to the genetic background of the lines in a national program will be introduced. Figure 4 shows that among varieties released by developing countries, those with CIMMYT ancestry have larger numbers of landraces in their pedigrees. Genealogical analysis of the bread wheat crosses grown in the developing world in 1990s reveals that landraces identified in the genetic background are as likely to have been those grown by farmers in countries now classified as high-income, the former Soviet Union or Eastern
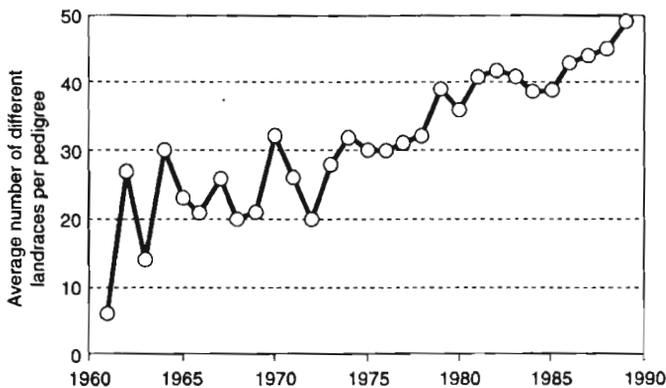
Figure 3. *Landraces in pedigrees of wheats released in developing countries. Source: Calculated from CIMMYT databases. Note: Includes approximately 800 wheat releases.*

Europe as by farmers in countries now classified as low-income (Smale *et al.*, 1996).

In summary, the relationship between the Green Revolution and genetic erosion is not well established. The evidence suggests that the replacement of traditional varieties by the products of plant breeding programs began early in this century in the major wheat-producing regions of the developing world. The concentration of area in leading cultivars has declined since then in the industrialized world, and since the early Green Revolution in the developing world. The smallness of the populations of traditional varieties still planted by farmers remains a cause for concern because these varieties are important for genetic resource conservation, although we are not sure what they may contain that will be useful for future generations of farmers or consumers. It is important to recognize, however, that modern wheats have genetic backgrounds with landraces from all over the world—and more so when international exchange of breeding materials is possible.

4. THE GREEN REVOLUTION AND GENETIC VULNERABILITY

The wheat rusts are the major diseases of wheat, although other diseases and stresses are emerging in importance as cropping systems evolve. Wheat has long been "vulnerable" to the rust diseases, and semidwarf wheats are less vulnerable than tall wheats and traditional varieties. The genetic basis of longer-lasting resistance is more fully understood today than in earlier decades. As with "genetic drift" the spatial distribution of varieties has important implications for rust epidemics but is most directly influenced by socioeconomic policies rather than by breeding programs.

(a) *Wheat is "vulnerable" to rust diseases*

The wheat rusts are old diseases; the Romans sacrificed red dogs to the god of grain, in the hopes that he would prefer meat to wheat and hold the
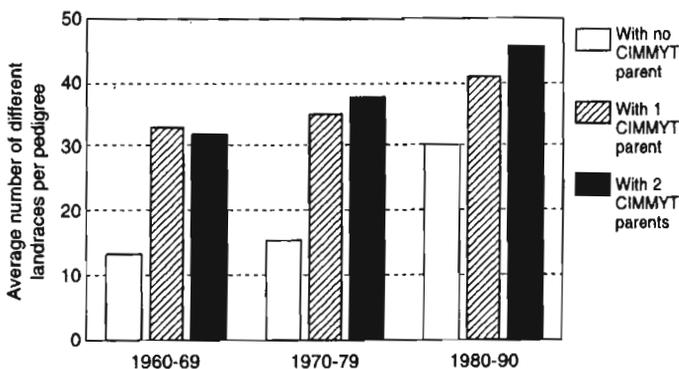

