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National and International Breeding Programs and Deployment of Plant Germplasm New Solutions or New Problems?

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INTRODUCTION

When we consider germplasm deployment and its subsequent adoption by producers, we focus explicitly on the changing area of utilization of the germplasm over time. The diffusion of germplasm over an area is determined by a set of factors that include the genetics of plants, the genetics of pathogens, and their interactions with each other and the environment. Because of the unique relationship between genetic resistance to pathogens, the area over which resistant cultivars are grown, and the pathogens themselves, I shall use the term *spaciogenic* to better describe the spatial phenomena of germplasm diffusion. Three geographic scales are important in spaciogenic aspects of agricultural systems: (1) intrafield considerations, where genetically similar or dissimilar plant genotypes are spatially distributed in a field; (2) interfield considerations, which account for the spatial separation of fields in an area; and (3) interregional factors, which deal with particular kinds of germplasm that are limited to specific regions (Mundt and Browning, 1985)

Plant breeders and pathologists have long been involved with the devel-

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opment of high-yielding, disease-resistant germplasm. But little attention has been given to the nature and consequences of how germplasm should best be deployed. Germplasm is often deployed indiscriminately and then allowed to find its niche. As Buddenhagen (1983) noticed, this may be because it is an exception to find plant pathologists participating directly in the release of disease-resistant germplasm. Germplasm is most often released from a breeding program along with a recommended area of production that is based primarily on breeders' plot field trials, where the germplasm had outyielded currently grown cultivars (Marshall et al., 1986). Even though these small-plot field trials are conducted over a number of years and locations, the actual amount of the germplasm tested is small compared to commercial production of the germplasm. Therefore, the germplasm is exposed to a relatively small number of potential pathogens, pathotypes, and environmental stresses. As a result, germplasm that seemingly has wide geographical adaptation may be quite limited to a specific area of adaptation.

The conventional breeding approach, especially in the cereal crops, has been to develop genetically uniform, pure-line germplasm. Pure-lines may be well adapted to a given set of biological and environmental factors, but they are unable to adjust when the set of factors change (Simmonds, 1962). It is the genetically static nature of pure-lines over space and through time that increases the probability of disease epidemics. Within most of the cereal-growing areas of the world are planted cultivars with similar genetic backgrounds, over large, contiguous areas (Harlan, 1972; NAS, 1972). In most instances, disease epidemics, ephemeral disease resistance, and the continuous replacement of cereal cultivars can be attributed to the extensive cultivation of pure-lines and the failure to direct their spatial diffusion over time (Johnson, 1961; Harlan, 1972). In this chapter we focus on wheat and, to a lesser extent, other cereals because of the pivotal role that breeding and germplasm deployment have played in the culture of these crops.

For the majority of time that man has been engaged in growing cereals, the crops have been spaciogenically diverse on all the aforementioned geographic scales (Jasny, 1944; Harlan, 1975). In North America, Australia, and Europe, it has only been in the past 80 to 100 years that spaciogenic uniformity was customary. Mechanization and large-scale specialization greatly decreased interfield and interregional diversity (Marshall, 1977), while the pure-line method of breeding cereals virtually eliminated intrafield diversity (Allard and Hansche, 1964; Harlan, 1972).

In some less developed countries of the world, a more abrupt shift was taken from the spaciogenic diversity of traditional agriculture employing landraces over to the production of pure-line cultivars grown under more intensive cultivation. The shift, in wheat, resulted from the timely development and rapid adoption of the semidwarf, photoperiod-insensitive germplasm developed in Mexico in the 1950s and early 1960s. The combined success of the semidwarf germplasm and the associated high-yield technology resulted in the

Green Revolution (Borlaug, 1981). This revolution made it possible to improve the living conditions of much of the world's population in the less developed countries. Without question, the benefits of the Green Revolution were, and continue to be, tremendous. The fact remains, however, that diseases are still a major component in the failure of cereals to yield their genetic potential. Furthermore, it is the cereal rust diseases (the diseases that pure-line cultivars were originally bred to control) that still cause epidemics throughout the world. As Borlaug (1981) aptly pointed out: "The current methods of relying on pure-line, disease resistant cultivars can be improved upon." The Green Revolution set the example. It must now be used as the starting point in the development of new, sustainable breeding and deployment systems. The question is: Can pathologists and breeders reestablish spaciogenic diversity, eliminate disease epidemics, provide durable disease resistance, and subsequently reduce the evanescent nature of cereal cultivars while maintaining and improving current production levels?

To answer this complex question, a reflection on past events is first needed in order to examine how and why wheat cultivation went from a state of spaciogenic diversity to spaciogenic uniformity and the effects that this has had on wheat diseases.

