CHAPTER EIGHTEEN

Wheat

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Wheat is grown worldwide and is the most widely adapted cereal. It exceeds all other cereals in total area and total production. The crop is mainly cultivated under rain-fed conditions where precipitation is less than 900 mm annually. Winter wheat is more extensively grown than spring wheat, with the greatest areas of production primarily in the United States, Western Europe, the Balkans, southern USSR, and China. Spring wheat is grown in cold, dry areas unfavorable for winter wheat, such as the northern plains of the United States, the Canadian prairies, Argentina, and central and northern USSR. Spring wheat also is grown as a fall-sown crop in countries with mild climates, such as Mexico, Brazil, India, Australia, and southwestern United States.

Several species of wheat were cultivated during early agriculture, but in modern agriculture only common wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* L.) are important. Common wheats are more widely adapted than durum wheats and can be used in a diversity of food products, including bread, cookies, cakes, crackers, and noodles. Durum wheats are used for macaroni, semolina, and some flat breads.

In the United States and elsewhere, five main wheat market classes are designated. They include the four common wheat classes: hard red winter, hard red spring, soft red winter, and white (which includes club). Durum is the fifth market class. The production environment usually influences which market classes of wheat are grown. The United States consists of four main geographic areas, and certain market classes are more or less confined to these regions. Hard red spring and durum normally are grown in the northern plains and hard red winter is grown in the central plains. Soft red winter is mainly grown in the East and South, but some white wheats are grown in the northeastern United States. The U.S. West produces all classes, but white is the main class.

TYPES OF CULTIVARS

Mode of Propagation

Cultivated wheat is a monoecious plant with perfect flowers. It reproduces sexually as an autogamous or self-pollinated crop. Cross-pollination does occur, but it is usually less than 3%. Wheat is propagated from sexually produced seed, and apomixis does not occur. Single wheat plants can be separated into clones derived from different tillers to facilitate seed increase. Usually four or more clones per plant may be obtained. Such clones generally tiller less and suffer slightly higher mortality rates than whole plants (Allan, 1980).

Past and Current Cultivar Types

Because wheat is highly self-pollinated, it is true-breeding and the genetic identity of the seed is the same as that of the plant which produced it. Wheat cultivars have been developed primarily by three means: introduction, selection, and hybridization. Introduction of wheats grown elsewhere has been an effective means of cultivar improvement, particularly during early establishment of wheat production areas. Introduced cultivars famous in North America include 'Red Fife' (hard red spring); 'Turkey' (hard red winter), 'Mediterranean' (soft red winter); 'Sonora' (white); 'Little Club' (club); and 'Kubanka' (durum). Introduced wheat cultivars have had significant impact, even in recent times. Cultivars developed by the International Maize and Wheat Improvement Center (CIMMYT) have had notable success. Several famous CIMMYT wheat cultivars introduced to more than 25 countries included 'Pitic 62,' 'Sonora 64,' 'Lerma Rojo 64,' 'Inia 66,' 'Ciano 67,' and 'Siete Cerros.' During the 1970s, 'Siete Cerros' and its synonyms were grown in more than 20 countries.

Many of the wheats introduced many years ago represented landraces that were heterogeneous mixtures of genetically different strains. Because most landrace cultivars had been repeatedly reproduced, individual plant selections from within them were homozygous and their progeny had a high degree of uniformity. Many wheat cultivars were selected as off-type plants from introduced wheat cultivars during 1840 to 1940 in North America. Some of the more important U.S. cultivars that were selections within introductions included 'Fultz,' 'Trumbull' (soft red winter);

'Kanred,' 'Cheyenne,' 'Blackhull' (hard red winter wheats); 'Goldcoin,' 'Big Club' (white spring); 'Haynes Bluestem,' 'Glyndon Fife' (hard red spring); and 'Mindum' (durum). More recently, numerous selections have been made from CIMMYT wheats. Dalrymple (1978) identified 31 cultivars developed by such selection that were used in 13 countries during 1967 to 1974.

Most modern wheat cultivars were developed by artificial hybridization or crossbreeding. Crossbred wheats first became important around 1890. A. E. Blount, W. J. Spillman, and L. R. Waldron were among the first in the United States to develop crossbred wheat cultivars. Among their more successful cultivars were 'Gypsum,' 'Hybrid 128,' and 'Ceres.' Farmer-breeder S. M. Schindel produced 'Fulcaster' from a cross between 'Fultz' and 'Lancaster' in 1886. In 1903, the Canadian C. E. Saunders developed 'Marquis,' a famous crossbred hard red spring wheat. Another famous wheat hybridizer was William J. Farrer of Australia. During 1886 to 1906, he produced numerous crossbred cultivars of which his most famous was 'Federation.'

Three types of wheat cultivars currently are grown for commercial wheat production: pure-line cultivars, hybrid cultivars, and multilines. Numerous new pure-line cultivars are released each year. The 1984 *Wheat Newsletter* described over 70 pure-line cultivars developed or registered in 14 countries that year. Hybrid wheat cultivars are now being grown to a limited extent. Hybrid wheats are produced in the United States by the use of cytoplasmic-genetic male sterility and by chemical gametocides. The percentage of commercial wheat produced with hybrid cultivars is still small, but it has increased yearly, especially in the Great Plains. In 1984, three commercial seed companies marketed 20 hybrid wheat cultivars in North America.

Multiline wheats also are being produced on a limited basis in a few countries. One type of multiline is a seed mixture of morphologically similar pure-line components which differ genetically for resistance genes to one or more wheat diseases. A second type of multiline or blend is a seed mixture of distinct cultivars. In the United States, a few small seed companies and farmer cooperatives market blends of cultivars under a brand designation.

EXTENT AND NATURE OF BREEDING PROGRAMS IN NORTH AMERICA

Many public and private groups breed wheat in North America. This is particularly true in the United States. According to USDA Agricultural Research Service (USDA-ARS) information, 37 state agencies conduct wheat breeding programs, several of which are joint efforts with the

USDA-ARS (Briggle, 1985). Kansas, Oregon, Montana, Texas, Washington, Utah, Idaho, and North Dakota each have two or more wheat breeders who are employed by public institutions. When there are several public breeders in a state, each may have responsibility for a different wheat market class.

Private cultivar development has increased in the United States since the enactment of the Plant Variety Protection Act in 1970. There are over 30 private companies developing wheat cultivars in the United States. In recent years, these companies have produced and marketed over 200 pure-line cultivars, hybrids, and blends of wheat.

In Canada, public wheat breeding programs are conducted by provincial, federal, and university scientists. More than 20 different breeding programs are carried out for improvement of spring bread, spring soft, winter, utility, and durum wheats. Private wheat breeding efforts in Canada are restricted because there is no legal system for protecting the rights of ownership of new cultivars.

In Mexico, INIA (Instituto Nacional de Investigaciones Agricolas) and CIMMYT conduct cooperative wheat breeding research at several locations. CIMMYT is an international agricultural institute with large programs conducted on common wheat, durum wheat, and triticale (*X Triticosecale* Wittmark). CIMMYT has linkages with wheat programs in over 100 other countries. The Mexican environment permits efficient wheat breeding research. The crop season at low elevation sites located above 24°N latitude extends from November to May. The crop season of the high elevation sites below 20°N latitude extends from May to November. These contrasting crop seasons allow for two generations of wheat each year and facilitate selection for agronomic and disease problems associated with the two locales.

BREEDING OBJECTIVES FOR CULTIVAR DEVELOPMENT

Usually wheat breeders attempt to improve 10 to 30 different characters. The main traits are yield, quality, adaptation, pest resistance, and environmental stress tolerance. The improvement of the main traits of wheat has been facilitated by the study of their inheritance.

The polyploid make-up of cultivated wheat often has impeded the genetic analysis of many traits. Because the cultivated forms are allopolyploids, there are often genes with related functions on the homoecologous chromosomes. In spite of the complicating effect of polyploidy, there is considerable information on the inheritance of most of the principal wheat traits (McIntosh, 1983). The information mainly has been obtained in two ways. Conventional genetic analysis has been used for many qualitative and quantitative traits, and aneuploid analysis has been used to identify which chromosomes or arms of chromosomes carry a specific trait. Wheat has aneuploid collections unequaled by any other crop. There are complete sets of nullisomics, monosomics, trisomics, tetrasomics, and telocentrics. These stocks have greatly facilitated cytogenetic studies and the assignment of genes to linkage maps. Table 18-1 lists the gene number and mode of genetic expression of several important traits in wheat.

Yield

Grain yield is recognized as a main trait and many studies have been conducted on its inheritance. The consensus of these studies indicates that grain yield is a complexly inherited trait of low to moderate heritability and strongly influenced by the environment. Biometrical genetic analyses using diallel crosses and generation means have been numerous. Although the conclusions from such studies have sometimes been conflicting, most have indicated that grain yield is primarily controlled by genes with additive effects and smaller portions of inheritance due to epistasis and dominance effects. Researchers have attempted to clarify the inheritance of grain yield by studying the main components of yield: spikes per unit area, spike number, kernels per spike, and kernel weight. Biometric genetic studies of these yield components usually have given results parallel to those of grain yield. Although some studies have not been conclusive, the yield component approach sometimes has identified the most important components for a production area. Harvest index, the ratio of grain weight to grain plus straw weight, relates closely to yield capacity and receives attention by several breeders, especially in high-production environments. Harvest index is closely associated with semidwarfism.

In the past 30 years, breeding has consistently increased grain yield. The increase has been nearly linear, amounting to about 0.74% per year (Schmidt, 1984).

Quality

Nearly all modern wheat breeding programs consider quality to be a high priority. Wheat quality characteristics are numerous and complex. Breeding goals for quality usually are aimed toward achieving acceptable standards for the trade. New cultivars must meet minimum milling and flour quality criteria.

Breeding for quality traits is complicated by the many uses made of wheat. Quality factors of bread and pastry wheats differ notably, and

Table 18-1 Inheritance of Some Qualitative Characters in Wheat*

Character	Number of genes	Expression				
		Dominance	Epistasis	Complementary	Additive	Multiple Alleles
Spike type	3–4	X	X			
Anthocyanin pigment	3	X	X			
Awnedness	3–5	X	X			
Glume color	3	X	X			
Grass clump dwarfness	4	X		X		
Reduced height (semidwarf)	10	X			X	
Hybrid necrosis	2	X	X	X		X
Hybrid chlorosis	2	X		X		X
Genetic male sterility	2	X				X
Meiotic pairing	2	X				X
Red grain color	3	X			X	
Response to photoperiod	2	X			X	X
Response to vernalization	5	X	X		X	
Restorers for cytoplasmic male-sterile	6	X			X	
Glaucousness	2	X				X
Resistance to *Erysiphe graminis*	9	X				X
Resistance to *Puccinia graminis*	37	X	X			X
Resistance to *P. recondita*	30	X	X			X
Resistance to *P. striiformis*	10	X	X			X
Resistance to *Tilletia* spp.	11	X			X	
Isozymes	50+	X				X

*Gene number obtained mainly from information cited by McIntosh (1983).

quality factors of durum wheats are unique to themselves. The genetic improvement of milling and baking quality was delayed until suitable experimental procedures were perfected that could be used to evaluate large numbers of progeny that most breeding programs generate. Several useful micro, semi-micro, and semi-macro tests are available to evaluate the key quality traits. There are at least 32 tests used to evaluate common wheat quality and several others to evaluate durum wheat quality (Wrigley and Moss, 1968). The basis for wheat quality can be classified into four types of measurements that embrace most of the various tests that are used: kernel hardness, flour strength, flour stability, and flour stiffness.

Milling quality relates to kernel hardness. It is measured as the percentage of flour and the rate it can be extracted from whole grain during milling. The higher the percentage of flour yield and the faster it can be extracted from the grain are economically important factors for the miller. Hardness traits, such as break flour release, pearling index, and particle size are parameters affecting milling and baking. These traits have been found to be primarily under genetic control and respond readily to selection. Flour strength is closely associated with protein content and dough extensibility. It is mainly affected by environmental conditions and is not highly heritable. Flour stability responds readily to genetic improvement and can be measured by the mixograph and the farinograph tests. Flour stiffness depends to some extent on flour stability, and both stiffness and stability are aspects of protein quality, particularly gluten content. Gluten protein consists of gliadin and glutenin. The gliadin composition for a particular wheat genotype remains relatively constant over diverse environments. The gliadin proteins probably account for much of the baking differences observed among cultivars.

Considerable evidence has been gained by aneuploid analysis on the inheritance of wheat quality traits. This evidence indicates that chromosomes of the D genome are largely responsible for many of the baking quality attributes of bread wheat. Such properties as loaf volume, dough mixing characteristics, baking absorption, and milling characteristics are influenced by several chromosomes and are complexly inherited.