Figure 4. *Landrace use through CIMMYT parents, wheat releases in developing countries. Source: Calculated from CIMMYT databases. Note: Includes approximately 800 wheat releases.*
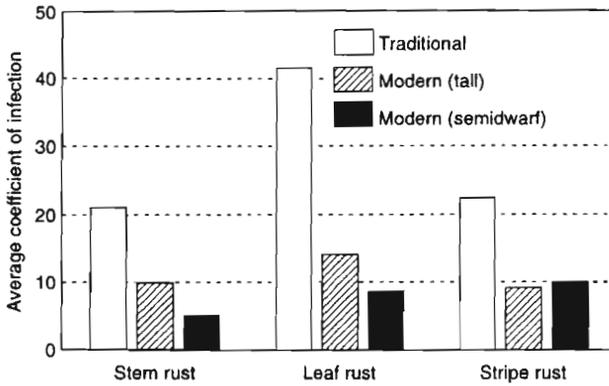
Figure 5. *Rust resistance by wheat type, 50 locations in 30 countries, 1980. Adapted from Rajaram et al.* (1988).

wheat rusts at bay (Large, 1962). In the Asian subcontinent, the first stem rust epidemic was recorded in 1786 (Nagarajan and Joshi, 1975), and concern for the magnitude of losses from rust was expressed in government documents from 1839, well before the initiation of scientific plant breeding at the turn of this century. According to government records, Indian landraces, which were planted to millions of contiguous hectares, were notably susceptible to rust. Average annual losses were estimated in one document at 10% of the value of the crop (Howard and Howard, 1909; Nagarajan and Joshi, 1985). Prior to the adoption of the first successful cultivars released by wheat breeding programs in the Asian subcontinent (during the 1920s and 1930s), the price of wheat was significantly correlated with the incidence of weather conditions favorable for the development of rust epidemics (Howard and Howard, 1909).

(b) *Some evidence on rust resistance*

Resistance to rust was an early goal in plant breeding (see Lupton, 1987). One of the attractions of the semidwarf wheats released in India in the 1960s was that they were less vulnerable to rust than the taller, later maturing, cultivars previously released by the Indian wheat breeding program (Pal, 1966; ICAR, 1978). The semidwarf wheats built on over 20 years of research in Mexico to incorporate resistance to the major rust diseases (Byerlee, 1994). In the early years of the Green Revolution there was heightened concern for the potential effects of widespread adoption of semidwarf wheats on the incidence of disease. In 1974, Saari and Wilcoxson found no apparent linkage between susceptibility to disease and dwarfing genes: "the semidwarf wheats have not increased the incidence of disease and no new

diseases have arisen because of them" (Saari and Wilcoxson, 1974, p. 51).

During 1978–81, in 50 locations in over 30 countries, CIMMYT tested semidwarf varieties, tall varieties released by breeding programs, and traditional spring wheats for stem, leaf, and stripe rust resistance. The average coefficient of infection (ACI), an index ranging from zero (disease free) to 100 (maximum infection), is shown in Figure 5 for each cultivar type (results are shown only for the 1980s, but are similar in other years). For leaf and stem rust, the semidwarfs were clearly superior to both tall cultivars released by wheat breeding programs and traditional cultivars. Data on stripe rust indicate that semidwarfs were on average less susceptible than traditional varieties but slightly more susceptible than wheat releases of tall stature (Rajaram *et al.*, 1988).

Data from screening nurseries for advanced breeding lines used in the developing world also show a gradual increase in the level of resistance to rust since the late 1960s. Of the six screening nurseries that CIMMYT annually distributes to cooperators in wheat-growing countries around the world, the nursery with the longest history is the International Bread Wheat Screening Nursery (IBSWN), initiated in 1967. The nursery contains 200–400 new, advanced lines from CIMMYT's bread wheat breeding Program. The percentage of advanced bread wheat lines with less than 10 ACI to leaf, stem, and stripe rust has an upward trend during 1967–92 (van Ginkel and Rajaram, 1993). Data for leaf rust resistance, which has been a major focus of CIMMYT's research, are shown in Figure 6.

