# Chapter 21

# Wheat

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Wheat is grown in almost all cropping environments of the world, except in the humid lowland tropics. Winter wheat under rain-fed conditions dominates in Europe, the USA, Ukraine and southern Russia, followed by spring-sown spring wheat in semi-arid conditions (Canada, Kazhakstan and Siberia) in the developed world. In the developing world, wheat is usually not a subsistence crop and its production is concentrated in several well-defined cropping systems: double-cropped with paddy rice in Asia (22 million ha) or with maize, cotton, soybean or berseem (15 million ha); with soybean in the Southern Cone (7 million ha). Only in the wetter parts of the developed world, such as the eastern USA, Europe and southern Russia, and in parts of the Southern Cone, is wheat grown in more complex rotational systems involving pulses, oilseeds, other cereals, alfalfa and pastures. An exception is southern Australia, where, despite low rainfall, complex rotations and ley farming are practised.

## BOTANY AND DISTRIBUTION

### Origin, Distribution and Diffusion

Wheat belongs to the genus *Triticum*, which originated about 10 000 years ago in what is now the Middle East. Polyploid *Triticum* arose when two diploid wild grasses crossed naturally to produce tetraploid wheat, which today includes cultivated durum wheat (*Triticum turgidum* L. var. group *durum* Desf. $2n=4x=28$). Tetraploid wheat later outcrossed to goat grass (*T. tauschii*, considered a troublesome weed in many wheat-growing areas) and gave rise to hexaploid bread wheat (*T. aestivum* L. em Thel. $2n=6x=42$).

*Triticum turgidum durum*, the main modern variety of tetraploid durum or macaroni wheat, is widely grown in drier areas of the world, such as those found in India, the Mediterranean Basin, the former Soviet Union, Argentina and the rain-fed areas of the North American Great Plains. The other tetraploid wheat, *T. timopheevi*, is only grown in some areas of the Transcaucasian regions. Cultivation of the diploid *T. monococcum* is restricted to some areas of the Middle East and Mediterranean regions.

*Triticum aestivum* is the most widely grown wheat in the world today. Generally called bread or common wheat, its flour is best suited for making bread. Bread wheat encompasses several thousand cultivars that are widely adapted over a range of environments and grown worldwide.

Placing the female parent first, durum and bread wheats are genomically represented as BBAA and BBAADD, respectively. The mode of chromosome pairing in triploid $2n=3x=21$ *T. turgidum x T. monococcum* and pentaploid $2n=5x=35$ *T. turgidum x T. aestivum* hybrids has revealed the diversity of ancestral species in the allopolyploid wheats. Chromosomal configurations at meiosis have unequivocally demonstrated that diploids, tetraploids and hexaploids have either one (AA), two (AABB) or three (AABBDD) sets of seven chromosomes each and that the A genome is common to durum and bread wheats. This led to the inference that bread wheat is an allohexaploid.

More recent indications are that *T. urartu* Tum., rather than *T. monococcum* L. subsp. *boeoticum* Boiss., a more widely spread diploid, is the source of the A genome in cultivated wheat. *Triticum urartu* inhabits areas in the Fertile Crescent from southern Lebanon to southern Syria, northward through southeastern Turkey into the Caucasus mountains and southeastward through northern Iraq into southwestern Iran. It was suggested as the A-genome donor by Johnson (1975) and more recently by Kerby and Kuspira (1987).

Wheat's B genome donor is thought to be similar to *Aegilops speltoides* Tausch., which grows wild throughout the Fertile Crescent. Another possible donor of the B genome is *Ae. searsii*, which is restricted to southern Palestine, but the issue is still somewhat unsettled. The source of the D genome is *T. tauschii*, which was readily accepted as the donor species based on analyses of synthesized and cultivated wheats that revealed certain genomic similarities.

The main centre of diversity and origin of *Triticum* is southwest Asia, around the Fertile Crescent hill sites, extending from the Mediterranean coast in the west around the Syrian Desert to the Tigris-Euphrates plain in the east. In that area, the diploid and polyploid *Triticum* species grow in mixed populations exhibiting a great diversity of morphological and ecological variation.