Considerable effort has been made to increase protein and lysine concentration of wheat grain, but both objectives have met with only limited success. Both traits generally have low heritability. Protein content is negatively correlated with grain yield and most modern cultivars differ little in total protein produced per unit area. Recurrent selection significantly increased grain protein concentration, but also gave a negative shift in yield (Loffler et al., 1983). The variability for lysine content has been rather narrow, and wheats high in lysine are almost always low in protein. After an exhaustive search among members of the primary wheat gene pool, a few promising parents were found. 'Atlas 66' and its derivatives are high for total grain protein and 'Nap Hal' is high in lysine content and moderately high for total protein.

Adaptation

Breeding for adaptation is usually a main consideration. Adaptive traits may be undefined for a production area, but by breeding for yield performance over time and space, cultivar adaptation is improved. Most breeders purposely choose experimental sites that represent the main agricultural environments of their respective production areas. Such sites may differ in rainfall, growing season, soil types, management practices or specific production problems. In the soft white winter wheat breeding program of the USDA and Washington State University, multiple-site trials are conducted. Diverse management practices are represented, such as irrigation, recropping after both legumes and small grains, wheat-fallow, various soil fertilization levels, and no-tillage. The sites vary from 120 to 210 frost-free days, 200 to 700 mm in rainfall and represent a diversity of soil types.

Many breeders from different U.S. states participate in uniform regional testing programs. Cooperators test their most promising advanced lines in regional interstate and intrastate nurseries. Performance in regional trials has been a key way to determine the adaptive properties of a potential cultivar. Similar regional or national testing programs are conducted by most major wheat-producing countries.

Adaptation is primarily a genetically complex trait. However, three major gene systems have had considerable impact on wheat adaptation. These gene systems are the reduced height or semidwarf (*Rht*) genes, the photoperiod response (*Ppd*) genes, and the vernalization response (*Vrn*) genes. Pugsley (1983) contends that these systems interact to the extent that their manipulation provides the main framework for adaptation of wheat to a wide array of agricultural environments. Qualset (1978) used these three gene systems as examples of quantitative traits that are controlled by major-effect genes, which also have an undetermined number of genes with small effects that facilitate broad adaptation of wheat.

The *Rht* semidwarf genes have contributed greatly to adaptation, as well as yield. The semidwarf wheats are efficient in partitioning photosynthate between straw and grain The phenomenal success and wide adaptation achieved by the CIMMYT wheats has been largely due to combining favorable semidwarf genes with photoperiod-insensitive genes. There are at least two major independent genes for response to photoperiod, each of which have several alleles (Klaimi and Qualset, 1973). Photoperiod insensitivity allows wheats to head and mature in short-day

Mediterranean type environments. Conversely, photoperiod sensitivity of wheats grown at extreme northern and southern latitudes coordinate the timing of reproductive growth with the period when the most optimum environmental conditions occur.

The vernalization response genes (*Vrn*) facilitate wheat adaptation to a range of climates. Different combinations of the *Ppd* and *Vrn* genes can provide the optimum heading date of wheat for a diversity of environments ranging from short-day tropical to long-day frigid. The genetic control of vernalization requirement is complex. Five different *Vrn* loci have been reported. Other workers report genes that act epistatically to one or two *Vrn* genes and either enhance or inhibit their effects.

Breeders developing wheat cultivars for distinctly different agricultural environments may use two different approaches to adaptive breeding. One strategy is to develop cultivars for a specific agro-ecosystem, such as irrigation or reduced tillage. With this approach, breeders may be able to reduce the number of traits with which they work. For instance, in the northwestern United States, wheat grown under irrigation has different production constraints than wheat grown under rain-fed or dry-land conditions. Irrigated wheat seldom is damaged by strawbreaker foot rot, cephalosporium stripe, snowmold, or dry-land root rot, and seedling vigor is not a problem. These can be serious limitations under rain-fed culture. In contrast, irrigated wheat must have high resistance to lodging and foliar diseases, which are minor problems under dry-land culture.

The second strategy for adaptive breeding is to select for broad adaptation or to develop wheat cultivars that perform well over diverse agricultural environments. This approach also has merit in wheat breeding. Because cultivated wheats are well-buffered polyploids, their makeup may allow for sufficient individual buffering or developmental homeostasis to be adapted to rather diverse environments. There are many examples of wheat cultivars that have broad adaptation, such as 'Centurk,' 'Nugaines,' 'Siete Cerros,' 'WW15,' 'Era,' and 'Blueboy.'

Pest Resistance

Pest resistance ranks high among a wheat breeder's objectives. The main effect of diseases and insects is reduction of yield or biomass. There are over 50 diseases of wheat that represent air-borne fungi, soil-borne fungi, bacteria, viruses, and nematodes. The diseases that are critical depend on the specific environment and the availability of alternate disease control measures. Genetic resistance has not been a viable control means for barley yellow dwarf virus, wheat streak mosaic virus, take-all (*Gaeumannomyces graminis* var. *tritici*), kernel bunt (*Neovossia indica*), dry-land root rot (*Fusarium* spp.) or cephalosporium stripe (*Cephalosporium gramineum*). For these diseases, either genetic resistance has not been identified or it is yet to be exploited.

Numerous arthropod pests attack wheat. In North America, over 30 species of insects and mites parasitize wheat. Genetic resistance to insects can be exploited for the Hessian fly (*Mayetiola destructor*), wheat stem sawfly (*Cephus cinctus*), cereal leaf beetle (*Oulema melanopus*), greenbug (*Schizaphis graminum*), and wheat curl mite (*Eriophyes tulipae*). As with breeding for disease resistance, permanence of insect resistance is a main consideration and biotypes of Hessian fly and greenbug have made it difficult to achieve lasting resistance.

The major diseases attacking wheat are the rusts, smuts, powdery mildew (*Erysiphe graminis* f. sp. *tritici*), speckled-leaf blotch (*Septoria tritici*), glume blotch (*Septoria nodorum*), take-all, strawbreaker foot rot (*Pseudocercosporella herpotrichoides*), black chaff (*Xanthomonas translucens* f. sp. *undulosa*), soil-borne wheat mosaic, wheat streak mosaic, barley yellow dwarf virus, and cereal cyst nematodes (*Heterodera avenae*). The rusts, powdery mildew, and most of the smuts show a high degree of specialization. Many physiological races have been determined for the pathogens causing leaf rust (*Puccinia recondita* f. sp. *tritici*), stem rust (*Puccinia graminis* f. sp. *tritici*), stripe rust (*Puccinia striiformis*), powdery mildew, dwarf bunt (*Tilletia controversa*), common bunt (*Tilletia caries*, *T. foetida*), loose smut (*Ustilago tritici*), and powdery mildew. Resistance to these highly dynamic pathogens frequently is simply inherited and produces hypersensitive reaction types. This type of resistance generally has had short-lived usefulness because virulent strains of the pathogen eventually appear. The inheritance of specific resistance to biotypes of the rusts, smuts, and mildew generally has been shown to be monogenic, dominant or partially dominant, and often complicated by epistatic effects.

Because the effectiveness of specific resistance is usually temporary, attention has been directed toward breeding for long-lasting resistance. This type is often called durable, nonspecific, or general resistance. To qualify as general resistance, the resistance must be effective against all variants of the pathogen. Genotypes with general resistance may slow or reduce the rate of development of the pathogen. Lines that are slow to rust or mildew or that allow for only partial smutting of their spikes often have general resistance. The inheritance of general disease resistance in wheat is not well documented. Some studies have shown that general resistance may be either simply or complexly inherited with genes imparting large and small effects. Heritability of general resistance is usually low to moderate.

Resistance to soil-borne wheat mosaic is controlled by one or two genes and can be selected readily. In contrast, attempts to breed resistant cultivars to wheat streak mosaic and barley yellow dwarf virus have met with limited success. Genotypes expressing partial resistance to the virus vectors and to the viruses have been identified.

Resistance to speckled leaf blotch seems to be simply inherited, but quantitative inheritance and additive gene effects have been reported. There may be no true resistance to glume blotch, but some cultivars exhibit tolerance. Its inheritance is largely unknown, although quantitative inheritance and additive gene effects have been suggested.

Wheat cultivars with very good resistance to strawbreaker foot rot have been bred in Europe, but most U.S. cultivars lack resistance. The main sources of resistance are from the common wheat, 'Cappelle Desprez,' and from lines that obtained resistance from *T. ventricosum*. Genetic studies indicate both simple and complex inheritance of resistance. Monosomic analyses showed that at least four chromosomes affected reaction to foot rot. The resistance of 'Cappelle Desprez' is located on chromosome 7A. Other studies report that resistance of several *T. ventricosum* derivatives is due to a single dominant gene.

The distant relatives of wheat, referred to as alien sources, have begun to make significant contributions to disease resistance (Knott and Dvorak, 1976). Alien sources, including various species of *Aegilops*, *Secale*, and *Agropyron*, have been used to gain genetic resistance to three rusts, common bunt, wheat streak mosaic, and foot rot.

Introduction of alien variation into wheat has been greatly facilitated by its tolerance for aneuploidy. Synthetic amphidiploids and chromosome addition and substitution lines may be used to bridge between the alien source and common wheat. The desired trait may be translocated to a wheat chromosome by ionizing radiation or by suppression of the *Ph* diploidization gene which allows some homoeologous chromosomes to pair and affect crossing over between the chromatids of wheat and the alien line.

Tolerance is reported to exist to a number of wheat diseases including rusts, powdery mildew, cephalosporium stripe, glume blotch, barley yellow dwarf virus, and cereal cyst nematodes. Few breeders purposely breed for tolerance to diseases, probably because it is difficult to evaluate and usually involves measurement of yield and detailed disease notes.

Tolerance to Environmental Stress and Weather-Induced Loss

Many environmental stresses and weather-induced losses affect wheat, but an individual breeder might only need to contend with a few. Important ones include damage caused by temperature extremes, drought, flooding, grain shatter, lodging, preharvest sprouting, stand failure, and nutrient imbalance caused by aluminum, manganese, and sodium toxicity.

Breeding for tolerance to stress environments may be complicated and elusive. Approaches may be either direct or indirect (Lewis and Christiansen, 1981). Indirect selection pressure undoubtedly occurs in performance trials conducted in the area of production where stress conditions exist. In the direct approach, breeders deliberately choose test sites that represent stress conditions reliably and uniformly. Wheat breeders have been successful in breeding for some environmental stresses. There has been considerable improvement in breeding wheats adapted to cold environs. In the Northern Great Plains of the United States and Canada, fall-sown wheat cultivars have moved into production areas previously limited to spring wheat cultivars.

Wheat cold hardiness is quantitatively inherited, and by consistent selection pressure on breeding material, genetic gain for enhanced cold tolerance has been realized. Cold hardiness is genetically complex, but selection for components of cold hardiness has been helpful. Selection for deep crown formation, slow spring growth recovery, prostrate growth, and low crown water content has improved cold hardiness of wheat. These traits generally are quantitatively inherited, although crown depth seems to be controlled by two major genes.

There has been considerable success in selecting wheats tolerant of acid soils and aluminum toxicity. Aluminum and acid soil tolerance have been reported to be controlled by one to three genes with major effects and several polygenes (Foy, 1983). Genotypes with tolerance to Al can be selected readily by using lab tests or by growing them in strongly acid field soils.

Improving stand establishment capabilities has been extensively studied, but genetic gain has been limited, especially among semidwarf cultivars. Little progress has been made in developing wheats with tolerance to heat, flooding, salt, alkaline soils, or reduced tillage. Some genotypes seem to have low or partial tolerance to some of these maladies. Several sources for tolerance to these problems belong to the secondary and tertiary wheat gene pools, and transfer of their tolerance to cultivated wheat has yet to be effected.

Breeding for resistance to preharvest sprouting has met with some success. Genotype differences exist, but none has complete resistance to sprouting damage under prolonged periods of rain. Although resistance to sprouting is environmentally sensitive, selection for high seed dormancy, certain plant morphological traits, and reduced rate of water uptake by wheat spikes are factors that respond to selection and impede preharvest sprouting.

Wheats highly resistant to shattering and lodging have been bred. The inheritance of resistance to lodging has been shown to be controlled by genes with major and minor effects. The main strategy for limiting lodging has been by reducing plant stature. The various *Rht* genes of wheat reduce plant height by about 10 to 50%. They are simply inherited, some act additively, and they vary in expression from recessive to partially dominant. Genes with minor effects control culm diameter and straw strength. Shatter resistance is a trait that has responded to cyclical breeding and selection. Wheat gene pool members range from completely free threshing to completely hulled types; hence, the needed genetic variability has been available to the breeder.

Summer drought in semiarid regions has been successfully avoided by selection for early heading. This approach is ineffective once maximum plant productivity is matched with maximum seasonal precipitation. Glaucousness (waxiness) of wheat leaves, stems, and spikes may be a positive attribute for yield in dry-land environments. The glaucous trait apparently is controlled by major and minor genes.