(c) *"Gene-hunting" and polygenic resistance*

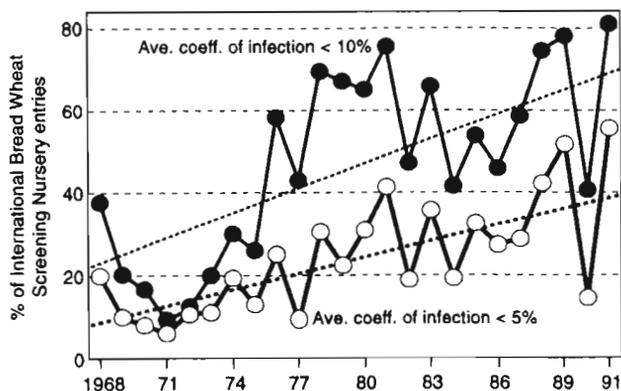Wheat breeders have recognized for some time

Figure 6. *Resistance of advance lines to leaf rust. Source: Updated from van Ginkel and Rajaram (1993).*

that developing monogenic resistance to such diseases as the wheat rusts contributes to a "boom-bust" cycle of resistance and vulnerability because the pathogen is able to mutate rapidly and form new strains. The effects of monogenic resistance (also known as race-specific, single-gene, or qualitative resistance) are generally easy to observe on a diseased plant. Breeding for this type of resistance is still practiced by many wheat breeders because it is relatively cheap and simple. When resistance is based on a single gene, the presence of the gene can be easily verified in the seedling as well as in the adult plant. In the long term, this strategy leads to a continual, expensive search for resistance genes, or "gene-hunting" (Singh and Rajaram, 1991).

Achieving resistance that endures through time is clearly a preferable objective. Increasingly, scientists breed for polygenic (as opposed to monogenic) resistance by accumulating diverse, multiple genes from new sources and genes controlling different mechanisms of resistance within single varieties. Diversity among genes that confer race-specific resistance does not assure resistance, however, since most of these genes will individually remain effective for only a short time. Longer-lasting resistance in wheat is believed to result from the additive interactions of a few unnamed, "slow-rusting" (Caldwell, 1968) genes, each of which has a minor visible impact but which together confer nonspecific resistance. The selection methodology used in the CIMMYT wheat breeding program is based on this strategy (van Ginkel and Rajaram, 1993). Most of the major varieties in the world today, and almost all of CIMMYT's bread wheat germplasm, contain what are currently understood as resistance genes for stem and leaf rust whose effects are likely to be or have been long-lasting (Singh and Rajaram, 1991; Singh, 1993; van Ginkel and Rajaram, 1993). Progress with the stripe rusts is less pronounced.

The challenge of breeding for durable, polygenic

resistance to the wheat rusts is well illustrated by examining the current effectiveness of named genes for leaf rust resistance in major cultivars released in South Asia. No single, named genes present in these cultivars still confer resistance (as measured at the seedling stage). Incorporation of new single genes, even when they are alien resistance genes, does not solve the resistance problem.[5] In each case, new pathotypes evolved shortly after the release of cultivars containing these genes (Singh, 1993). Where cultivars remain resistant, their resistance is partial and is conferred by more than one known gene, each of which has a minor additive effect, as well as unknown genes or mechanisms of resistance in the genetic background of the cultivars. As an example, five cultivars in South Asia contain only a single named gene (*Lr*13) for leaf rust resistance. Four of these cultivars are now completely suscep-tible to leaf rust at both the seedling and adult plant stage; a fifth, HUW234, still carries moderate resistance, perhaps because of unknown, background resistance (Singh and Rajaram, 1991; Singh, 1993; R. Singh, personal communication).

(d) *Some evidence on background resistance*

Rust pathogens evolve. As noted above, although some of the genes that confer race-specific and non-race-specific resistance at a given point of time can be identified, other sources of resistance in the genetic background of a cultivar may be expressed only when pathogens change.