HISTORICAL PERSPECTIVE

The first human consumers and users of wheat were those neolithics who gathered the plants from natural, mixed populations. After some migration, the early farmers sowed and later harvested mixed cereals in tiny plots (Ucko and Dumbleby, 1969). This simple farming system probably began and slowly moved away from an area near the present-day borders of Iran, Iraq, and Turkey (Clark, 1969). The first cultivated small grains were wild einkorn (*Triticum boeoticum*), wild emmer (*T. dicoccoides*), and wild barley (*Hordeum spontaneum*). Interestingly, these species may originally have been grown for their vegetative biomass for use as animal fodder rather than for grain (Bohrer, 1972). From about 3000 to 1850 B.C., the size of individual fields is fairly unknown, but they were necessarily small because farmers could only work as much ground as their primitive tillage implements and animals permitted (Fussell, 1965). As a result, the spatial separation between fields was large. Within fields, spaciogenic diversity between plants was high and the crops probably resembled the diverse cereal populations now found in natural stands in parts of the Middle East (Vavilov, 1951; Wahl et al., 1985).

From the writings of Cato (Brehaut, 1933) we learn something about the size of agricultural fields in the Mediterranean region from 500 B.C. to A.D. 500. The commercial crops of the time were olives and grapes. The average vineyard was 100 *jugera* (25.3 ha) in size. However, wheat fields were much smaller, ranging from 2 to 7 *jugera* (0.5 to 1.7 ha), and were grown in family,

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subistence farming operations. The wheat and other cereal crops grown during this period were the archetypal landraces. The landraces were genetically heterogeneous populations that had adapted over the years to a changing biological environment, local soil types, climatic fluctuations, and cultivation practices (Dorst, 1957). Landraces were very reliable inasmuch as they produced fairly consistent yields from year to year. Most historical accounts relate that the yields of landraces were rather low (Vavilov, 1951; Dorst, 1957). However, records show that in central Iraq in 2400 B.C., wheat yields averaged 72 bushels of grain per hectare (Jacobsen and Adams, 1958). This can be compared with the wheat yields in Texas in 1980 of 62 bushels per hectare! Most important, the landraces enabled subsistence farmers to survive and persist (Lozano and Schwartz, 1981). Both qualitative and quantitative forms of disease resistance existed in the landraces (Vavilov, 1951; Qualset, 1975; Damania, 1985; Negassa, 1987). The individual components of a landrace were adapted not only to the environment but to each other as well (Witcombe and Gilani, 1979; Damania et al., 1985). Therefore, within the prevailing conditions of a region, in a given year and field, there would be some plants that compensated for others that were at a disadvantage. In the next year or field, the stresses might be different, and other components of the landrace population would reproduce differentially. Thus the landraces possessed a high degree of intrafield, spaciogenic diversity that helped protect them from disease epidemics (Harlan, 1975). Additionally, the landraces were adapted to the cultural conditions of traditional agriculture, namely low soil fertility and low plant populations. As a result, "crowd diseases" such as the rusts were inconsequential.

The landraces continued to evolve and adapt through the centuries to become local varieties or cultivars. They were still genetically heterogeneous and generally variable in appearance, but each was identifiable and locally named (Hunter and Leake, 1933). In the eighteenth century mechanized row cropping and seed drilling helped to stimulate wheat expansion in western Europe and North America. Stem rust was epidemic on wheat in Italy in 1766, particularly in the district of Tuscany (Fontana, 1767). Fogs during the cool nights followed by hot, sunny days provided optimal environmental conditions for infection by *Puccinia graminis tritici*. Tozzetti (1767) wrote that during the Tuscany stem rust epidemic, the wheat in the wheat-rye and wheat-vetch mixtures had less severe stem rust than did the wheat in pure stands. Apparently, given a highly conducive environment, rust epidemics could occur on the local cultivars of the mid-eighteenth century.

The epoch from about 1850 to 1910 had a great impact on wheat production, especially in the United States. Large areas of land in the Great Plains were being sown to wheat because land was cheap and available and farm mechanization was ever improving (Fussell, 1965). Interfield and interregional diversity began a rapid decline. Wheat was becoming spatially contiguous from Texas to the Canadian provinces of Alberta and Saskatchewan. In 1877,

the foundation of the hard red winter wheat industry was established in the Great Plains with the introduction of the Turkey landrace from southern Russia by Mennonite immigrants (Salmon et al., 1953). The Turkey landrace was rather uniform in physical appearance, but was variable for many physiological traits, including disease resistance. In 1887, the U.S. Congress passed the Hatch Act, which provided the framework for public support of agricultural research and created the agricultural experiment stations. Much of the early work of wheat researchers in the state experiment stations in the Great Plains involved testing different lots of Turkey and selections from it and other landraces (Salmon et al., 1953).

From the late nineteenth century to 1920, most of the improvement in wheat was by means of introductions and subsequent selection. In the United States, the use of selection to improve wheat dates back at least 100 years before the Hatch Act, to 1787, when a hard winter wheat was selected from an unknown landrace in Virginia (Destler, 1968). Some researchers in the 1890s began to cross lines that they had selected from the landraces. The progeny of the crosses were allowed to self-pollinate over several generations and individual head selections were made. The first extensively grown pure-line cultivar of hybrid origin in North America was the hard red spring wheat Marquis, developed by C. E. Saunders of Canada and released in 1912. Marquis resulted from a cross between a selection from Hard Red Calcutta, an Indian landrace, and Red Fife, a selected landrace of Gaelic origin (Salmon et al., 1953). The farmers' acceptance of Marquis was slow at first, but its area of production increased rapidly, until by 1929, it occupied 90% of the northern Great Plains spring wheat area.