STEPS IN CULTIVAR DEVELOPMENT

Three types of wheat cultivars are currently being developed. They are pure lines, multilines, and hybrid wheats. Procedures for developing each type differ somewhat and warrant separate discussion.

Pure-line crossbred cultivars are by far the most common of the three kinds. The development of pure lines and the other two kinds of cultivars begins with a plan that should include: (a) the need for a cultivar, (b) identification of traits to be improved and some knowledge as to their inheritance, (c) choice of parents, and (d) selection of a breeding approach.

In gathering information, breeders often rely on their judgment as to the current limitations of existing cultivars for user acceptance, yield potential, adaptation, and disease resistance. Wheat producers are a good information source. Their preferences should not be ignored, because many cultivars fail due to lack of farmer acceptance. The literature should be consulted to determine if a trait is amenable to genetic manipulation. It may be necessary to conduct preliminary genetic studies prior to breeding. Because priorities sometimes change, breeding plans should be flexible. Production constraints and user preferences may fluctuate in their relative importance over time. By having a comprehensive program that addresses most main problems and by approaching them by more than one strategy, the breeder's efforts are apt to remain relevant to changing needs.

The main steps in pure-line cultivar development are choosing the parents for development of genetic variability, development of pure lines, and pure line evaluation, purification, and release. The choice of parents, whether two or several, is extremely important because the genetic differences between the parents ultimately affect the spectrum of genetic recombinations obtained among the offspring.

Hybridization of the parents is the next step, the mechanics of which are discussed later. Hybridization is the main means of obtaining genetic variability for all of the principal wheat breeding procedures. It allows the breeder to advantageously exploit the ingredients of mendelian genetics, which are segregation, recombination, linkage, dominance and epistasis. The development of the new cultivar begins with union of the parental germ cells to form the F_1 hybrid. The F_2 generation represents the key generation because it contains the total potential genetic variability of the cross.

The next step involves choice of a breeding procedure. Because wheat is self-pollinated, procession toward pure-line development occurs automatically in wheat after hybridization. Self-pollination ensures intensive inbreeding, which leads to high levels of homozygosity. For each generation of selfing, the percentage of heterozygous individuals decreases and the percentage of homozygous individuals increases.

Evaluation or testing of candidate pure-line cultivars occupies the major part of the breeder's time and resources. Wheat breeding procedures differ primarily in the amount of evaluation that takes place as populations attain homozygosity.

Because breeders contend with traits that are either genetically simple or complex, they need to design their evaluation procedures to handle both types of traits. Complex genetic traits, such as yield and quality, are undoubtedly regulated by many genes and strongly influenced by the environment. That is why it is necessary to conduct yield and quality tests during several crop years at different sites and under diverse management practices. Simply inherited traits, such as spike type and plant height, do not require extensive and repeated evaluation.

Pure-line cultivars must be purified before they are released. Although wheat is self-pollinated, there is the likelihood that off-types may be present in the seed stock as it undergoes testing. It is the breeder's job to remove off-types. The usual way to do this is by selecting typical plants or spikes, growing them out in a block, and comparing them for genetic uniformity.

The development of multilines is similar to that of pure-line cultivars. Multilines are mixtures of two or more components which are actually pure lines of wheat. The components of multilines may be isolines, related lines, or actual cultivars. Breeding, testing, and increase procedures for these multiline components are very similar to those followed for pure-line cultivars.

The concept of multiline cultivars was put forward over 30 years ago as a way to effect lasting disease resistance to highly dynamic pathogens, such as the rust fungi. Actual development of multilines for commercial production has been very limited. The unpopularity of multilines is probably due to several reasons. Their development takes considerable time and resources. Their worth as a means of managing resistance genes has not been extensively tested. Because they are mixtures of pure lines, multilines may not be readily accepted by seedsmen as an alternative to highly uniform pure-line cultivars.

Production of hybrid wheat requires a means to alter the wheat flower so that it can be readily cross-pollinated rather than self-pollinated. This can be done on a mass scale by either the cytoplasmic male-sterile method (CMS) or the chemical hybridization agent method (CHA). Both methods require the development of male and female lines. For the CHA method, the considerations and procedures are nearly the same as for those of pure-line cultivars, although emphasis on selection for specific traits for hybrid wheat parents may be quite different than for those of pure-line cultivars. Breeding of lines for use in the CMS method is more complicated than for the CHA method and requires development of three different types of lines: (a) a CMS line or female; (b) a fertility restoring line or male; and (c) a maintainer line used to perpetuate the female line. These two hybrid wheat systems are described in more detail in the section on breeding procedures.

SOURCES OF GENETIC VARIABILITY

Types of Parents and Populations

Wheat has the largest gene pool of cereals and is notable for its diversity. It belongs to the Triticeae tribe of the Gramineae or grass family. This tribe includes seven genera in each of the subtribes Hordeinae and Triticinae. There are at least 27 species of *Triticum* with ploidy levels of 14, 28, and 42 chromosomes (Feldman and Sears, 1981). Harlan (1975) described three subgene pools of wheat. Primary gene pool members cross readily with one another and consist of all *Triticum* species. A large secondary gene pool consists of *Secale*, *Haynaldia*, some species of *Agropyron*, and former genus designated as *Aegilops*. A tertiary gene pool comprised of *Hordeum* and several species of *Agropyron* and *Elymus* represent potential useful variability. Successful hybrids have been made between *Triticum* with certain genotypes of *Hordeum*, *Elymus*, *Taeniatherium*, *Agropyron*, *Haynaldia*, *Secale*, and *Eremopyron* (Table 18-2). Table 18-3 lists the cultivated forms of wheat and several representative wild *Triticum* species. Ploidy levels and the key genomes of *Triticum* are indicated.

Both common and durum wheat are allopolyploids. Common wheat is a hexaploid with 42 somatic chromosomes and durum wheat is a tetraploid with 28 somatic chromosomes. Of the hexaploids, four variety groups are cultivated: *T. aestivum*, *T. compactum*, *T. spelta*, and *T.*

Table 18-2 Genera of the Tribe Triticeae Which Have Been Successfully Hybridized with Triticum*

Subtribe	Genus	Number of Species	Ploidy Level (x = 7)	Growth Habit† Peren.	Peren./Annu.	Annu.	Mode of Pollination Cross	Cross/self	Self	Distribution
Hordeinae	*Hordeum*	25	2x–6x		X			X		Worldwide
	Elymus	60	2x–12x	X				X		Worldwide
	Taeniatherum	2	2x			X			X	Mediterranean Basin Central Asia
Triticinae	*Agropyron*	100	2x–10x	X			X			Worldwide
	Haynaldia	2	2x, 4x		X		X			Mediterranean Basin Central Asia
	Secale	6	2x		X		X			Mediterranean Basin Central Asia
	Eremopyrum	5	2x, 4x			X			X	Mediterranean Basin Central Asia
	Triticum	27	2x–6x			X		X	X	Mediterranean Basin Central Asia

**Source:* Data from Feldman and Sears (1981).

†Peren. and Annu. refer to perennial and annual growth habits, respectively.

Table 18-3 Classification of Cultivated Wheats and Closely Related Wild Species*

Species	Genomes†	Common Name	Use
Diploid species (2n = 14)			
T. monococcum var. *monococcum*	*AA*	Einkorn	Cultivated
T. monococcum var. *boeoticum*	*AA*	Wild einkorn	Wild
T. dichasians	*CC*	—	Wild
T. tauschii	*DD*	—	Wild
T. comosum	*MM*	—	Wild
T. speltoides	*SS*	—	Wild
T. umbellutum	*UU*	—	Wild
Tetraploid species (2n = 28)			
T. turgidum L. var. *dococcon*	*AABB*	Emmer wheat	Cultivated
T. turgidum L. var. *durum*	*AABB*	Durum wheat	Cultivated
T. turgidum L. var. *turgidum*	*AABB*	Poulard wheat	Cultivated
T. turgidum L. var. *polonicum*	*AABB*	Polish wheat	Cultivated
T. turgidum L. var. *carthlicum*	*AABB*	Persian wheat	Cultivated
T. turgidum L. var. *dicoccoides*	*AABB*	Wild emmer	Wild
T. timopheevii araraticum	*AAGG*	—	Wild
T. cylindricum	*DDCC*	—	Wild
T. ventricosum	*DDMM**	—	Wild
T. triunciale	*UUCC*	—	Wild
T. ovatum	*UUMM**	—	Wild
T. kotschyi	*UUSS**	—	Wild
Hexaploid species (2n = 42)			
T. aestivum L. var. *aestivum*	*AABBDD*	Common wheat	Cultivated
T. aestivum L. var. *spelta*	*AABBDD*	Spelt wheat	Cultivated
T. aestivum L. var. *compactum*	*AABBDD*	Club wheat	Cultivated
T. aestivum L. var. *sphaerococcum*	*AABBDD*	Shot wheat	Cultivated
T. syriacum	*DDMM*SS**	—	Wild
T. juvenale	*DDMM*UU*	—	Wild
T. triaristatum	*UUMM*MM**	—	Wild

*Much of the information in this table was obtained from Feldman and Sears (1981).

†Genomes designated by * are modified.

sphaerococcum. Of these, *T. aestivum* is the largest and most extensively cultivated variety group, but club, spelt, and shot wheat are grown in some regions (Table 18-3). Durum wheat is the chief tetraploid; additional tetraploids known as emmer, poulard, polish, and persian wheats were once cultivated, but they are no longer important.

The exact origin of wheat remains incomplete, although it is known that cultivated durum and common wheats evolved through amphiploidy. The center of origin and diversity of the genus *Triticum* is southwestern Asia, primarily the Fertile Crescent. Tetraploid emmer wheat originated before hexaploid wheat from hybridization of the wild diploid *T. monococcum* L., donor of the A genome, and an unknown diploid, probably of the Sitopsis section which was the donor of the B genome. Durum wheat presumably originated from cultivated emmer by several sequential mutations that reduced glume toughness to the point of free threshing (Feldman, 1976). Hexaploid *T. aestivum* probably originated soon after the domestication of the diploid and tetraploid forms. Wild Emmer (*T. turgidum* L. var. *dicoccoides*) with the *A* and *B* genomes probably repeatedly hybridized with forms of *T. tauschii*, the *D* genome donor. The addition of the *D* genome expanded the range of cultivated wheat beyond the Near East to continental climates. Spontaneous mutations of *T. aestivum* forms apparently gave rise to *T. compactum* and *T. sphaerococcum*. The origin of *T. spelta* is still uncertain.

Several countries maintain wheat collections. The International Board for Plant Genetic Resources lists 15 countries committed to long-term storage of wheat germ plasm. The USDA-ARS Wheat Small Grains Collection has over 39,000 accessions. About 50% of the accessions are landraces, 25% are of breeders' lines or cultivars, and the rest are undetermined. These stocks are available to bonafide wheat breeders at no cost. The documentation and evaluation of these collections are mostly incomplete. Portions of the USDA-ARS wheat collection have been evaluated for reaction to rusts, smuts, powdery mildew, glume botch, speckled-leaf blotch, Hessian fly, cereal leaf beetle, greenbug, and wheat stem sawfly. A part of the collection has been classified for heading date, growth habit, awn expression, and straw, chaff, awn, and kernel color.

The choice of parents for hybridization is an important decision that all wheat breeders must make. Precise guidelines for parent selection are lacking. However, several general principles are used. When making two-way crosses breeders generally choose at least one locally adapted parent so that a portion of the progeny of the cross also will be well adapted. A breeder's own material often is a good source of potential parents. It is accessible and perhaps the best evaluated germplasm available for the environment of interest. The other parent has one or more desired traits lacked by the well-adapted parent and it may or may not have adaptive traits as well. As a rule, the best basic parents are nearly always good cultivars or near-cultivars because their breeding value and phenotype are correlated. However, outstanding combinations cannot always be predicted by parental performance. Invariably, some crosses between good parents give poor progeny. Foreign wheat germplasm sometimes produces immediate potential utility for improved yield and adaptation. The most useful foreign sources often derive from places with environments similar to that of the breeder's area of responsability (Simmonds, 1979). This has been strikingly borne out by the near universal adaptation of Mexican-bred CIMMYT wheats to nearly all torrid zone countries.

Knowledge concerning the inheritance of the desired traits greatly enhances wise parent selection. For instance, several reduced height (*Rht*) genes give nearly identical phenotypes. If the breeder knows the *Rht* genes of the parents, crosses can be planned to produce progeny that will express either maximum or minimum variability for plant height.