Genealogical indexes based on coefficients of parentage have been used as indicators of "latent diversity" or the potential for resistance to unknown pathogens in the genetic background of a set of cultivars (Souza et al., 1994). The coefficient of parentage estimates the probability that a random allele taken from a random locus in one cultivar is
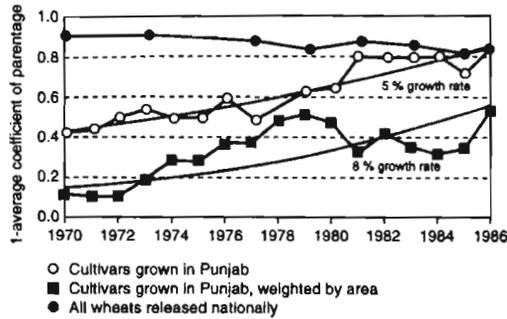
Figure 7. *Latent diversity in wheat, Indian Punjab.*

identical, by descent, to a random allele taken from the same locus in another cultivar. The coefficient of diversity is calculated as one minus the coefficient of parentage, and ranges from zero (a cultivar with itself) to one (no known ancestral relationship).[6] The average coefficient of diversity is the mean value of the pairwise coefficients for a given group of cultivars. The average coefficient of diversity can be weighted by the percentage of area planted to each cultivar in order to express the effects of the spatial distribution of cultivars on latent diversity.

Evidence suggests that Indian wheats released by the national program have had a high level of latent diversity over the past 70 years, with some slight decrease within a small range (Smale *et al.*, 1996). Figure 7 shows that the latent diversity among cultivars actually planted by farmers in the Punjab of India from 1970 ranges around a much lower level than those released by the national program but increases significantly over time. When weighted by the percentage of area planted to each cultivar, the level of latent diversity drops considerably, but it too rises over the past few decades.[7]

The difference between the weighted and un-weighted measures of diversity crudely reflects the effects of factors related to varietal adoption, such as seed distribution systems. Farmers will choose to grow the variety that is most attractive to them (in terms of profits or other measures of economic value), but the range of their choice is often limited by the few seed types that are locally available. Policy factors that affect the rate of release of cultivars, and the policy, institutional, and behavioral factors that determine the varieties that farmers plant and their rate of varietal replacement, are principal determinants of wheat diversity in farmers' fields. These factors are generally outside the influence of plant breeders and require more careful study by social scientists.

The extent of contiguous cultivation of a genotype affects the probability of disease outbreak and the progress of an epidemic should an outbreak occur. For example, the concentration of planted area

among leading modem wheats in the Indian and Pakistani Punjabs still causes concern to plant pathologists (Dubin, personal communication). As preventive measures, plant breeders and pathologists recommend spatial diversity of cultivars and cultivar combinations that change over time (see D.N. Duvick, 1984; Brennan and Byerlee, 1991). Public policy plays an important role in the course of disease prevention, since the successful implementation of many of the strategies devised by scientists depends on decisions by governmental or public institutions and the allocation of public resources (NRC, 1972; for an example, see Dubin and Torres, 1981). "Curative" strategies, or control once disease occurs, are also essentially matters of public policy. Disease reconnaissance and monitoring are important in enabling rapid responses to outbreaks. The best means of controlling the spread of disease (chemically or otherwise) once an epidemic is diagnosed is increasingly a source of policy debate.

Wheat scientists have made progress in breeding for host-plant resistance to the wheat rusts, which are major diseases of wheat. Semidwarf cultivars are generally more resistant to rusts than either previously released, tall varieties or traditional varieties. The resistance of advanced breeding lines used by developing countries has improved, as well as the background resistance of cultivars grown in the Indian Punjab. Breeders working for public institutions, and in particular CIMMYT wheat breeders, work increasingly with polygenic, durable resistance which is based on the accumulation of genes with partial resistance from diverse sources. The genetic basis of resistance remains incompletely understood, however, and as concluded in the preceding section, the fairly high concentration of wheat area among cultivars remains cause for concern.

5. CONCLUSIONS

A causal relationship between genetic erosion in bread wheats and the Green Revolution cannot

be established, because of the difficulties in defining and measuring genetic erosion and proving causality with multiple intervening factors. Over the past 100–200 hundred years, the increasing cultivation of wheat varieties released by plant breeding programs has undoubtedly affected the structure of genetic variation in farmers' fields. The implications of this shift for the availability of genetic combinations that are key to plant expression—in accessions, fields, or in the genetic backgrounds of advanced lines—is unclear.