Generally, the adoption by producers of new germplasm, or any new technology or innovation, follows a logistically-shaped curve (Luce and Raiffa, 1958). The pattern of adoption can be defined by the time when the germplasm is introduced and the rate of adoption (Byerlee and de Polanco, 1982). Once germplasm is released, its acceptance as a cultivar is often slow at first. But if the cultivar performs well during the first years following release, its acceptance by producers and its acreage undergo a phase of rapid increase. The acreage planted to a cultivar levels off and often decreases following shifts in the pathogen populations and/or the release of new and improved cultivars.

Gould (1965) described the acceptance of breeder-recommended cultivars by farmers in Kilimanjaro, Tanzania, as a process of learning with partial reinforcement. This means that even though the acceptance of new cultivars decreased the probability of sustaining damage from rust, such acceptance did not ensure a good crop because of other production risks. As shown in Fig. 1, prior to 1943, less than 5% of the Kilimanjaro wheat-growing area was planted to recommended pure-line cultivars, because local cultivars and landraces predominated. When more virulent forms of *Puccinia graminis tritici* arose, the pure-line cultivars were found to have major gene resistance that

Figure 1 Percent of area planted to breeder-recommended cultivars in Kilimanjaro from 1943 to 1963 (after Gould, 1965)

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Figure 1 Percent of wheat acreage planted to breeder-recommended wheat cultivars in Kilimanjaro, Tanganyika, from 1943 to 1963 (after Gould, 1965).

protected their yield; therefore, farmers recognized those cultivars as superior and grew them in subsequent years. However, as the area of the pure-lines increased, selection pressure was placed on the *P. graminis tritici* population, which resulted in an increase of new races able to overcome the resistance in the pure-lines. As a result, the wheat farmers were caught in a boom-and-bust cycle. By 1963, essentially all the acreage was planted to breeder-recommended cultivars because other alternatives were unavailable.

Most of the wheat breeding programs in the world pursued similar courses of action from the 1940s through the 1980s. Pure-line breeding and, when needed, incorporation of major-effect genes for rust resistance were the norm. The recommended cultivars were planted on adjacent, expansive acreages. Many new cultivars were developed, released, and subsequently lost, mainly because of adaptation in the rust populations.

As wheat pure-lines and their associated seed industry intensified, some researchers were questioning the practicality of dependence on intrafield spaciogenic uniformity in self-pollinating cereals. Harlan and Martini (1929, 1938) pioneered early work on increasing genetic diversity in cereals by means of cultivar mixtures. Jensen (1952) promoted intrafield diversity as a means of obtaining stability in oat cultivation. Borlaug (1953) and Borlaug and Gibler (1953) reported on the development of spaciogenetically diverse multilines as a means of controlling stem rust epidemics in wheat. Borlaug's work on multilines at CIMMYT (International Maize and Wheat Improvement Center) was concomitant with research on semidwarf, photoperiod-insensitive germplasm. The multilines were based on standard-height germplasm that did not have the yield potential equivalent to that of the semidwarfs under intensive cultivation, as yields of 90% or better than standard-height cultivars were realized with the semidwarfs (Borlaug, 1981).

Following widespread acceptance and phenomenal success in Mexico in the 1950s, the CIMMYT semidwarf germplasm and its intensified management system were adopted in many of the less developed countries in Asia and Africa (Saari and Wilcoxson, 1974). The adoption curve of the semidwarf germplasm in Bangladesh, India, Nepal, and Pakistan (Fig. 2) indicates that the most rapid rate of adoption was between 1966 and 1971. This can be compared to the rate of adoption of semidwarf germplasm in Texas during the same period (Fig. 2). The Texas semidwarfs, developed mainly by K. B. Porter and his colleagues (Atkins, 1980), experienced a rapid acceptance just after their initial introduction, and another large increase in 1980 following the release of TAM 105 wheat in 1979.

Throughout the 1970s and 1980s, cereal breeding by private companies in the United States increased rapidly, both in the number of lines released and number of companies involved. The Plant Variety Protection Act of 1970 provided greater incentive to private companies to breed and release cereal cultivars. It is to the advantage of the commercial breeders to develop cultivars that will later need replacement, since it is much easier to promote a new cultivar with some improvements than to extoll the virtues of an already cultivated line. Hybrid small grains, whether produced cytoplasmically or by chemical hybridizing agents, advance the purchasing of new seed to an annual occurrence. The benefits of hybrids to commercial concerns are obvious. Spacio-genic diversity has not been a high priority among private concerns, nor, for that matter, public institutions.

It is evident that pure-line development and release has received most of the attention of small grain breeders from the very initiation of breeding programs. Although the present system has several positive attributes, some difficult problems, particularly related to genetic vulnerability to disease, have been created (NAS, 1972).