Population Development by Hybridization

Populations used to develop crossbred wheat cultivars range from simple two-parent (P) crosses to complex populations with several parents. As dictated by breeding objectives, many breeding programs exploit the full array of crosses, e.g., two-way (P1 × P2), three-way (P1 × P2) × P3, four-way [(P1 × P2) × P3] × P4, backcross (P1 × P2) × P1 and complex crosses of many parents. Whatever the type of population a breeder uses, the parents must collectively embrace the necessary genetic diversity to allow for desired recombinant progeny to be obtained. Some breeders tend to restrict their crossing among indigenous lines that represent their most recent successes, a situation that could lead to narrowing of the genetic base and reduction of long-term genetic gain. Breeding approaches to avoid narrowing of the gene base will be discussed in the section Breeding Procedures, Recurrent Selection.

Wheat is relatively simple to hybridize manually. Crosses can be made either directly in the field or in environmentally controlled facilities. Crossing nurseries in the field are planted in easily accessible locations. Wide within- and between-row spacing of plants simplifies handling of material during hybridization and enhances plant growth. Artificial lighting may be used in the field to induce photoperiod-sensitive wheats to flower in short-day environments. Adequate supplies of water and soil nutrients are needed for normal floral development and successful hybridization.

When wheat plants are grown in greenhouses or growth chambers, photoperiods of 14 to 16 hours with mean daily radiation values of 6×10^6 J/m^2 provide optimum conditions for seed set. Proper lighting is essential 1 to 5 weeks prior to anthesis. Temperatures between 15 to 20°C during the day and 10 to 15°C at night are optimal for fertilization and kernel development.

Winter wheats require vernalization. When held 6 to 8 weeks outdoors at temperatures of 1 to 10°C, most wheat strains will vernalize. Seeds on moist filter paper in Petri dishes will usually vernalize after 6 to 10 weeks storage in a refrigerator held at 3 to 7°C and given an 8- to 10-hour photoperiod.

The inflorescence of wheat is a determinate composite spike (Fig. 18-1). Spikelets are alternately arranged on the rachis. Each spikelet has two bract-like empty glumes that enclose two to nine florets. The outer parts of each floret consist of a lemma and a palea. They enclose the sex organs which are three stamens, a pistil, and two lodicules (Fig. 18-1). Each stamen comprises a filament and an anther. The pistil consists of an ovary with two short styles and a branched feathery stigma. The uppermost and lowermost spikelets of a wheat spike are often nonfunctional, as may be one or more of the upper florets of each spikelet.

Flowering generally begins midway on the spike and proceeds upward and downward. The primary floret develops first, the secondary is next, and the tertiary is last. The florets within the spikelet often flower on successive days. Anthers may dehisce inside the floret, but as much as 80% of the pollen may be shed outside the florets (Allan, 1980).

The only tools needed for artificial hybridization are forceps and scissors. If the two parents have contrasting alleles for useful marker genes, the female parent to be emasculated should have the recessive allele. This will help to confirm successful hybridization. Useful morphological wheat traits are listed by McIntosh (1983).

Choice of spikes for emasculation requires care. Emasculation should be timed 1 to 3 days before normal anthesis. Anthers should be well developed and light green, but not yellow or cream. The stigmas should be nearly fully developed. A check of spikelets in the middle of the spike will help determine its floral development stage. One to three of the basal and upper spikelets may have nonfunctional flowers and should be excised. All but the primary and secondary florets of the remaining spikelets are removed. This is done by gently pulling the tertiary floret downward and outward with the forceps. Awns are removed with scissors. Anthers can be removed from each floret by inserting the forceps between the lemma and palea and spreading them. The three anthers are removed carefully with the forceps to avoid crushing them or injuring the stigma. Emasculated spikes should be immediately covered with a glassine bag or wrapped with bond typing paper. Another emasculation procedure involves removal of the upper one-third of each floret by cutting it off with scissors to expose the sex organs. Forceps are used to remove anthers from the top of the floret. This method works well in cool, humid environments.

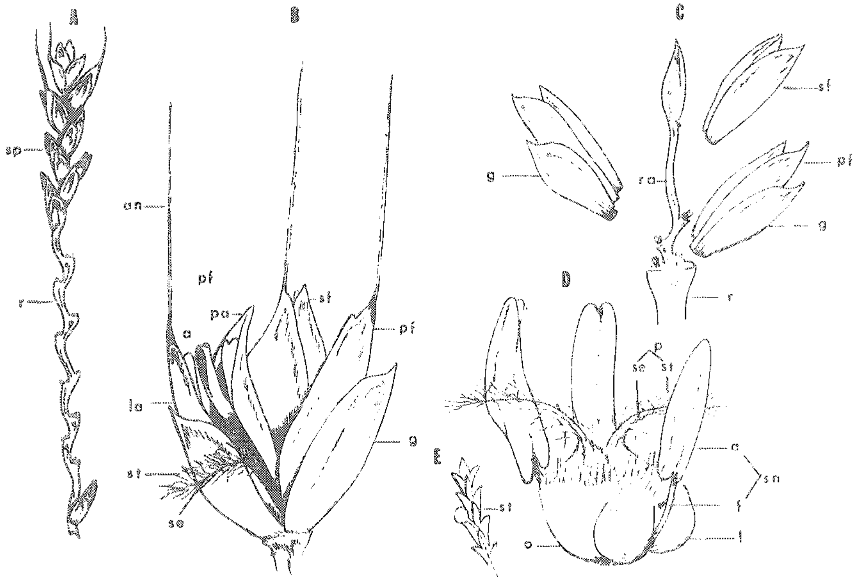

Figure 18-1 Wheat spike and parts. (A) Wheat spike with several spikelets (sp) removed, showing rachis (r). (B) Wheat spikelet showing primary floret (pf) and secondary floret (sf), awn (an), lemma (la), palea (pa), anther (a), stigma (st), style (se), and glume (g). (C) Wheat spikelet (sp) showing sterile glumes (g), primary florets (pf), secondary florets (sf), rachilla (ra), and rachis (r). (D) Organs of a wheat flower including the pistil (p), stigma (st), style (se), ovary (o), stamen (sn), anther (a), filament (f), and lodicule (l). (E) Close-up of stigma (st) and a pollen grain.

Wheat flowers may be pollinated 2 to 4 days after emasculation. Florets should have well-developed, feathery stigmas when they are pollinated. Spikes with suitable pollen exhibit a few freshly extruded anthers, and mature pollen may be obtained from florets of spikelets adjacent to those with extruded anthers. Anthers are removed with forceps from the florets just before anthesis. If male spikes need to be saved, anthers are removed from florets and transported immediately to the female in the crease of the hand or in a small petri dish. If the male spike is not needed for production of selfed seed, it can be detached from the plant and taken to the female spike.

Pollen can be applied several ways. The standard method is to remove the bag from the female spike, grasp (with the forceps) an anther that has just begun to shed pollen, and brush it on the stigmas. One good anther can be used to pollinate three to four florets. When pollen is abundant, the pollination procedure is repeated to increase seed set. Two other ways to pollinate female spikes are the twirl and approach method (Allan, 1980). The twirl method is rapid and can be mastered quickly. The top of the bag covering the female spike is cut off and a pollinating male spike is inverted into the bag parallel to the female spike. The male spike is vigorously rotated by twirling its peduncle between the thumb and forefinger, and the bag is resealed. The approach method usually gives high seed set and can be used effectively during bad weather. In this method, the female spike is positioned slightly below the male spike and both spikes are covered with a bag. Detached male spikes can be kept alive to shed pollen for 2 or more days by placing their culms in water. Novice breeders have better success with the approach method than with the anther transfer or twirl method.

After pollination, the spike is recovered immediately to minimize accidental pollination. Paper tags are used to record the cross number, the parents, dates of emasculation and pollination, and the worker's initials.

Wheat hybrids may be made by using parents with genetic and cytoplasmic male sterility, although their use is still infrequent. Several sources of genetic sterility are now available. Male-sterile female spikes are identified at anthesis and bagged. They can be pollinated by the same procedures already described. Procedures have been outlined for utilization of both recessive (Driscoll, 1983) and dominant (Sorrels and Fritz, 1982) genetic male-sterile systems.

Mutagenesis

After years of intensive research that yielded few tangible accomplishments, mutation breeding in wheat has begun to make a significant impact. Mutation breeding is now being used to complement other wheat breeding approaches, rather than as a stand-alone approach to wheat breeding.

Ionizing radiation, ultraviolet light, and chemical mutagens have all been used successfully for mutation breeding in wheat. Ionizing radiations (X-rays, gamma rays, thermal and fast neutrons) may be used on wheat seeds. Ethyl methane sulfonate (EMS) and diethyl sulfate (DES) are effective chemical mutagens for wheat which pose minimal safety hazards.

Several wheat cultivars have been developed exclusively by mutation breeding (Konzak, 1985). Examples include 'Els' (France), 'Sharbati Sonora' (India), 'Stadler' (United States), 'Nanjing No. 3' (People's Republic of China), 'Novosibrskaya 67' (USSR), 'Shirowase-Komugi' (Japan), 'Ruso' (Finland), 'Caroline' (Chile), and 'Castelnuovo' (Italy). A number of other cultivars have been developed using induced mutation and cross-breeding.

Evaluations of mutagenized materials are generally made in the M_2.

The size of M_2 population to screen is difficult to determine. However, a skilled person can visually screen in one season several hectares of M_2 or M_3 wheat for several traits (Konzak, 1984). The main traits of wheat for which useful mutations have been secured include changes in morphology, physiology, reproductivity, chemical composition and disease resistance. Desired morphological changes that have been obtained include reduced height, spike type, plant form, awnedness, glume shape, grain size, and grain color. Beneficial physiological induced mutations include early maturity, photoperiod insensitivity, response to vernalization, and male sterility. Mutations have been obtained for increased protein and lysine content, as well as increased glaucousness of wheat spikes, stems, and leaves. Resistance to leaf, stem, and stripe rust has been induced in wheat. The male-sterile recessive mutant Cornerstone is used extensively to facilitate recurrent selection, and a scheme has been proposed for its use to produce hybrid wheat. A dominant genetic male-sterility mutant was induced in a *T. aestivum* stock carrying *T. tauschii* cytoplasm.

Some of the most potentially useful mutants have been several reduced plant height (*Rht*) mutants in wheat. None of the *Rht* mutants dwarf the coleoptile or the first foliar leaf, hence they do not adversely affect seedling vigor and stand establishment, as is the case with the naturally occurring Rht_1, Rht_2, and Rht_3 semidwarf genes..

It is likely that wheat mutation breeding will continue to be used. It has been shown to be of special value to augment natural variability. The best way to use mutation breeding is as a complementary method to other traditional breeding approaches.

BREEDING PROCEDURES

The normal sequence of approaches used for wheat improvement in a particular production area has been (a) introduction of landrace cultivars, (b) selection within introductions, and (c) hybridization among selections. Direct introduction may still hold potential, particularly when the introductions are made from well-established wheat breeding programs to programs just being established and where the two programs have common production environments and limitations.

Hybridization is the key feature of backcrossing, pedigree, single-seed descent, bulk, recurrent selection, and composite-cross breeding methods. They will be addressed here primarily for their utility for obtaining specific wheat breeding goals. Almost no wheat breeding programs follow exactly the same breeding procedures. This diversity of approaches is desirable because it lends stability to wheat improvement and lessens the danger of different wheat programs developing genetically similar products with mutual genetic vulnerabilities.

Backcrossing

Backcrossing is a breeding method used to transfer one or a few genes from one parent or cultivar to another parent or cultivar. Often the parent that is to receive the desired genetic trait possesses a high preponderence of desirable genes for other traits. Backcross-derived wheats have most frequently represented cultivars to which genes for specific resistance to a particular disease have been added. For example, stem rust resistance and common bunt resistance were added to 'Baart' to produce 'Baart 38.' Genes for stripe rust (Yr_7), leaf rust (Lr_9), and stem rust (Sr_6) were backcrossed into 'Lemhi' to produce 'Lemhi 66.' The leaf rust gene Lr_{24} and stem rust gene Sr_{24} were added to 'Parker' to produce 'Parker 76.' The semidwarf gene Rht_2 and a stripe rust gene were added to 'Omar' to produce 'Paha.' The development of 'Baart 38' cultivar by the backcross method is outlined in Table 18-4.

The advantages of backcross breeding are its simplicity and predictability. Progress may be increased by making additional backcrosses in the greenhouse or in winter nurseries. Backcrossing works best for simply inherited traits. Most important wheat traits are genetically complex and are not easily manipulated by backcrossing. The opportunity to recover progeny that transgress both parents for a complexly inherited trait is low in backcrossing. The recurrent parent imposes a genetic ceiling for most important traits that are polygenically controlled. In practice, few wheat breeders rely on the backcross method alone. Rather, it is used to develop improved parental lines, to produce components for multilines, or to eliminate defects of otherwise useful genotypes.