In many major wheat-producing areas of the world, varieties bred by scientists replaced the traditional cultivars grown by farmers early in this century. The concentration of planted area among leading cultivars in these areas has also declined over time, reflecting higher rates of release of new varieties and a greater capacity for seed systems to meet farmers' needs by making a range of seed types available. The percentage of area planted to leading varieties, and their spatial distribution, continue to be cause for policy concern because (a) small plant population sizes are associated with "genetic drift" and (b) spatial distributions of cultivars carrying similar genetic sources of resistance have implications for the outbreak and spread of disease. Social scientists need to understand better how various policies and determinants affect the spatial distribution of varieties.

Pedigrees of modern wheats have become increasingly complex as materials are exchanged among breeding programs throughout the world, containing in their genetic background a growing number of ancestors from diverse sources. Advances have been and continue to be made in breeding for host-plant resistance to the wheat rusts, although the genetic basis of that resistance is not completely understood.

It is not clear, however, what this evidence implies for wheat genetic diversity, its use, and conservation. There are many "windows" or perspectives on genetic diversity, from allele frequencies to patterns among the plant populations grown on farms in a locality, nation, or region. Since social scientists will often work with the analysis and design of policies designed to influence farmers' decisions, it is important for us to remember that the relationship between the visible characteristics on which farmers' varietal choices are based and the variation that can be observed in a laboratory of molecular biology is complex. Farmers do not choose wheat cultivars based on DNA sequences, since these sequences are unobservable to them. Most economic policies are therefore blunt instruments for the issue at hand.

NOTES

1. The genome is the complete genetic code for any individual species. The International Plant Genetic Resources Institute (IPGRI, 1991) defines it as a collective term for all the genes carried by a single representative of each of all the chromosome pairs.

2. Alleles are alternate forms of a gene. Loci are gene positions on the chromosome.

3. These estimates are based on CIMMYT data from a global survey conducted in 1990, and Aquino *et al.* (1996).

4. Refers to the spontaneous cross that occurred in a farmer's field, translocating the short arm of chromosome 1R of rye and the long arm of chromosome 1B of wheat.

5. Examples include $Lr26$, present in the 1B/1R translocation from rye to wheat, and $Lr19$, from the wild grass species *Agropyron*.

6. The accuracy of the index reflects the accuracy of the pedigree information and the extent of our knowledge of the origin and relationships among ancestors.

7. The upward trends in both series of Figure 7 are statistically significant with a first-order autoregressive time-series model.

REFERENCES

Aquino, P., Hernández, V. and Rejesus, R. M. (1996) Selected wheat statistics. Part III, *CIMMYT 1995/6 World Wheat Facts and Trends.* CIMMYT, Mexico, D.F.

Bagnara, D., Bagnara, G. L. and Santaniello, V. (1996) Role and value of international germplasm collections in Italian durum wheat breeding programs. Presented at the CEIS-Tor Vergata Symposium on the Economics of Valuation and Conservation of Genetic Resources for Agriculture, Rome.

Brennan, J. P. and Byerlee, D. (1991) The rate of crop varietal replacement on farms: Measures and empirical results for wheat. *Plant Varieties and Seeds* 4, 99–106.

Brown, A. H. D., Clegg, M. T., Kahler, A. L. and Weir B. S. (ed.) (1990) *Plant Population Genetics: Breeding and Genetic Resources.* Sinauer Associates, Sunderland, Mass.

Byerlee, D. (1994) *Modern Varieties, Productivity, and Sustainability: Recent Experience and Emerging Chal-*

lenges. International Maize and Wheat Improvement Center (CIMMYT), Mexico, D.F.

Byerlee, D. and Moya, P. (1993) *Impacts of International Wheat Breeding Research in the Developing World, 1966–90.* International Maize and Wheat Improvement Center (CIMMYT), Mexico, D.F.