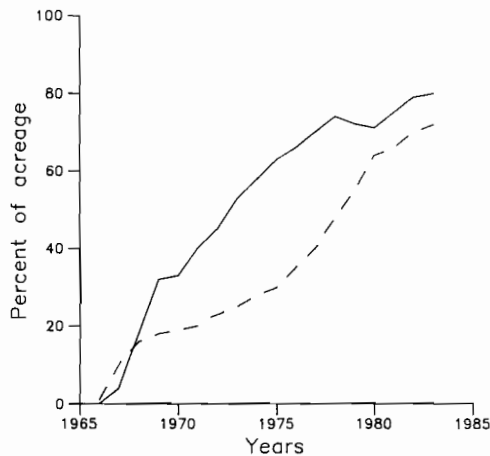


Figure 2 Percent of wheat acreage planted to semidwarf wheat cultivars from 1966 to 1983. The solid line represents semidwarf wheats in Bangladesh, India, Nepal, and Pakistan (after Dalrymple, 1986). The dashed line represents semidwarf wheats in Texas.

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NEW PROBLEMS

One of the most underrated phenomena in agriculture is the introduction or intensification of new and unsuspected problems associated with changes in agricultural practices (Hunter and Leake, 1933). It is clear that wheat breeding and cultivar deployment has had a major effect on the occurrence and intensity of wheat diseases. As some diseases have abated, others have intensified. The risk of disease epidemics will remain high as long as a lack of spaciogenic diversity exists. This is not to say that wheat breeding programs have been unsuccessful. On the contrary, breeding programs have been highly successful within the framework of pure-line development. There are some areas, delimited by climate and geography, that are less of a risk to problems caused by spaciogenic uniformity than are other areas (Lozano and Schwartz, 1981). The lower-risk areas usually have drier environments, such as the western Great Plains of the United States. The rate of disease progress of moisture-requiring pathogens is less in such areas. These areas also have less overwintering of pathogens, particularly the rusts. On the other hand, it is probable that the detrimental effects of other diseases, insect pests, and abiotic stresses could be minimized through planned intra- and interfield diversity (Jensen, 1978; Gill et al., 1984).

The high-risk areas are climatically and edaphically diverse. Incidence and severity of diseases are closely related to the ecology of high-risk areas. In such areas, the relationship between the areal extent of a cultivar and the intensity of diseases peculiar to that cultivar is intimately linked. The space occupied by a genotype is a determinant of disease development as much as disease development is a determinant of the space occupied by the genotype.

The core of the dilemma in breeding disease-resistant cereals is adaptation. Breeders and pathologists cross, select, and develop germplasm that is best adapted (highest yielding; disease resistant) over a number of testing locations and years. Pathogens then adapt to the new germplasm as its use intensifies. The greater the area over which the germplasm is cultivated, the more opportunities the pathogen has to combine overall fitness traits with increased virulence (Watson, 1970). Changes in virulence probably arise continually in pathogen populations. Most of these changes remain undetected because they occur at low frequencies and are often in a genotype that may be less fit. Here, fitness means the per capita rate of increase of an organism (Fisher, 1930), and adaptedness means the inclination of the organism to survive and reproduce (Michod, 1986). Fitness is really the deciding factor in whether or not a virulence change will become pervasive in a population because it tells how much more or less a type will produce over time on a per capita basis (Michod, 1986). Vanderplank (1984) has called pathogen adaptation following widespread production of a cultivar "epidemiologic mutation." Once the pathogen combines the appropriate fitness and virulence traits, its further increase and spread are dependent to a large degree on the spatial extent of its host, given

a conducive climate. Thus a biological phenomenon takes on properties of a spatial diffusion problem. Two factors are characteristic of such problems. First, for a pathogen to spread over large areas, it must be disseminated in some way. Carriers include wind, rain, living and dead plant material, and human beings and their equipment. Second, the rate at which a pathogen spreads over space will be influenced by barriers of various kinds. These barriers can be physical (mountains, oceans), biological (nonhosts), climatic (temperature, moisture), political (farm programs, price supports), or cultural (innovative farmers).

The wheat rusts are among the most intensively studied diseases that consistently cause major epidemics. The rusts are highly adaptable to the physical and biological environment, have high reproduction and survival rates, wide genetic variability, and are capable of long-distance dissemination (Johnson, 1978). A recent set of books by Roelfs and Bushnell (1985) has collated the literature on wheat rust epidemics. A major concern of wheat breeders in the first half of this century was the development of wheats resistant to stem rust (Salmon et al., 1953). The breeding method taken to combat the disease was to cross lines containing major-effect genes for resistance into adapted genotypes and produce pure-line cultivars. This led to the cycling of pathogen adaptation and cultivar replacement (Stakeman, 1957; Johnson, 1961).

Along with selection for stem rust resistance, breeders were selecting for wheat genotypes that matured early (Borlaug, 1954). Early maturity added another level of protection to stem rust, because the plants were in a more advanced developmental stage when temperatures became warm enough for rapid stem rust increase. Stem rust causes a greater loss in yield when severities are high at early growth stages (Kirby and Archer, 1927). Thus, by combining genes for stem rust resistance with those for early maturity, epidemics of stem rust have been mitigated since the late 1950s in North America (Roelfs, 1985).