Pedigree Selection

Because wheat is an autogamous crop, it is well suited to pedigree or line breeding. In its strictest sense, the pedigree method involves alternate parent-progeny testing commencing with the F_2 generation and continuing to advanced generations. This system yields accurate progeny performance records and allows for direct progeny and parent comparisons. In the pedigree system, the breeder selects several hundred F_2 plants and grows 10 to 50 progeny plants from each of these. In the F_3, several plants or spikes are selected from the best $F_{2:3}$ lines. In the F_4 and subsequent generations, the same procedure is followed. Table 18-5 illustrates the development of the cultivar 'Compton' by the pedigree method.

A high percentage of segregates may be discarded in the pedigree system. This may be good or bad depending on how a particular trait is inherited. If heritability of the trait is low or controlled by additive or recessive genes, selection in early generations may actually discard useful genotypes.

Table 18-4 Development of 'Baart 38' Cultivar by the Backcross Method

Year	Nursery	Generation	Activity*
1930	Spring		Original 'Hope' × 'Baart' cross was made and 20 seeds were obtained.
1931	Spring	F_1	BC_1 made to 'Baart' and 49 seeds were obtained.
1931	Summer	BC_1F_1	Rust test; three heterozygous resistant BC_1F_1 plants were used for BC_2 to 'Baart' and 66 seeds were obtained.
1932	Spring	BC_2F_1	All 60 plants were used for BC_3 to 'Baart' and 904 seeds were obtained.
1932	Summer	BC_3F_1	Rust test; 31 heterozygous resistant BC_3F_1 plants were selected.
1933	Spring	BC_3F_2	Without rust test, 405 BC_3F_2 plants were selected on basis of agronomic characters.
1933	Summer	BC_3F_3	Rust test; 180 BC_3F_3 plants were selected from homozygous resistant $BC_3F_{2:3}$ lines.
1934	Summer	BC_3F_4	$BC_3F_{2:4}$ lines were subjected to rust; 14 plants were selected for BC_4 to 'Baart' and 240 seeds were obtained.
1935	Spring	BC_4F_1	Twenty-eight plants were selected for BC_5 to 'Baart 35'† and 588 seeds were obtained.
1935	Summer	BC_5F_1	Two hundred and ninety plants were selected.
1936	Spring	BC_5F_2	Plants were inoculated with bunt; 1056 bunt-free BC_5F_2 plants were saved.
1936	Summer	BC_5F_3	Rust test; 1056 $BC_5F_{2:3}$ lines in three row blocks were grown; 340 were homozygous for stem rust resistance.
1937	Spring	BC_5F_3	Remnant seeds of the 340 stem-rust-resistant lines were used to test for bunt resistance. The 157 lines homozygous for bunt resistance were bulked as 'Baart 38.'

*Source: Data from Hayes et al. (1955).
†'Baart 35' is a bunt-resistant strain of 'Baart' developed independently from 'Martin' × 'Baart'[7].

Rigid pedigree breeding is slow, labor intensive, and tedious for large numbers of crosses or their progenies. Several breeding programs handle their hybridized populations in some procedure which represents a combination of pedigree and bulk breeding. A popular method is the F_2 progeny bulk system. In this method, F_2 plants or spikes from F_2 plants are selected and grown as plant or head rows the next season. In the F_3 to F_5 generation, selection is done on a row basis. The entire row rather than a few plants are harvested each generation and a sample of this bulk seed

Table 18-5 Development of the 'Compton' Cultivar by the Pedigree Method

Year	Generation	Activity*
1966–1967		Single cross was made between two elite breeding lines, IN5879-189-3 × IN6111E5-5-3. These lines were selected from a series of crosses involving 20 cultivars and breeding lines.
1967	F_1	F_1 plants were vernalized and three plants were transplanted in the spring; each plant was harvested separately.
1968	F_2	About 1250 plants were grown; 44 plants based on resistance to leaf and stem rust, early maturity, and short-stiff straw were selected.
1969	F_3	Forty-four $F_{2:3}$ lines were grown and evaluated for agronomic type. Seven lines were selected and the rows were cut individually in bulk. Diseases did not occur, so plant selections were not made.
1970	F_4	Seven $F_{2:4}$ lines were grown and evaluated for reaction to leaf and stem rust, maturity, and agronomic type. Thirty-one plants from three lines were selected.
1971	F_5	Eighteen $F_{4:5}$ lines with the best seed appearance of the 31 plants selected in 1970 were grown. Twenty plants were selected from 4 of the 18 lines. Selection was based on resistance to leaf and stem rust, a low expression of brown necrosis, and better agronomic type. The lines were tested for reaction to Hessian fly biotypes B and D.
1972	F_6	Three $F_{5:6}$ lines with the best seed appearance of the 20 plants selected in 1971 were grown. The two best lines in agronomic type were harvested separately in bulk. The lines were retested for resistance to Hessian fly biotype B.
1973	F_7	Two $F_{5:7}$ lines in a disease nursery were grown, and one was selected. The line was cut in bulk for preliminary yield trials.
1974	F_8	The selection was multiplied for preliminary yield trials.
1975–1976	F_9,F_{10}	Preliminary yield trials of the F_5-derived line were conducted for 2 years. Trials were conducted at one location with two replications each year. Plot size was 1.5 m^2. Disease data included seedling resistance to leaf and stem rust and adult plant resistance to *Septoria tritici* and powdery mildew. Agronomic data included winter hardiness, height, maturity, straw strength score, yield, test weight, and grain quality.
1977	F_{11}	Five F_{11} plants were selected from the line.

Year	Generation	Activity*
1978	F_{12}	The five F_{11}-derived lines were multiplied. Disease reactions and agronomic type were observed.
1979	F_{13}	Four lines were tested in preliminary yield trials, as described for the F_9 and F_{10} generations. One hundred spikes for head row multiplication were selected from the line designated 6728A3-22-4-2-1-2.
1980	F_{14}	One hundred head rows were grown and observed for disease reaction and agronomic type; 78 of 100 rows were composited for breeder seed.
1981	F_{15}	Composited seed of 6728A3-22-4-2-1-2 was multiplied.
1980–1983		The line was tested in advanced nursery yield trials, with three or four replications at one location. The bordered plots had a harvest area of 1.9 m^2.
1981–1983		The line was tested (a) in intrastate drill plots at four or five locations with four replications (plot size was about 0.013 ha) and (b) in the regional uniform Eastern Soft Red Winter Wheat Performance Nursery at about 18 to 20 locations per year.
1982		Breeder seed of the line was multiplied.
1983		Foundation seed of the line was multiplied. The line was named 'Compton' and released to the Indiana Certified Seed Producers.

**Source:* Data from Patterson (1985).

is sown the succeeding generation. The system permits the tracing of a line back to a specific F_2 plant. It has the advantage of not needing to grow out individual progeny each generation. With this method, there is less likelihood of discarding favorable genotypes in early generations. Because the F_2 progeny rows are bulk-harvested, there usually is sufficient seed to start evaluations of quality, adaptation, and yield earlier than with the conventional pedigree system.

Single-Seed Descent

The single-seed descent system recognizes that extensive genetic variability is expressed among F_2 individuals in a population. Other breeding procedures tend to lose some of this variability via natural and artificial selection. With single-seed descent, the objective is to get through the early generations rapidly. The method capitalizes on growing more than one generation per season in the field, greenhouse, growth chamber or in winter nurseries. The mechanics of the system require growing out a large number of F_2 plants and selecting one seed from each plant. These seeds are bulked to form the F_3 population from which one seed is again selected from each plant and bulked to form the F_4.

Strict single-seed descent has not become popular among wheat breeders. In the case of winter wheats and long-day wheats, it is bothersome to use artificial vernalization and supplemental photoperiod to grow populations in controlled environments. When single-seed descent is attempted in the field, the risk is high that poor stands may occur. Genetic drift can result if a significant proportion of the original F_2 population is lost. Selecting single kernels of wheat is slow and tedious.

Some wheat breeders prefer to use a single-spike descent method, also referred to as a single-hill procedure of single-seed descent. One spike is harvested from each F_2 plant, which is usually maintained as a separate line thereafter. About 10 to 30 seeds from each F_2 plant are sown in pots in the greenhouse or in hills in the field and a single spike is harvested from the line to be used for the next generation of selfing. Spike selection is fast and allows the breeder to keep a seed reserve in case of incomplete vernalization, poor emergence, winterkill, and hail. The procedure requires more space than strict single-seed descent, but gives the breeder more flexibility and helps ensure that progeny of each F_2 plant will survive to the selection generation.

Some wheat breeders use a combination of single-spike descent and early-generation selection. If the opportunity arises for advantageous selection for a particular trait, such as rust resistance or semidwarf stature, they may choose to advance only lines possessing the desired trait. Once the F_5 to F_7 has been reached, a large number of lines can be subjected to selection for most traits, regardless of their heritability. Table 18-6 outlines the development of the cultivar 'Manning' by the modified single-spike descent method.

Bulk Breeding and its Modifications

In the bulk breeding method, an F_2 population of several hundred plants is grown. The larger the F_2 population the better. Populations are harvested in bulk, and a sample of the seed is used to make a similar planting the following year. This cycle can be repeated several times, at least until the F_5 generation when a high degree of homozygosity would prevail and individual plant selections could be made. Table 18-7 outlines the development of 'Weston' cultivar by the bulk method.

Table 18-6 Development of the 'Manning' Cultivar by the Modified Single-Spike Descent Method

Year	Generation	Activity*
1967		Single cross was made between two elite breeding lines. Obtained about 20 F_1 seeds.
1968	F_1	Grew 12 space-sown F_1 plants. Bulk harvested seed from all plants with no selection.
1969	F_2	Grew about 3000 space-sown F_2 plants. Selected about 400 spikes from plants of medium short height with bronze, awned, inclined spikes. Bulk threshed selected spikes.
1970	F_3	Grew about 3000 spaced-sown plants from F_3 seed inoculated with composite of common bunt races. Selected about 300 spikes from agronomically acceptable plants expressing resistance to common bunt and stripe rust and bulk threshed them.
1971	F_4	Repeated procedure of F_3.
1972	F_5	Repeated procedure of F_4.
1973	F_6	Grew about 3000 spaced-sown F_6 plants. Two spikes each were selected from approximately 300 F_6 plants with emphasis on the same criteria used in the F_2 to F_5. The spikes were threshed individually.
1974	F_7	Seed of one spike from each pair was sown at two sites. Site 1 provided reaction to dwarf bunt and site 2 gave agronomic observations. About 50 of the $F_{6:7}$ lines were selected based on disease reaction, agronomic appearance, protein content. Each selected line was bulk harvested.
1975	F_8	The 50 $F_{6:8}$ lines were grown in unreplicated four-row plots. Yield, test weight, milling and baking quality were used to select the line UT 89099.
1976–1978	F_9–F_{11}	UT 89099 ('Manning') was tested in intrastate and regional performance tests.
1978		Plant rows to obtain breeder seed of 'Manning' were produced from 200 F_{10}-derived spike selections taken from plants judged to be true to type. Uniform rows were composited.

**Source:* Data from Dewey (1985).

Bulk breeding may be used to accomplish specific objectives in a wheat breeding program. Natural selection is the key feature of this method and the individuals that survive in bulk populations are those that are the most competitive. Whether this competitiveness will necessarily correlate with agronomic worth will decide if bulk breeding is compatible

Table 18-7 Development of 'Weston' Cultivar by the Bulk Method

Year	Generation	Activity*
1966		Crossed 'Bezostaja' to an elite breeding line. Important attributes of 'Bezostaja' were stiff straw, high yield, and strip rust resistance. The elite breeding line, a selection from the cross 'Burt' × PI 178383 gave resistance to stripe rust, dwarf bunt, and common bunt.
1967	F_1	Grew about 20 F_1 plants. The hybrid was impressive for stiff straw and stripe rust resistance. Bulk harvested seed from all plants.
1968	F_2	Grew a F_2 population of about 3000 plants and bulk harvested their seed.
1969	F_3	Grew a F_3 block of about 3000 plants at one location. Severe snowmold and other wet soil maladies reduced stands. Seeds of the surviving plants were bulk harvested.
1970	F_4	Planted early and late sown plots of 2000 to 4000 plants each at one site. Undefined wet soil problems reduced stands. Seeds of surviving plants were bulk harvested.
1971	F_5	Plots were sown at three sites. Each plot consisted of 2000 to 3000 plants. Snowmold severely reduced stands at two sites, but had minor effect at the third site. From each site, about 200 spikes were selected from vigorous plants.
1972	F_6	From about 600 spikes, 180 spikes were selected based on kernel type and their progeny were sown. Seven of the $F_{5:6}$ lines were selected based on stripe rust resistance, vigor, straw strength and overall agronomic appearance. The selected lines were bulk harvested.
1973	F_7	Planted the 7 $F_{5:7}$ lines in unreplicated four-row plots at one site. Harvested two lines based on overall agronomic appearance.
1974	F_8	The two $F_{5:8}$ lines (Sel. 55-19 and Sel. 55-20) were placed in replicated performance trials at several sites. One site in southeast Idaho experienced severe snowmold damage and dwarf bunt infection. Sel. 55-19 and Sel. 55-20 rated better than most other germplasm for resistance to these two diseases. Seed from the southeast Idaho site of both lines was bulk harvested.
1975	F_9	Continued replicated performance trials of both Sel. 55-19 and Sel. 55-20. Quality tests indicated Sel. 55-20 was superior to Sel. 55-19.
1976	F_{10}	Replicated performance trials were continued at multiple sites. Increase plots of Sel. 55-19 and Sel. 55-20 were made at a high elevation site. Only Sel. 55-20 matured in time to be bulk harvested.
1977	F_{11}	Replicated performance trials were continued at multiple sites. A second increase of Sel. 55-20 was made at a site with a long growing season. The seed of this increase was bulk harvested as breeder seed of 'Weston'.