Caldwell, R. M. (1968) Breeding for general and/or specific plant disease resistance. In *Proceedings of the Third International Wheat Genetics Symposium,* eds. K. W. Finlay and K. W. Shepherd, Australian Academy of Sciences, Canberra, Australia.

Ceccarelli, S., Valkoun, J., Erskine, W., Weigand, S., Millaer, R. and van Leur, J. A. G. (1992) Plant genetic resources and plant improvement as tools to develop sustainable agriculture. *Experimental Agriculture* **28,** 89–98.

Cooper, D., Vellvé, R. and Hobbelink, H. (1992) *Growing Diversity: Genetic Resources and Local Food Security.* Intermediate Technology Publications, London.

Dalrymple, D. G. (1988) Changes in wheat varieties and yields in the United States, 1919–1984. *Agricultural History* **62**(4), 20–36.

Dalrymple, D. G. (1986) *Development and Spread of High-Yielding Wheat Varieties in Developing Countries.* Bureau for Science and Technology, U.S. Agency for International Development, Washington, D.C.

de Cillis, E. (1927) *I grani d'Italia.* Tipografia della Camera dei Deputati, Rome.

Dubin, H. J. and Torres, E. (1981) Causes and consequences of the 1976–77 wheat leaf rust epidemic in N.W. Mexico. *Annual Review of Phytopathology* **19,** 41–49.

Duvick, D. N. (1984) Genetic diversity in major farm crops on the farm and in reserve. *Economic Botany* **38**(2), 161–178.

Falconer, D. S. (1981) *Introduction to Quantitative Genetics.* Second edition. Longman Group Limited, Essex, U.K.

Food and Agricultural Organization of the United Nations (1996) *The State of World's Genetic Resources for Food and Agriculture (Background Documentation for the International Technical Conference on Plant Genetic Resources, Leipzig, Germany, 17–23 June, 1996).* FAO, Rome.

Fowler, F. J. and Mooney, P. (1990) *The Threatened Gene: Food, Policies and the Loss of Genetic Diversity.* The Lutterworth Press, Cambridge.

Frankel, O. H. and Bennett, E. (ed.) (1970) *Genetic Resources in Plants—Their Exploration and Conservation.* Blackwell, Oxford.

Harlan, J. R. (1992) *Crops and Man.* American Society of Agronomy, Inc., and Crop Science Society of America, Inc., Madison, Wisconsin.

Hawkes, J. G., (1983) *The Diversity of Crop Plants.* Harvard University Press, Cambridge.

Howard, A. and Howard, G. L. C. (1909) *Wheat in India: Its Production, Varieties and Improvement.* Thacker, Spink and Company, for the Imperial Department of Agriculture in India, Calcutta.

Indian Council of Agricultural Research (1978) *Wheat Research in India 1966–1976.* ICAR, New Delhi, India.

International Board for Plant Genetic Resources (1991) *Elsevier's Dictionary of Plant Genetic Resources.* Elsevier, Oxford.

Jaaska, V. (1993) Isoenzymes in the evaluation of germplasm diversity in wild diploid relatives of cultivated wheat. In *Biodiversity and Wheat Improvement,* ed. A. B. Damania, Wiley-Sayce. Chichester, U.K.

Large, E. C. (1962) *The Advance of the Fungi.* Dover Publications, New York.

Lupton, F. G. H. (1987) History of wheat breeding. In *Wheat Breeding: Its Scientific Basis.* Chapman and Hall, London.

Lupton, F. G. H. (1992) Wheat varieties cultivated in Europe. In *Changes in Varietal Distribution of Cereals in Central and Western Europe: Agroecological Atlas of Cereal Growing in Europe,* Vol. 4. Wageningen University, Wageningen, the Netherlands.

Macindoe, S. L. and Walkden Brown, C. (1968) Wheat breeding and varieties in Australia, Science Bulletin No. 76, Third Edition, New South Wales Department of Agriculture, Sydney, Australia.

Nagarajan, S. and Joshi, L. M. (1975) An historical acccount of wheat rust epidemics in India and their significance, J. G. Manners (ed.). *Cereal Rusts Bulletin* **3**(2), 29–33.