In connection with the epidemic nature of stem rust in the Great Plains of the United States, the following observations were made during the 1985-1986 wheat-growing season. In that year, the wheat acreage along the south Texas Gulf coast doubled, from 24,000 acres to 48,000 acres, mainly due to weak markets in other commodities (Findley, 1985). The predominant cultivars recommended and grown were soft red winter wheats that possessed resistance to leaf rust (caused by *Puccinia recondita*), the most prevalent disease of the area. Fall infections of stem rust were evident by mid-December on wheat planted in early November. When spring temperatures rose, the pathogen proliferated, resulting in the complete destruction of some south Texas wheat fields. As the inoculum migrated northward, some genetic and climatic barriers slowed the rate of spread. However, heavy disease levels were found in Kansas by May, where wheat breeders at Kansas State University were in the process of releasing a new, high-protein wheat called Sumner. Throughout its many years of testing, Sumner was never exposed to such an intensity of stem rust inoculum. As a result, the Kansas wheat breeders recalled the cultivar

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(R. G. Sears, personal communication). Because of contiguous wheat cultivation, the lack of spaciogenic diversity, a mild winter, and a "forgotten" disease problem, there were unnecessary losses in yield and germplasm.

Spaciogenic uniformity has contributed to two of the most costly epidemics of leaf rust in North America in modern times. In the 1976-1977 epidemic in Mexico, Jupeteco 73 was planted on 75% of the Sonoran wheat acreage (Dubin and Torres, 1981). To the credit of the Mexican government and CIMMYT, catastrophic losses were averted in Sonora because of timely applications of fungicides. However, losses of more than 40% were realized in some Mexican wheat fields that were not treated (Dubin and Torres, 1981). The cultivar Probrand 812 occupied 63% of the acreage in central and south-central Texas in 1984-1985, when leaf rust caused approximately a 50% loss in yield in the Texas Blacklands and a 28% loss in yield statewide (Marshall, 1988). Both Jupeteco 73 and Probrand 812 were good agronomic and disease-resistant cultivars at the time of their release. It was the growing of these cultivars over large contiguous acreages in high-disease-risk areas that resulted in the epidemics.

Spaciogenic uniformity and wheat intensification have contributed to making some local disease problems regional or even continental. This can be said of septoria tritici blotch, caused by *Mycosphaerella graminicola* (Fuckel) Schroeter (anamorph, *Septoria tritici* Rob. ex Desm.). In this disease, primary infections on seedlings result mainly from propagules produced on debris from the previous years' crop (Shipton et al., 1971). Infections are established on lower leaves and secondary inoculum is later dispersed by splashing rain. The disease tends to develop and the pathogen spreads more rapidly in dense canopies and is favored by long periods of leaf wetness and cool temperatures (Shaner and Finney, 1976).

Septoria tritici blotch had been known to occur on landraces and cultivars in many parts of the world, but rarely had caused severe disease prior to 1960 (Saari and Wilcoxson, 1974). The Mexican semidwarf wheats and the intensified agriculture of the 1960s and 1970s unfortunately served to increase the incidence and severity of the disease in some areas. This was due primarily to the relative susceptibility of the germplasm coupled with conducive climates. High levels of susceptibility were found in Inia 66 in Ethiopia and Tunisia, Siette Cerros in Morocco, and Lerma Rojo and Super X in Turkey (FAO, 1974). The original semidwarf germplasm from Mexico, as a whole, was rather susceptible to *S. tritici* because the germplasm was selected in the near-absence of the pathogen.

Recent evidence suggests that aggressiveness and virulence in *S. tritici* varies with geographic location. Here, "virulence" refers to the ability of the pathogen to produce disease on a cultivar and aggressiveness as the relative amount of damage the pathogen is able to cause. Marshall (1985) found that within the United States, aggressive populations of *S. tritici* were found in north-central California and northern regions of Indiana and Ohio. On a

global basis, highly virulent isolates of *S. tritici* were found in Brazil, Mexico, Uruguay, Israel, Tunisia, Turkey, Ethiopia, and Oregon (Eyal et al., 1985). In *S. nodorum*, virulence frequency was high in most isolates from the United States, Canada, and South America, while European isolates were relatively less virulent (Scharen et al., 1985). These works suggest that spaciogenic diversity, in the form of strategic placement of germplasm, could aid in reducing regional spread of the *Septoria* diseases. Previously, Jeger et al., (1981) determined that intrafield spaciogenic diversity could serve to reduce the spread and incidence of septoria nodorum blotch. In a three-year study, Karjalainen (1986) found that disease levels caused by *S. nodorum* were lower in cultivar mixtures than the arithmetic mean of the pure line. However, the mixtures were less effective when disease pressure was high.

Vavilov (1951) cited the case of the pure-line cultivar Svalofs Panzer in Germany in the early 1920s. When the acreage of the cultivar was low, the biotypes of *Puccinia striiformis* virulent on it were absent or strictly limited in their distribution. As the cultivar became more widely grown, biotypes developed that were adapted to the cultivar, producing a serious epidemic of stripe rust in 1923.

In other cereal crops, spaciogenic uniformity has also resulted in numerous disease epidemics. IR-8 and other nitrogen-responsive, semidwarf cultivars developed by IRRI (International Rice Research Institute) were shown to be quite susceptible to bacterial leaf streak and bacterial blight (Singh, 1969; Srivastava, 1967). In India, bacterial blight was unknown in all but two states prior to the introduction of IR-8. Following widespread plantings of the cultivar, the disease became pandemic within two years (Srivastava, 1967). Additionally, the rice semidwarf germplasm reduced the genetic diversity of several Asian breeding programs, as 80% of the crosses made in 1974-1975 carried the same gene for dwarfism (Hargrove, 1979).