**Source:* Data from Pope (1985).

with the breeding goals. Bulk breeding is an ideal way to handle crosses between spring and winter wheats. At Pullman, Washington, spring types are eliminated if spring × winter populations are sown in the fall because they cannot survive the winter. Winter types do not undergo vernalization, fail to set seed, and are eliminated when spring × winter wheat populations are sown in the spring.

Wheat breeders must sometimes deal with intangible problems that manifest themselves infrequently or whose cause is so poorly understood that informed selection for the trait is not possible. In such instances, bulk breeding may be a useful approach. Examples in wheat include breeding for resistance to cold injury or sprout injury in areas where these problems may occasionally be severe, but occur infrequently. The materials can be carried in bulk until the appropriate conditions prevail, at which time natural selection should favor the survival of the most resistant genotypes.

Bulk populations of wheat can be selected readily for spike type, plant height, awn expression and kernel color. In fact, some selection may be necessary to preserve the desired genetic traits. When bulk populations contain plants that have opposite alleles for plant height, awn type, and spike type, only a few semidwarf, club, or awnless plants may survive until the F_6. The bulk population can be subdivided into several phenotypic groups, such as semidwarf, nonsemidwarf, club spike, and lax spike, to prevent the loss of less competitive genotypes.

Artificial mass selection with self-pollination can be used with the bulk method, sometimes referred to as the selected-bulk method. Bulks may be mechanically separated for seed weight and size. They can be harvested at two or more height levels to separate tall, medium, and short plants.

Lines generally are derived from bulk populations in the F_5 to F_8. When using a combination of random and selected-bulk breeding, Qualset and Vogt (1980) advocate selecting individuals in the F_5. They found there is actually little genetic gain past the F_4 for this breeding procedure.

Recurrent Selection

The breeding procedures already described mainly fit short-term goals of cultivar development. Wheat breeders also need to have long-term goals for future germplasm improvement. Several ways have been described to broaden the genetic base of wheat breeding populations. They are referred to as parent building, prebreeding, and evolutionary breeding. All represent a form of recurrent selection, which is a cyclic process alternating between selection and hybridization. Recurrent selection has had limited use in wheat breeding, but it should gain more general use in the future.

When recurrent selection is used by wheat breeders, they may not make all possible intermatings among parents of a given cycle or they may delay selection in one or more generations to get sufficient seed to evaluate lines for yield or quality. Recurrent selection has been used successfully in wheat to increase grain protein content, reduce heading date, lower strontium content, and increase tillering, seed weight, and test weight (Avey et al., 1982; Busch and Kofoid, 1982). Qualset and Vogt (1980) suggested using recurrent selection to enhance inherent yield capacity with little consideration for its stability. They suggested that backcrossing to adapted parents could be used to eliminate defects.

A form of recurrent selection called the diallel selective mating system (DSM) was suggested by Jensen (1970). He proposed this system to overcome several inherent deficiencies of the commonly used approach of selection in two-parent crosses. The two-parent system is characterized by narrow genetic variability, low recombination potential, and intensified linkage blocks, whereas the DSM system provides for broad use of germplasm, exploitation of recombination, release of genetic variability, breakage of linkage blocks, and creation of gene pools (Jensen, 1978). In spite of the strong arguments proposed for the DSM system, very few wheat breeders have used the method.

Development of Hybrid Wheat

Several companies produce commercial hybrid wheat in the United States, but no public institutions are engaged in its commercial production. Commercial hybrids are produced by the CMS and CHA methods. The CMS method was the first system developed, and is the most complicated in terms of breeding. The CMS system requires three different lines. The female parent, or A line, is male sterile due to a factor carried in its cytoplasm. The A line's female sex organs are functional, but not its male sex organs. The male line, or R line, is used to cross-pollinate with the female line to produce hybrid seed. The R line has one or more nuclear genes which override the CMS trait of the A line. It is the male-fertility restoration trait that allows F_1 hybrid wheat plants to function autogamously to produce a normal crop. In the CMS system, only the F_1 hybrid population would have normal seed set. If a farmer were to plant seed from an F_1 hybrid, it could be highly undesirable because the F_2 would segregate for male sterility and perhaps for numerous other plant traits that could adversely affect performance. Because the F_1 hybrid seed is the only generation suitable for planting, the seed dealer is assured of repeated sales.

The third component of the CMS system is the maintainer line for an A line, known as the B line. The nuclear constitution of the B line would be nearly identical to that of its A line. The B line possesses normal, rather than male-sterile cytoplasm. In the current CMS system, the cytoplasm that imparts male sterility comes from the wild species, *T. timopheevi*.

In the sequence of developing B and A lines, the breeder first develops a normal pure line that serves as the B line. Because this line has normal cytoplasm and is male fertile, it may be bred by procedures identical to the development of conventional wheat cultivars. It should possess the usual attributes expected of pure-line cultivars. In addition, B lines must have good combining ability to make suitable hybrid parents. The B line should possess traits that enhance its ability to serve as an effective pollinator of its A line. This may require selection for degrees of anther extrusion and of pollen shedding duration. Once suitable B lines are produced, A lines are developed by backcrossing. The stock with *T. timopheevi* cytoplasm becomes the female and repeated backcrosses are made using the B line as the male and recurrent parent. Winter nurseries and greenhouses can be used to speed A line development.

R lines of CMS hybrids must have two key attributes. First, they must combine well with one or more A lines to produce a superior hybrid. Second, the R line must function as a potent restorer of the CMS trait. R lines also have the cytoplasm of *T. timopheevi*, but they function as self-fertile plants because they have male-fertility restoration genes that overcome the CMS trait. The development of dependable R lines that consistently restore male fertility over diverse environments has been an elusive problem to breeders of CMS hybrid wheat. Dependable restoration is multigenically controlled, and background genes often mask restoration. R lines require more breeding attention than do B and A lines. As with the A and B lines, they must have a balance of all of the genetic traits that affect productivity, adaptation, and quality. To ensure that they possess potent restorer genes, R lines must be test crossed to a number of A lines and their F_1 hybrids must be carefully observed for complete self-fertility. The restoration effectiveness of R lines must be checked with test crosses at multiple locations for several years. Test crosses can give preliminary performance data on yield, disease reactions, and quality, and help identify those combinations worthy of large-scale tests.

Dominance is extremely important in hybrid wheat. If a desired trait such as rust resistance or semidwarf height is completely dominant, only one parent may need the desired allele for it to be expressed in the hybrid. If the trait is expressed as a recessive or partially dominant trait, then both parents need the desired alleles to ensure expression in the F_1 hybrid. For example, most genes for common bunt resistance are recessive. If A and R line parents each have single but different genes for resistance, the F_1 would be susceptible to the fungus. Both parents must have the same allele of one or both genes to express resistance. The Rht_1 and Rht_2 semidwarf genes are weakly dominant. Hybrids between one parent with a gene for semidwarfness and another that is not semidwarf usually have excessive plant heights and straw weights. Productive hybrids usually have parents with at least one semidwarf gene in common.

CHA hybrid development is less complicated than that of CMS hybrids and should be faster. For the CHA method, appropriate parents must be developed and tested in various combinations to identify the hybrids with the best performance. The parents are developed by procedures identical to conventional pure-line wheat breeding. Parents also must have attributes that facilitate cross-pollination. Female lines require floral structures conducive to cross-pollination. Tendencies toward cleistogamy are selected against. Males need to shed profuse amounts of pollen for extended durations. As with the CMS hybrids, thorough knowledge concerning parental genotypic makeup for disease resistance, morphological traits, and other criteria would help identify the best hybrid combinations.

Thorough testing of both CMS and CHA hybrids is essential. The performance of wheat hybrids cannot be predicted from their parental performances, except for a very few traits. The section on seed production, later in this chapter, deals with the mechanics of hybrid seed production.

Development of Multilines

Multilines are mixtures of pure lines of wheat. The pure lines can be isolines, related lines, or cultivars. Normally, isolines and related lines are used as components of multilines to provide resistance to an airborne disease, such as stripe rust.

Isoline components of multilines are developed by the backcross method. Ideally, several genetically different sources of specific resistance to the disease pathogen would be selected as donor or nonrecurrent parents. They are crossed to a recurrent parent which lacks specific genes for disease resistance. The recurrent parent should excel for agronomic traits, adaptiveness, and quality. Most specific genes for disease resistance are dominant, hence backcrossing may progress rapidly. Winter nurseries or greenhouse facilities would shorten the time required to develop components. The number of components contained in a multiline depends on the availability of different genes for resistance. Eight components usually is considered a minimum. Table 18-8 outlines the development of 'Crew,' a multiline comprised of three cultivars and seven near-isolines, each developed by backcross breeding.

A criticism of multilines made up of closely related isolines is their conservativism. These multilines are normally structured for single disease resistance. CIMMYT breeders have undertaken a composite-cross multiline approach involving over 500 cultivars in crosses with 'Siete Cerros,' a widely-adapted spring wheat (Rajaram and Dubin,

Table 18-8 Development of 'Crew' Multiline Wheat

Year	Activity
1967	Crossed stripe rust susceptible cultivar 'Omar' (P1) to nine stripe rust resistant parents: 'Webster' (P2), 'Spaldings Prolific' (P), 'Falco' (P4), 'Ibis' (P5), 'Ministre' (P6), Sel. 2629 (P7), 'Druchamp' (P8), *T. spelta*/'Coastal' (P9) and Sel. 3602 (P10). The resistant parents putatively had different gene(s) for resistance.
1968	BC_1 made to 'Omar' on F_1 plants of the nine populations.
1969	Grew BC_1F_1 plants of nine populations. Made BC_2 to 'Omar' on 20 to 30 stripe resistant BC_1F_1 plants of populations with resistance from P9 and P10.
1970	Grew BC_1F_2 progeny of the P2 to P8 populations. Selected 300 to 400 spikes from each population. Grew BC_2F_1 plants with P9 and P10 resistance and bulk harvested each population separately.
1971	Inoculated $BC_1F_{2:3}$ spike rows of the P2 to P8 populations with a composite of stripe rust races. Selected 10 to 25 resistant rows from each population and crossed them to one of two stripe rust susceptible lines, Sel. 68342 (P11) or Sel. 68749 (P12). P11 and P12 were near-isolines of the 'Omar'-type with one gene for semidwarfness. Grew BC_2F_2 populations with P9 abd P10 resistance and made 300 to 400 spike selections from each.
1972	Grew BC_2F_1 plants of the P2 to P8 populations and bulk harvested each population separately. Grew about 300 $BC_2F_{2:3}$ spike rows of the P9 population. Selected 25 lines with stripe rust resistance and crossed them to P12. Grew 300 $BC_2F_{2:3}$ spike rows with P10 resistance and selected 57 which were stripe rust resistant, awnless, club spike, and one-gene semidwarf.
1973	Grew BC_2F_2 plants of the P2 to P8 populations. Selected 200 to 300 spikes from plants with phenotypes of awnless, club spike, and one-gene semidwarf. Grew BC_3F_1 plants with P9 resistance and bulk harvested their seed.
1974	Grew $BC_2F_{2:3}$ spike rows of populations with resistance derived from the P2 to P8 parents and inoculated them with race CDL-1 of stripe rust. Selected 15 to 35 lines with stripe rust resistance, club spike, and one-gene semidwarfness. Grew F_2 plants of BC_3 with P9 resistance and selected 300 spikes.
1975	Grew single 2.6-m^2 plots of 15 to 35 $BC_2F_{2:4}$ lines of the P2 to P8 and P10 populations at one site. Bulk harvested the plants within plots of three to eight lines from each population which had the resistant (R), moderately resistant (MR), or intermediate (I) type of stripe rust reaction. Plant types were awnless, club spike, and one-gene semidwarf with white kernels. Grew about 300 $BC_3F_{2.3}$ spike rows with P9 resistance and selected 40 lines with R reaction to stripe rust and the desired phenotype.
1976	Grew 40 $BC_3F_{2.4}$ lines with resistance derived from P9 in single 2.6-m^2 plots. Bulk harvested plants within plots of five lines with R reaction to stripe rust.