### Classification

The Triticeae tribe is comprised of approximately 350 species, of which about 250 are perennials. Perennials not only include many important forage grasses but also serve as a vital genetic reservoir for improving annual Triticeae species, which include the major cereals – bread wheat, durum wheat, triticale (X *Triticosecale* Wittmack, a man-made cereal resulting from a cross between wheat and rye), barley (*Hordeum vulgare* L.) and rye (*Secale cereale*).

The genomic system for classifying the perennial Triticeae (Dewey 1984) recognizes ten genera with defined genomes or genome combinations. The ten genera, with their type species and genome compositions, are: *Agropyron (A. cristatum*; P), *Pseudoroegneria (P. strigosa*; S), *Psathyrostachys (Ps. lanuginosa*; N), *Critesion (C. jubatum*; H), *Thinopyrum (T. junceum*; J-E), *Elytrigia (E. repens*; SX), *Elymus (E. sibiricus*; SHY), *Leymus (L. arenarius*; JN), *Pascopyrum (Pa. smithii*; SHJN) and *Secale (S. montanum*; R).

Annual plants of the Triticeae are confined largely to the *Triticum* and *Aegilops* species, with the notable exception of certain species belonging to *Hordeum, Secale, Haynaldia, Eremopyrum, Heteranthelium, Taeniantherum* and *Henrardia*. The large number of generic and specific names of the interrelated *Triticum* and *Aegilops* groups has led to considerable confusion over the years. The multitude of names not only expresses the opinions of various taxonomists, but also represents the diversity of the species themselves. To clear up the confusion, Kimber and Feldman (1987) compiled a synonym list of the most commonly used names among the *Triticum/Aegilops* groups.

## GERMPLASM CONSERVATION AND USE

CIMMYT's wheat genebank contains almost 122 000 accessions representing more than 50 years of breeding, collecting and acquisition. The collection includes different types of Triticeae genetic resources, as shown in Table 21.1. Currently (1996), the entire collection is maintained as an active collection. However, hexaploid wheat and triticale germplasm recently have been stored in both base and active collections. Durum wheats and wild relatives are maintained as active collections, in accordance with the ICARDA-CIMMYT agreement. Barley (*Hordeum vulgare*) germplasm is stored at CIMMYT as a working collection for the ICARDA-CIMMYT Barley Program.

Multiplication and regeneration are accomplished in a screenhouse at CIMMYT headquarters in El Batan, Mexico. This facility expedites the production of quality seed for medium- and long-term storage. It also minimizes accidental mechanical mixing and other handling errors by allowing sowing to be programmed year-round rather than strictly by the annual crop season. Thus, a manageable number of accessions can be multiplied through sequential plantings.

CIMMYT's Seed Health Unit inspects all introductions before planting, and any samples presenting a potential quarantine risk are destroyed. If no problems are encountered, introductions are released for planting in the greenhouse or designated introduction fields. All introductions are inspected periodically during the crop cycle, and fungicides and insecticides are routinely applied.

The key to most wheat genetic resources work in the future is the development of a database, or an interconnected system of databases, with the capacity to manage and integrate all wheat information, including passport, characterization and evaluation data. In the early 1990s, CIMMYT's Wheat Program established just such a strategy for integrating and managing all data pertaining to germplasm regardless of where they were generated. The goal was to facilitate the unambiguous identification of wheat genetic resources and remove barriers to handling and accessing information. As a result, the International Wheat Information System (IWIS), a system that seamlessly joins conservation, utilization and exchange of genetic material, came into being. The system is fast, user-friendly and is available on an annually updated CD-ROM.

IWIS has two major components: the Wheat Pedigree Management System, which assigns and maintains unique wheat identifiers and genealogies, and the Wheat Data Management System, which manages performance information and data on known genes.

The power of IWIS has been demonstrated in several ways. For example, it has been used to trace genealogies of modern cultivars to their parental landraces or to lines of unknown pedigrees. The system has also revealed that the number of parental landraces in CIMMYT's bread wheats has increased markedly over four decades, from six ancestors in Yaqui 50 to 68 ancestors in Weaver. Using information generated by IWIS, cytoplasmic diversity in CIMMYT wheats was found to be restricted. Other analyses using the system have demonstrated that landraces from certain regions of wheat's centre of origin do not, or only rarely, appear in the pedigrees of modern wheats. Such genealogical analyses, which could have broad implications for genetic resources utilization, are evidence of the system's great utility and many potential applications.