Perhaps the most destructive epidemic in terms of amount of plant material lost was the well-documented southern corn leaf blight in the United States in 1970. *Helminthosporium maydis* race T was present and had favorable environmental conditions prior to 1970; however, because of the spaciogenic uniformity of the corn crop, the epidemic occurred (Ullstrup, 1972).

NEW SOLUTIONS

The links between spatial and other aspects of germplasm utilization are only now being forged. Multidisciplinary approaches to cultivar development should be encouraged. Pathologists need to participate more in cultivar release and deployment. Moreover, because plant breeding and plant disease epidemiology have profoundly influenced each other, scientists should be trained in a combined discipline focusing on epidemiological plant breeding. Such trained

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scientists would be concerned with the breeding *and* deployment in space and time of germplasm engineered to eliminate plant disease epidemics.

It is clear that spaciogenic uniformity has been an important component in the disease epidemics of cereal crops. Pure-line cultivars do not have the ability to evolve or respond to shifts in pathogen populations. Extensive contiguous plantings of pure-line cultivars in disease-prone areas furthers the risk of incurring severe losses due to plant diseases. Improvement is needed in the methods used to breed disease-resistant germplasm and the strategies practiced to deploy it. Spaciogenic considerations in plant breeding and germplasm utilization offer alternatives to the avoidance of risks in cereal production. Schemes to increase diversity will be most effective if their research and implementation is planned and directed toward solving problems.

Pure-Line, Disease-Resistant Germplasm

It would be counterproductive to regress in any way from the great strides and successful achievements that have been realized in the breeding of pure-line, disease-resistant germplasm. However, the effectiveness of currently practiced methods could be increased if viewed as part of a larger program to achieve spaciogenic diversity.

Several of the cereal breeding programs in the world have been pursuing strategies of host plant resistance to direct and stabilize the evolution of pathogen populations. For clarity, the following terms and definitions will be used in this discussion: race-specific resistance is resistance that is effective against some races of the pathogen but not others; general resistance is resistance that does not interact differentially with races of the pathogen. Most cases of race-specific resistance are studied by Mendelian genetics, while most cases of general resistance require study by biometrical means. The pathogen counterpart of host race-specific resistance is virulence, while pathogen aggressiveness is the counterpart of host general resistance. Major-effect genes are those genes that most often correspond with race-specific resistance. Minor genes most often correspond with general resistance.

The accumulation of resistance genes, whether they be of major or minor effect, into breeding lines and germplasm pools has been a widely practiced and effective breeding method (Rajaram and Torres, 1986). This method could be made more effective if greater effort was placed on the identification of the genes being accumulated. A line may contain a single, major-effect gene even though it has a diverse pedigree and has tested resistant over many locations and years. Resistance gene identification must be coupled with identification and frequency information of virulence genes in the pathogen. This combined information allows researchers to monitor and direct pathogen evolution. Much research has been concentrated in this area and should be continued in order to develop superior breeding lines.

An approach that could aid in breeding for general resistance would be to develop a set of "differentials" for the disease in question and to test these at multiple locations and against various pathotypes, in comparison with breeding lines. The differential set should contain a spectrum of lines ranging from the highest level of general resistance to complete susceptibility. Genes for race-specific resistance should not be in any of the lines of the differential set. Coupled with this research should be an aggressiveness survey of the pathogen. Aggressiveness could be tested on a fully susceptible line, as, for example, infection frequency or sporulation capacity. Such an aggressiveness survey, conducted over a long period, would help determine if shifts in aggressiveness occur as cultivars with higher levels of general resistance are planted on larger acreages.

The breeding of germplasm with durable resistance (Johnson, 1978) is a useful concept, but cultivars possessing this type of resistance can be identified only in a historical sense. The durability of resistance can be shown only after wide cultivation of germplasm for a long period under environmental conditions that favor disease. The underlying mechanisms of durable resistance in those cases studied have been shown to be quite diverse (Johnson, 1984). Perhaps the most useful method to breed for durable resistance is to use proven sources of durability as parents in crosses and subsequently select for the resistance traits of the durably resistant parent.

Most of the resistance breeding methods in this brief discussion have aided in the protection of pure-line cultivars from diseases. However, the effectiveness of these methods could be increased if used as part of a diversification and deployment program. The present methods of producing disease-resistant germplasm are totally miscible with methods to increase spaciogenic diversity.

Intrafield Spaciogenic Diversity

Browning (personal communication) has emphasized that one of the major constraints on the use of diversity for intrafield disease management is a paradigmatic one. That is, the underlying basic idea of cultivar uniformity is so fixed that it may actually prevent scientists from researching and understanding the potential benefits of diversity. Clearly, rethinking is needed about the generalized concepts concerning how much uniformity is really needed in a given crop. As Frankel (1950) stated, ". . . the purity concept has not only been carried to unnecessary lengths, but . . . may be altogether inimical to the attainment of highest production."