Table 18-8 *continued*

Year	Activity
1977	Tested three to eight BC_2-$BC_3F_{2.5}$ lines of the P2 to P10 populations with stripe rust resistance in a yield test of four replications at one location. Conducted initial quality tests. Checked seedling stripe rust reaction to two races.
1978	Tested two to four BC_2-$BC_3F_{2.6}$ lines of each of the nine populations in replicated performance tests at four locations. Selected one line from each population based on its agronomic and quality performance. Selected lines were morphologically similar.
1979	Composited equal amounts of seed by volume of nine BC_2-$BC_3F_{2.7}$ lines which obtained stripe rust resistance from P2 to P10. Included the cultivar 'Faro' in the composite. 'Faro' is a one-gene semidwarf with the Yr_{10} gene for stripe rust resistance derived by backcrossing to 'Omar'. The composite of the nine lines and 'Faro' was designated WA 6472.
1980–1982	WA 6472 was tested extensively in replicated intrastate and regional performance trials during this period. In October 1982, it was released to growers in Idaho and Washington as the 'Crew' multiline.

1977). The 500 cultivars were chosen for their diverse origins and proven resistances to four airborne diseases. The system involves multiple double crosses between 'Siete Cerros' and the disease-resistant parents. Backcrossing is avoided. Disease resistant segregants are saved that are phenotypically similar to 'Siete Cerros.' The scope of the double-cross multiline approach allows for development of cultivars with plant-to-plant heterogeneity for multiple disease resistance and lessens the problem of a narrow genetic base associated with backcrossed-derived cultivars.

Components of multilines require evaluation for yield, quality, and other important criteria. This is especially true if the number of backcross generations is low. Alternate components for multilines should be developed continuously so they can be substituted for components that are susceptible to new and prevalent disease races.

There are two very different philosophies concerning deployment of multilines. The two strategies are called the "clean-crop" and the "dirty-crop" approach. In the clean-crop approach, all components of the multiline would be resistant to all prevalent races of the disease to be controlled. If a component becomes vulnerable to a new race, it is replaced by a new resistant component. The clean-crop approach attempts to retain complete resistance to the disease pathogen.

In the dirty-crop approach, the components of the multiline also have a single gene for resistance, but none of the lines is completely resistant to all races of the pathogen. Dirty-crop multilines may become partially rusted. Dirty-crop multilines may act to stabilize the race structure of the pathogen. Many different races would have opportunity to survive, and because the components have only single resistant genes, the surviving population of the pathogen should be composed mainly of simple races. Selection pressure for races for multiple genes for virulence should remain low. This phenomenon is called stabilizing selection. Arguments favoring one or the other approach are mainly theoretical and probably will not be resolved until multiline production becomes of sufficient quantity to actually test the theories.

Components of blends may be pure-line cultivars or advanced breeding lines. Their development is identical to procedures used to develop pure-line crossbred cultivars. For components of blends to be compatible, they usually need to have similar plant heights, maturity dates, and threshing characteristics. Blends comprised of components with different morphological traits may not be acceptable to farmers. Therefore, components usually are similar for spike type, awn expression, and straw and glume color.

The yield of blends generally approaches the average of the individual yields of their components. Often the difference is a 1 to 5% increase in yield in favor of the blend. Blends may have utility when no single pure-line cultivar has all the needed traits to ensure optimum production over unpredictable environmental conditions. In such instances, blends can reduce risk and minimize yield fluctuations. Some farmers in the state of Washington blend the cultivars 'Stephens,' 'Daws,' and 'Lewjain' to cope with unpredictable seasonal vagaries. If the winter is mild and the summer dry, 'Stephens' usually yields best. If the winter is cold, 'Daws' normally yields best. When the season favors foliar and soil-borne disease, 'Lewjain' yields best. This three-cultivar blend often yields better than one or two cultivars each season and occasionally yields equal to the best cultivar.

Most studies on blends in wheat and other small grains indicate that they often outyield their component means, but very seldom exceed the yield of the highest component. Blends frequently are more stable for yield than their average component, but they are seldom more stable than their best component. It is unlikely that the use of wheat blends will increase, but they may have value for short-term emergencies.

FIELD-PLOT TECHNIQUES FOR GENOTYPE EVALUATION

Wheat breeders often use different approaches for yield evaluation. There is considerable interaction between grain yield and the environment. Because environment strongly affects yield, tests must span several years over diverse environments to identify which lines are genetically superior for yield.

The grain yield the farmer obtains is on a per-unit-area basis, and selection for yield in a breeding program is only effective when measured on that basis. Yield cannot be evaluated on a single-plant basis (Knott, 1972).

Wheat breeders do not agree on when to begin to evaluate lines for yield potential. Some breeders advocate early-generation testing beginning with progeny of F_2 plants, whereas others delay selection until the F_5 or later generations. Many studies have been made on the value of early testing for wheat grain yield. Most studies concluded that early-generation testing had limited value and usually did not correlate closely with yield performance in later generations (Knott, 1979). This is not surprising because the heritability of grain yield is moderate to low. Most studies of genetic variance reveal that yield is mainly controlled by additive effects which could be masked in early generations by dominance and epistatic effects.

A typical approach of wheat breeders is to select for highly heritable traits in the F_2 to F_4 and begin replicated yield tests in F_5 to F_7. Traits such as photoperiod response, semidwarfism, awn expression, shatter resistance, harvest index, and numerous disease reactions generally have moderately high heritabilities and are amenable to early-generation testing. These traits all directly or indirectly affect yield. By emphasizing selection of these traits in the early generations and delaying selection for yield until later, a greater proportion of the lines placed in the initial yield tests are agronomically acceptable and more seed is available for testing.

There is a possible disadvantage by delaying yield selection until the F_5 to F_7 because some useful genetic variability for yield may be inadvertently lost, even with single-seed descent. The evaluation of F_2-derived lines in the F_3 is the earliest time that sufficient seed could be obtained to conduct yield tests on a plot basis. Perhaps the main reason against early-generation testing is the lack of evidence that it is effective.

Nature of Environments Utilized

The number of locations and replications breeders employ for yield tests vary due to personal philosophy and the specific situation. The greatest source of variability in yield is caused by genotype × year interactions, followed by genotype × location interactions. Ideally, breeders should opt for more yield tests spread over seasons than over locations within a season. This is seldom feasible because additional years delay cultivar development.

Some breeders conduct their initial yield evaluation at one site and others make their initial tests at multiple sites. Often this decision depends on seed availability and resources. In environmentally diverse production areas, breeders frequently begin initial yield tests with F_3- or F_4-derived lines, which they test at multiple sites. Additional sites are favored over increased replications per site. Several breeders initially yield test their lines in single replications at multiple sites, but often at least two replications per site are included. When one site is used for the initial yield test, it should be the one most typical location of the production area.

After the initial yield test, the number of sites and replications and the size of plots usually are increased. For instance, in the USDA-ARS soft white wheat program of Pullman, Washington, the initial yield and observation tests of 500 to 700 F_4-derived lines in F_5 are conducted in one replication at each of five sites in 0.3 m^2 plots. At one site, a single plot of 5.5 m^2 is grown for seed increase and for yield, test weight, and quality evaluation. For the second year of testing, between 50 to 100 F_4-derived lines in F_6 are advanced to yield tests at eight sites. Entries are replicated five times at each site and plots are 3.0 m^2. The third year of testing includes 20 to 40 lines evaluated at 13 sites. Plot sizes and replications are the same as the second year. Several of these same lines may be concurrently placed in the Western White Wheat Regional Nursery which is grown at 20 sites in four states. One to four promising lines may be entered into 26 tests of the cooperative extension programs of two states.

The yield-test environments should collectively sample or represent the production area. The more variable the wheat production area, the more test sites are required. In western North America and elsewhere, production environments are extremely diverse due to differences in rainfall, elevation, growing season, soil type, and management practices. These variables often differ within small geographic locales. The major management practices used by farmers must be represented. In the northwestern United States, this would include annual crop, wheat fallow, no-till, and irrigation. In contrast, large areas in the U.S. Great Plains are more environmentally uniform and require proportionately fewer test sites.

Plot Types

The most common plot type used for wheat yield evaluation consists of one or more rows. Hill plots also have been used for the initial yield tests on a limited basis. Yield evaluation in hill plots may be feasible for some environments, but its utility should be evaluated thoroughly for the specific situation before its adoption. Although spacing between hills varies, 30- to 75-cm spacing is typical. Seeding rates range from seed of one spike (0.6 to 1.0 g) to 5.0 g.

Row plots are sown at seeding rates comparable to those used commercially. For wheat, this can vary from 40 to 200 kg/ha. Although single-row plots are sometimes used, interplot competition may occur which can bias an entry's performance. Planting a common border between the individual rows or separating rows by 0.6 to 0.9 m reduces interrow competition. Another way to reduce interplot competition is to sort genotypes into gross physio-morphological classes, such as dwarf, semidwarf, normal, club spike, lax spike, and heading date.

When sufficient seed is obtained, most wheat breeders opt for using plots of multiple rows with rows interspaced at distances comparable to those used by farmers. Such plots usually consist of 3 to 10 rows. Multiple-row plots have border rows that minimize interplot competition. The border rows can be removed prior to harvest. Some breeders do not remove border rows, but harvest the entire plot. They are willing to accept some error caused by interplot competition to gain the savings in time and labor. If border rows are not removed, grouping genotypes into physio-morphological classes should be employed. Most wheat breeders use plot sizes varying from 0.7 to 6.0 m^2, with the most common size about 3.0 m^2.

The number of new entries chosen for yield evaluation each year varies among wheat breeding programs, and depends on available resources, type of selection method, and the breeder's personal philosophy. The numbers may range from 50 to 1000 lines. If a large number of lines are to be yield tested, they may be subdivided into several separate tests that contain a common check or checks to allow for comparison between tests. Useful subgroups are dwarf, semidwarf, normal; clubs, commons; and early, medium, and late maturity.

Experimental Designs

Wheat breeders use both complete-block and incomplete-block designs. They often employ different designs for their initial and advanced yield tests. For the initial tests, three frequently used designs are randomized complete-block, incomplete-block or lattice, and systematic designs. Randomized complete-block designs are used mainly when moderately few lines, usually less than 100, are evaluated and when intratest variability is reasonably low. When large numbers of lines are evaluated for initial yield performance, some type of lattice design frequently is used. Lattice designs usually reduce experimental error compared with complete block designs, especially when there are many entries and intratest variability is large. Some breeders employ systematic designs for the initial yield evaluations. A common practice is to replicate each genotype once or twice at one or more test sites. Often a common check cultivar is repeated frequently throughout the test to facilitate direct comparisons to neighboring lines being evaluated.

A more elaborate nearest-neighbor analysis has been described recently (Wilkinson, et al., 1983). This design features a moving-block type of error control and is claimed to be more efficient on the average than complete block or incomplete block experiments. LeClerg (1966) has provided a comprehensive review of experimental designs as they apply to plant breeding.

Considerations in Data Analysis and Use

Efficient data management is an important part of wheat breeding and essential for yield tests. Rapid and accurate analysis of yield data is a necessity in winter wheat breeding programs where the time between harvest of current year yield trials and planting of the yield trials for the next year may be only a few days. A computerized data system enhances the efficiency of wheat breeding. For any system to be useful, its format should be structured to facilitate future analysis, summarization, and decision making. A good system needs to be consistent, accurate, and give rapid output. It needs to be able to collate yield data across tests and summarize all the key criteria the breeder uses for saving or discarding lines. Several computerized record systems, which vary in degree of sophistication, are now available. Some systems do nearly all phases of record keeping, including printing notebooks, pedigrees, bag and stake labels, randomization, and seed inventory. Notes often are recorded in field books and entered later into the computer. Some breeders use portable data entry devices taken directly to the field. Many breeders now obtain yield weights on electronic scales that automatically access the yields into a computer. A few breeders have computerized scales mounted directly on their combines.

The breeder who contemplates use of the computer for records and data analysis should become familiar with several proven systems. Computers will increase efficiency, but they should be used wisely so that the intuitive insight of the breeder is not lost.

Equipment Utilized for Field Operations

Most equipment used for tillage, seed bed preparation, and fertilizer and herbicide application is identical to that used by farmers. The equipment breeders use to sow, tend, and harvest yield trials is for the most part modified and miniaturized versions of commercial machines. Scaleddown equipment helps to ensure a good relationship between experimental results and performance in commercial situations.