Nagarajan, S. and Joshi, L. M. (1985) Epidemiology in the Indian subcontinent. In *The Cereal Rusts: Volume 2. Diseases, Distribution, Epidemiology, and Control,* eds. A. P. Roelfs, and W. R. Bushnell. Academic Press, London.

National Research Council (1972) Committee on Genetic Vulnerability of Major Crops, *Genetic Vulnerability of Major Crops.* National Academy of Sciences, Washington, D.C.

Oldfield, M. (1984) *The Value of Conserving Genetic Resources.* U.S. Department of the Interior, National Park Service, Washington, D.C.

Pal, B. P. (1966) *Wheat.* Indian Council of Agricultural Research, New Delhi, India.

Pretty, J. N. (1995) *Regenerating Agriculture: Polices and Practice for Sustainability and Self-Reliance.* Joseph Henry Press, Washington, D.C.

Porceddu, E., Ceoloni, C., Lafiandra, D., Tanzarella. O. A. and Scarascia Mugnozza, G. T. (1988) Genetic resourcs and plant breeding: problems and prospect. *The Plant Breeding International, Cambridge Special Lecture.* Institute of Plant Science Research, Cambridge.

Rajaram, S., Singh, R. P. and Torres, E. (1988) Current CIMMYT approaches in breeding wheat for rust resistance. In *Breeding Strategies for Resistance to the Rusts of Wheat,* eds. N. W. Simmonds and S. Rajaram. International Maize and Wheat Improvement Center (CIMMYT), Mexico, D.F.

Rejesus, R., van Ginkel, M. and Smale, M. (1996) Wheat breeders' perspectives on genetic diversity and germplasm use: Findings from an international survey. *Plant Varieties and Seeds* **9**(3), 129–147.

Saari, E. E. and Wilcoxson, R. D. (1974) Plant disease situation of high-yielding dwarf wheats in Asia and Africa. *Annual Review of Phytopathology* **21,** 49–63.

Shiva, V. (1991) *The Violence of the Green Revolution.* Zed Books, London.

Singh, R. P. (1993) Resistance to leaf rust in 26 Mexican wheat cultivars. *Crop Science* **33,** 363–637.

Singh, R. P. and Rajaram, S. (1991) Resistance to *Puccinia recondita f. sp. tritici* in 50 Mexican bread wheat cultivars. *Crop Science* **31,** 1472–1479.

Smale, M. (1996) with contributions from P. Aquino, J. Crossa. E. del Toro, J. Dubin, R. A. Fischer, P. Fox, A. Mujeeb-Kazi, M. Khairallah, K. J. Nightingale, S. Rajaram, R. Singh, B. Skovmand, M. van Ginkel and G. Varughese. *Understanding Global Trends in the Use Wheat Genetic Diversity and International Flows of Wheat Genetic Resources.* Economics Working Paper 96-02. International Maize and Wheat Improvement Center (CIMMYT), Mexico, D.F.

Souza, E., Fox, P. N., Byerlee, D. and Skovmand, B. (1994) Spring wheat diversity in irrigated areas of two developing countries. *Crop Science* **34**, 774–783.

Sukhatme, P. V. (1945) *Random Sample Survey for Estimating the Outlook of Wheat in Punjab.* Indian Council of Agricultural Research, New Delhi, India.

van Ginkel, M. and Rajaram, S. (1993) Durability of disease resistance. In *Durability of Disease Resistance*, eds. Th. Jacobs and J. E. Parlevliet, Kluwer Academic Press, Dordrecht, the Netherlands.

Villareal, R. L., Rajaram. S., Mujeeb-Kazi, A. and del Toro, E. (1991) The effect of chromosome 1B/1R translocation on the yield potential of certain spring wheats (*Triticum aestivum* L.). *Plant Breeding* **106**, 77–81.

Wilson, E. O. *Biodiversity.* National Academy Press, Washington, DC.

Wood, D. and Lenné, J. (1997) The conservation of agrobiodiversity on-farm: Questioning the emerging paradigm. *Biodiversity and Conservation* **5**, 109–127.