Even though pure-lines grown over vast areas have been the root of many cereal crop epidemics, some pure-lines are actually somewhat genetically diverse. Pure-line cultivars are usually uniform only for several, highly recognizable traits (Jensen, 1978). The level of actual genetic homozygosity depends on which generation the plants were bulked together for Breeders Seed increase and whether or not any selection had occurred. Some released cultivars

are quite variable in their response to disease. The variability of cultivars are grown in different environments or biological conditions also cause the resistance to be heterogeneous (Johnson et al., 1965) and Harland (1978) has shown that in some pure-line cultivars over long periods of time there is a change in resistance and therefore a change in the potential for disease. The use of germplasm, particularly in the form of way crosses. One of the reasons for the grains used for

It is clear that the resistance over the long term in wheat, it is true, is not the product of producers for cultivars evolved dependent on Jensen (1978) preparation and the presence of "off-type" is so because of the handling of seed in regular, repeated

Moreover, the economic traits, such as intrafield spaciogenic diversity, the mixing of near "multicross" material, spatial differences (1978) showed that to protect the crop, the management relative to monogenic resistance of the multigenic resistance stated best by Jensen (1978) specific resistance in genotypes with

Another benefit of the use of mass selection and evolutionary-based breeding programs are crossed

are quite variable because they were the result of an unselected F_2 or F_3 population. The variation in such cultivars is usually most apparent when the cultivars are grown in areas remote from their original testing locations. Environmental or biological stresses to which the cultivar had not been exposed may also cause the recognition of previously unrecognized traits. Examples of some heterogeneous cultivars are Clinton oats (Morey, 1949), Scout wheat (Johnson et al., 1965), Siouxland wheat (W. D. Worrall, personal communication), and Harland barley (Jain and Qualset, 1976). One could speculate that a reason some pure-line cultivars have been successfully grown over large areas and long periods was because the cultivars were heterogeneous for disease resistance and thereby had the "buffering" of a population. Research is needed on the potential spaciogenic effects of releasing unselected, early generation germplasm, particularly when the population is the progeny of two- and three-way crosses. Obviously, genetic drift would occur. But, for example, in small grains used for forage, this would not be a concern.

It is clear that plant breeders and pathologists can have a degree of influence over the level of spaciogenic diversity present in agricultural fields. In wheat, it is true that there are pressures exerted by the seed industry and some producers for crop uniformity. However, the seed industry developed and evolved dependent on the pure-line cultivars provided by plant breeders. As Jensen (1978) pointed out, there are inherent problems associated with the preparation and maintenance of cultivar purity in small grains. The appearance of "off-types," even in highly homozygous material, is not unusual. This is so because of meiotic irregularities, low-level outcrossing, and mechanical handling of seed. The roguing of Breeders and Foundation seed fields is a regular, repeated event for most seed producers.

Moreover, reasonable if not total levels of uniformity for some key agronomic traits, such as height and maturity, need not be sacrificed to obtain intrafield spaciogenic diversity. The breeding of multiline cultivars, whether by the mixing of near-isogenic lines (Browning and Frey, 1969), or the CIMMYT "multicross" multilines (Dubin and Rajaram, 1982), serves to increase the spatial difference among like-genotypes in a field. Politowski and Browning (1978) showed that even though multilines use race-specific resistance to protect the crop, the epidemiologic effect was to slow the rate of disease development relative to the susceptible check. Thus although individual oat plants had monogenic resistance to *Puccinia coronata*, it was the epidemiological resistance of the multiline population that effectively slowed the disease. It has been stated best by Browning (1974) and Parlevliet (1981) that monogenic, race-specific resistance should be used only in diverse populations and, preferably, in genotypes with high levels of general resistance.

Another breeding strategy to increase intrafield, spaciogenic diversity is the use of mass breeding or composite crosses. Suneson (1956) proposed the evolutionary-based method of breeding where selected parents of diverse origin are crossed, bulked, and grown as a population for many generations.

These composites would have different genotype distributions dependent on where they were allowed to undergo natural selection (Suneson and Stevens, 1953; Taylor and Atkins, 1954). A similar mass breeding approach to obtaining high levels of general disease resistance and spaciogenic diversity was proffered by Beek (1986), who obtained increased resistance to several small-grain diseases by a bulk-seed selection technique. In Texas, Marshall (1987) has developed an approach to producing *directed landraces* in which germplasm possessing different types of resistance to many diseases is best matched agronomically by means of statistical pattern recognition. These matched lines are hybridized for two to three cycles in the field using male gametocides. The resulting seed is then separated into various lots and each lot is subjected to a different disease pressure. Each harvested lot is selected for high kernel weight/high kernel density seed. Finally, the lots of seed selected are recombined. The result is a directed landrace possessing spaciogenic diversity and reasonable agronomic uniformity.

Some practical and theoretical breeding strategies have been devised to select plants that perform better in mixed than in pure-line culture (Hamblin et al., 1976; Eagles, 1983; Wright, 1985). These mixture-selection schemes seek to develop lines that produce higher yields when grown under competitive conditions and that are adapted to their competitors. Mixture breeding is a rather uncharted area in the cereal crops, and further research is needed to determine the feasibility of the approach.