Several innovative machines have been developed by plant breeders or commercial manufacturers for use as seeders and harvesters of wheat yield plots. Seeders used for experimental yield trials need to have several characteristics. Before obtaining an experimental seeder, breeders should determine which devices perform satisfactorily for their particular wheat production area. They must give moderately uniform seed distribution, sow plots of variable size at different seeding rates, and clean out entirely between plots. Their design must facilitate rapid sowing of multiple plots without error. This may be accomplished by preloading seed containers in the laboratory in a manner prescribed by the specific design of the yield trial. Useful planter innovations include self-leveling devices for hilly terrain, variable row widths, interchangeable furrow openers, and fertilizer attachments.

Before harvest, border rows may be removed, and alleys are established or the ends of the plots are trimmed off. This is done to reduce experimental error caused by variable interplot competition. End trimming ensures that all plots are of a uniform size. It is best to delay border row removal or plot trimming at least until the wheat spikes begin to turn from green to yellow. Some breeders do not remove guard rows because they have ascertained that the reduction in experimental error gained from their removal is slight. The evidence is rather overwhelming, however, that border effects exist in most small grain-yield trials.

A number of functional self-propelled wheat plot harvesters are sold. Essential specifications of a harvester are that it be transportable, minimize seed mixtures between plots, conform to standard plot widths, require few operators, and harvest plots rapidly with low grain loss. A new breeder should consult with established wheat breeders to determine which machines are best for local conditions. Some harvesters work better than others on slopes, or for cutting lodged grain or harvesting wheat plots of high biomass.

Small yield plots may be cut by hand or with mechanical binders and threshed with stationary threshers. A few commercial companies manufacture these pieces of equipment. Harvest of total plot biomass facilitates determination of harvest index. Some breeders harvest plots at ground level and record total sheaf weights. The sheaves are threshed to obtain grain weights. Harvest index is the ratio of grain to sheaf weight.

PROCEDURES FOR SEED PRODUCTION

The release, multiplication, distribution, and maintenance of new wheat cultivars normally are handled by following carefully established guidelines. These guidelines may differ somewhat among various public or private agencies, and political regions (states, provinces, and countries), so it is essential to know the specific local requirements.

Cultivar release procedures differ between private and public agencies. Public agencies, such as experiment stations, universities, and federal groups, usually convene a committee to review a recommendation by the breeder for release of a candidate cultivar. The breeder usually assembles pertinent data to support release of the proposed cultivar.

The release of private cultivars also is based on favorable data which demonstrate the genetic superiority of the potential cultivar, but the economics of cultivar development and recovery of research costs are paramount. Release decisions by private companies usually involve heavy input and recommendations from the breeder, but the economics of the current market and potential demand will receive major consideration.

In the United States and Canada, state and federal seed certification agencies oversee seed production of wheat cultivars. In the United States, these agencies are usually state crop improvement associations. Their purpose is to make high quality seed available to the public via seed certification. Seed multiplication is achieved by assigning specific standards to different classes of seed considered by the International Crop Improvement Association. These classes are designated as breeder, foundation, registered, and certified seed. Each certifying agency sets procedures and quality standards for the production of each class of seed. They enforce the standards by inspection during growing and harvesting of the crop.

Methods for Producing and Maintaining Breeder Seed

Breeder seed is produced under the direct control of the wheat breeder. It is the basis for the initial and future increase of the cultivar. The procedure for breeder seed production is usually the prerogative of the breeder. For pure-line cultivars, the breeder is expected to develop a product that is genetically homozygous for the agronomically important traits for which it has been evaluated and for common morphological traits, such as plant height, awn expression, kernel, and glume color. Usually the breeder has the option of describing genetic heterogeneity if it may be either advantageous or functionally neutral. For example, tall off-type plants often occur at frequencies of 0.1 to 0.5% in semidwarf wheats which have the Rht_1 gene. Rigid selection generally fails to remove these off-types and their occurrence has little economic consequence. By describing a tolerance level for these off-types, the uniformity of the cultivar can be maintained within reasonable standards.

Most breeders increase candidate cultivars and components of multilines and blends in isolation from other wheat to minimize outcrossing or mechanical contamination. Isolation distances vary with the production environment and with the genotype. At Pullman, Washington, male-sterile wheat lines have experienced outcrossing of 3% at distances of 40 m and 7% at 20 m. In the USDA-ARS and Washington State University wheat breeding program, candidate pure-line cultivars are grown in increase blocks at least 30 m from other wheat to produce the seed used to grow breeder seed. Usually these increase plots are comprised of spike or plant selections chosen by the breeder from the candidate line. The number may vary from a few to over 100 spikes or plants. Their seed is individually sown as progeny rows in the increase plot, and they are closely observed by the breeder for variability throughout the growing period. Atypical rows are discarded. Some breeders simply grow bulk increases of their potential cultivars upon which they impose rigid selection against off-types.

From the seed increase plot, the breeder usually makes between 100 to 1000 spike or plant selections which are given to persons responsible for subsequent increase of actual breeder seed. These individual spikes or plants are threshed and planted in progeny rows the following season. Isolation from other wheat is usually imposed. However, the minimum distance varies among organizations charged with seed increase. Atypical progeny rows are discarded before harvest. It is often desirable to harvest these individual progeny rows separately to ascertain kernel color and kernel hardness prior to bulking because heterogeneity for these traits is not tolerated.

Commercial Seed Production and Marketing

Foundation seed is derived from breeder seed. Its production is carefully supervised or approved by seed producers of the parent seed agency. This agency could be an agricultural experiment station or a state or federal crop improvement group. Public breeders sometimes oversee foundation seed production, and may be called upon to verify cultivar trueness to type. Foundation seed is used to produce registered or certified seed. Some agencies have adequate land to produce foundation seed themselves, but usually they will contract with qualified seed growers to grow the seed.

Registered seed is progeny of the foundation or registered class of seed produced under the control of the certifying agency. Certified seed may be produced from foundation, registered, or certified seed classes. Certified seed is the class produced for large-scale commercial sale, and must meet the minimum seed quality standards of the certifying agency.

Seed production procedures differ for multilines and hybrid wheat cultivars compared with pure-line cultivars. With multilines, breeder seed of each component is produced separately, then the components are mixed in specified proportions. For the multiline 'Crew,' ten near-isoline components were blended on an equal seed number basis to form breeder seed. Sometimes the proportions of each multiline component is based on its disease reaction type and severity. Multiline wheat cultivars may experience shifts in the percentages of the components after one or more generations of multiplication. To minimize the effect of component shift, a limited number of generations of multiplication are used. Generations of 'Crew' are limited to three generations from breeder seed: one each of foundation, registered, and certified seed.

Presently, only a few private seed companies and no public agencies are developing hybrid wheats. Guidelines for development of hybrid wheat vary somewhat among companies. The B and R lines of CMS hybrids and parents of CHA hybrids can be multiplied and maintained by procedures similar to pure-line cultivars. Isolation is desirable, but because these lines behave autogamously, outcrossing is low. The A lines are increased by cross-pollination with their B line maintainer. This is accomplished in cross-pollinated A line production fields where alternate strips of female A lines are grown with strips of male B lines. Information on strip size and the ratio of A line to B line is scant and their proportion depends on the specific environment and their inherent floral and reproductive traits. Typical ratios of A line to B line include 2:1, 1:1, and 1:2. A lines may differ in pollen receptivity. B lines differ in the amount and duration of their pollen shed. It may be necessary to adjust the A line to B line ratio to compensate for suboptimal receptivity and pollen-shedding ability. Seeding rates are often very low (13 kg/ha) to maximize size of the seed field. Isolation from other wheat is necessary, with 50 m considered minimum. Extreme care must be practiced in harvesting A line and B line seed from the seed field to avoid their mixture.

The F_1 seed of CMS hybrids may be produced much the same way the A line seed is increased. In the hybrid seed production field, the R line is alternated with strips of the A line. Sowing rates of the A and R lines are kept low to optimize tillering and enhance seed production per plant. Isolation requirements of CMS hybrid seed production fields are the same as for A-line seed maintenance fields. Two or more A lines may be planted with a common R line in a single seed field to produce several hybrids. Extreme care is required at harvest to guard against mechanically mixing seed from A line and R line strips. After their initial increase, the R lines may be harvested from the same production fields used to produce F_1 hybrid wheat seed. Guidelines for CHA hybrid seed production would be similar to those for CMS hybrid seed production.

Marketing of public and private cultivars differs mainly in approach. Private companies must recover their investment costs; hence they market seed aggressively, usually by extensive advertisement. Marketing of public developed cultivars generally is less aggressive. Some states and provinces annually publish bulletins recommending specific wheat cultivars for their various agricultural environments. Other experiment stations use field days and workshops to describe the performance of both public and private cultivars. Some certifying agencies distribute publications that contain comparative performance rankings of various cultivars they certify.

FUTURE PROSPECTS FOR CULTIVAR DEVELOPMENT

Future wheat cultivar development will continue to be directed toward enhancement of yield, improved quality, pest resistance, and tolerance to unfavorable environments. It is likely that wheat yields will continue to increase, but the rate may be slower than in the past. Past yield advances mainly have been achieved by improved partitioning of photosynthate and by protecting inherent yield potential through pest resistance. An important future need will be to increase the total wheat biomass while maintaining optimum partition via high harvest index and securing better yield protection. Over 20 years ago, the world wheat yield record of 14,700 kg/ha was attained in Washington State. Yields of even 75% of this level are still rare today, mainly due to inadequate pest resistance and tolerance to adverse environments. It seems likely that attention will shift from maximum productivity to optimum productivity, as dictated by the economics of wheat farming. Wheat genotypes will probably be bred that can most efficiently use inputs (Schmidt, 1984).

Specific resistance genes continue to be compromised by virulent races and their future use may be limited. More attention already is being directed toward breeding for durable or general resistance and tolerance. This trend should increase. Pyramiding polygenes for pest resistance will be aided by recurrent selection by genetic male sterility. Intravarietal and intervarietal diversity may eventually be the only way to use specific resistance genes once they become compromised. In the case of intravarietal diversity, use of bulk hybrid or composite-cross populations may prove to have more long-term potential than multiline cultivars (Marshall, 1977).

Can wheat be bred for even higher cold, heat, or drought tolerance? Future breeding of wheat for tolerance to adverse environments could become the main wheat breeding objective to benefit the most from biotechnology. In vitro tests performed on one or a few cells of wheat may provide the basic knowledge needed to understand the exceedingly complicated interactions between plants and adverse environments.

Wheat genetic improvement most likely will continue. Plant breeding is a methodical science which leads to applied plant evolution. Cyclical breeding permits the stepwise improvement of an array of traits. The system invariably works as long as the desired trait has reasonable heritability and some new variability for the trait is periodically infused into the working gene pool.

To ensure introgression of useful genetic variability, future wheat breeding prospects probably will focus on three areas: (1) systematic utilization of the genetic diversity found in the wild relatives of wheat; (2) genetic, cytoplasmic, and chemical manipulation of the reproductive system of wheat to facilitate evolutionary breeding methods and exploitation of heterosis; and (3) the integration of biotechnology as an information source and as a tool to aid conventional wheat breeding.

Wheat is endowed with enormous genetic variability. Despite past exploitations of the wheat gene pool, much of this diversity is probably yet to be used. This is particularly true of its secondary and tertiary gene pool members. Prospects for more effective and systematic introgression of genomes of the wild and weedy relatives of wheat are excellent. The strong foundation of basic knowledge of wheat cytogenetics and the extensive aneuploid stocks have begun to yield significant breeding accomplishments. Manipulation of the diploidization gene of chromosome 5B is a proven means of infusing alien DNA into cultivated wheats. Although alien wheat relatives have been primarily exploited for their disease resistance, their genes will be sought for many traits in the future. Alien germplasm has tremendous variability for genes affecting quality, adaptation, photosynthetic efficiency, and environmental stress tolerance.

Cyclic breeding procedures such as recurrent selection, and bulk hybrid or composite-cross breeding will undoubtedly increase now that several means can be used to make large-scale hybridizations in wheat. Wheat germplasm collections are becoming more static. It is not possible to merely return to the centers of diversity of wheat when new variability is needed. The various cyclic breeding procedures should provide guided evolution via alternating sequences of outbreeding and inbreeding. Creation of specific wheat gene pool parks may be a future way to ensure continued evolution.

Biotechnology already has begun to enhance wheat breeding by improving our knowledge of gene structure, function, and plant development. Such studies have given a better understanding of the biochemistry of seed storage proteins, the molecular organization of chromosomes, and the metabolic pathways of nitrogen assimilation. So far, direct applications to breeding have been few. Perhaps the most immediate potential will come from dihaploid breeding, especially via wheat anther culture (Schaeffer et al., 1984). Dihaploid breeding would have special advantages in achieving homozygosity after hybridization and provide a means to facilitate mutagenesis and selection programs. With mutation breeding, it would not be necessary to undergo repeated selfings to achieve homozygosity of induced mutations. Haploid cells perhaps could be used in biochemical screening techniques for selecting plants tolerant of herbicides, excess minerals, or disease toxins.

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