In addition to breeding strategies designed to increase spaciogenic diversity, a promising deployment strategy that utilizes existing pure-lines is the use of cultivar mixtures (Wolfe, 1985). When the components of a mixture are selected for similar agronomic characteristics, diseases can be managed while yields are maintained and occasionally increased (Wolfe, 1983). The fact that cultivar mixtures use germplasm that is currently available means that spaciogenic diversity can be increased immediately via this method. Cultivar mixtures would allow producers to extend the period of utilization of susceptible germplasm because the susceptibles could be grown with resistant cultivars without the risk of severe yield loss. Because of the interaction between genotype and environment for each cultivar, mixtures have a more stable performance across environments than do pure lines (Wolfe and Barratt, 1980).

Interfield and Interregional Spaciogenic Diversity

Cultivar recommendations are made to a greater or lesser extent by most state agricultural experiment stations and extension services in the United States and by other government agencies throughout the world. Most often, these recommendations are based on yield results over several locations and years. Greater input by pathologists on cultivar recommendations for an area could effectively increase the level of interfield spaciogenic diversity. It is through cultivar recommendations that pathologists can have a significant im-

impact on interfield diversity in the United States. The need for cultivars for European and other regions, especially for the diversification of germplasm on a 1000-acre scale, is a protection and acreage data recently released (1986). Although the importance has increased to the production of risk populations.

On a national level, only certain breeding strategies have been established. This approach to development is, however, involved, such as to achieve national objectives.

Cultivar mixtures for wheat and wheat stem rust are mainly on the basis of the pathogen. It establishes epidemics of mildew of wheat in the winter. It is known as other diseases and strategies toward

CONCLUSIONS

It seems reasonable to state that the maintenance of diversity in crop uniformity is a gamble for

pact on interfield diversity. The National Institute of Agricultural Botany in the United Kingdom releases information annually on the recommended cultivars for England and Wales in addition to information on how to choose a cultivar, explanations of disease epidemiology, and methods for varietal diversification (NIAB, 1982). Growing four or five genetically different cultivars on a 1000-acre wheat farm in the Great Plains of the United States provides protection against the ravages of a disease epidemic. Based on pedigree and acreage data, there appears to be an increase in diversity among the more recently released red winter wheat cultivars in the United States (Cox et al., 1986). Although this does not necessarily mean that diversity for disease resistance has increased, it does indicate that more choices are available. The risk to the producer is lessened when cultivars that complement each other in regard to risk aversion are grown on a farm. The risk is still less when diverse populations are grown or when genotypes are mixed prior to planting.

On a regional scale, breeders and pathologists have cooperated in using only certain sources of resistance for specific areas (Browning et al., 1969). The breeding approach to the deployment of resistance genes effectively established genetic barriers over and between large geographical areas. Intuitively, this approach works best when few people are involved in the breeding and development of germplasm, such as is the case with oats in the United States. However, when many people from both public and private concerns are involved, such as in wheat breeding, a type of legislative action may be necessary to achieve resistance-gene deployment (McDaniel, 1985).

Cultivar deployment strategies have been developed in India and Cyprus for wheat leaf rust (Reddy and Rao, 1979; Hadjichristodoulou, 1981) and wheat stem rust control (Bahadur et al., 1984). These strategies are based mainly on knowledge of the epidemiology of the diseases, virulence patterns of the pathogens, and resistance genes in the cultivars. Cultivar deployment establishes genetic barriers to the spread of pathogens such that large-scale epidemics can be averted. In Europe, different resistance genes for powdery mildew of barley have been recommended because of spaciogenic uniformity of the winter and spring crops (Slootmaker, et al., 1984). Much more needs to be known about the effects of deploying cultivars to control one disease on other diseases in an area. Clearly, it is better to use several diversification strategies toward all the potential diseases in an area, to minimize production risks.

CONCLUSIONS

It seems reasonable to assume that a change in the basic philosophy that dictates the methods of cereal breeding to include greater levels of spaciogenic diversity could result in the potential elimination of disease epidemics. Genetic crop uniformity over large, disease-prone areas has proven to be a high-risk gamble for both producers and consumers of agricultural products. Crop sta-

bility has not been achieved with the widespread cultivation of pure-line cultivars, and it is unlikely that stability will be met should we continue on the same strict course.

At the beginning of this chapter, the question was posed as to whether production levels could be maintained and increased while concurrently extending the useful life of cultivars, providing durable resistance, eliminating epidemics, and reestablishing spaciogenic diversity. If some of the suggested solutions presented here were fairly and adequately tested, it is highly probable that the question could be answered affirmatively.

Methods to increase diversity within and between fields and regions should be incorporated into the current methods of developing and releasing germplasm. Each breeding program should evaluate and research methods to incorporate spaciogenic diversity into resistance breeding techniques and alternative methods of germplasm release and deployment. No single strategy will be appropriate for all breeding programs, nor even for individual objectives within a single program. The most useful strategies to implement diversity will be, in themselves, diverse. The degree of diversity that is needed will vary, but in areas where disease epidemics are a major threat, diversity is more apt to solve the problem.

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