Byerlee and Moya (1993) have indicated that 40 million ha in the developing world are sown to wheat cultivars originating directly from CIMMYT crosses or from national agricultural research systems (NARS) crosses using a CIMMYT parent. In industrialized countries, at least 20 to 25 million ha are sown to cultivars of CIMMYT ancestry. These cultivars are the direct result of active seed exchange between NARS and CIMMYT over the last three decades, which has made it

Table 21.1. Numbers of accessions in the CIMMYT Wheat Germplasm Bank by species as of February 1995.

| Crop | No. of accessions |
|------|-------------------|
| Bread wheat (*Triticum aestivum* L. em Thell.) | 71 171 |
| Durum wheat (*T. turgidum* L.) | 15 940 |
| Triticale (X *Triticosecale* Wittmack) | 15 200 |
| Barley (*Hordeum vulgare* L.) | 9 084 |
| Rye (*Secale cereale* L.) | 202 |
| Primitive wheats (*T. monococcum* L., T. dicoccon Schrank) | 7 245 |
| Wild relatives (*Triticum* spp.) | 4 549 |
| **Total** | **121 944** |

possible to introduce important traits into widely adapted germplasm. There is no indication that seed exchange will become less important in the future; on the contrary, it probably will be of greater importance. IWIS will assist in the exchange of seed and associated information, increase efficiency and minimize unnecessary duplication of evaluations.

Finally, IWIS makes it possible to estimate the degree of relatedness among wheats, allows breeders to increase genetic diversity by selecting materials of divergent parentage for crosses, thereby reducing wheat's vulnerability to diseases and climatic changes, and automatically updates family trees as additional ancestry is discovered.

About 640 000 accessions of *Triticum* spp., *Aegilops* spp. and X *Triticosecale* can be found in collections around the world (Table 21.2). The degree of duplication in these collections is difficult to ascertain without some type of global wheat genetic resources database. Given this situation, the level of priority that should be placed on collecting more materials is uncertain, except where there is a real threat of genetic erosion to native species in specific areas. Accessions in collections around the world may or may not be preserved properly, and some may not even be catalogued. It may thus be more cost-effective to place such collections into secure storage than to collect more materials in the field.

Several accessions of diploid wild relatives that have the A, B or D genomes are potential candidates for use in interspecific crosses. Accessions with other ploidy levels and partial genomic similarity are also good candidates. CIMMYT maintains working collections of these wild grass accessions.

The different genepools within the annual and perennial grasses of the Triticeae tribe also provide tremendous genetic variability for improving wheat (Dewey 1984). However, in contrast with the annual *Triticum/Aegilops* spp., the perennial genera we use in our intergeneric crosses are genomically quite diverse and rather difficult to cross with wheat. Hence, accomplishing beneficial alien transfers through intergeneric hybridization is quite time consuming.

*Evaluation*

Two evaluation approaches are used by the genetic resources unit. One is demand-driven, meaning that evaluations are conducted for specific traits or characteristics where the breeding programmes lack variation. Demand-driven evaluations may be requested by CIMMYT and national programme breeders. The other approach is systematic evaluation of germplasm groups that the Bank considers potential sources of variation for use in breeding programmes. The systematic evaluation of groups of germplasm as potential sources of variation for use in breeding programmes is done by selecting a specific set of underutilized germplasm and evaluating it for all possible characters.

Table 21.2. Number of accessions available in collections around the world.

| Type of wheat | No. of accessions |
|---|---|
| Hexaploid | 266 589 |
| Tetraploid | 78 726 |
| Diploid | 11 314 |
| Unspecified *Triticum* | 252 530 |
| *Aegilops* spp. | 17 748 |
| Triticale | 23 659 |
| Total | 640 603 |

Source: Information collated from IBPGR (1990).

## Pre-breeding

Genetic resources available for wheat improvement include perennial and annual grasses belonging to the tribe Triticeae. Their enormous genetic inheritance can be used for improving wheat thanks to the patterns of relationships within the tribe and to the possibility of making wide crosses. Wide crosses of wheat have received considerable attention because of the crop's global importance and the availability of a wide range of wild species; also, wide crossing techniques and subsequent genetic manipulations are well established.

Wheat wide crossing at CIMMYT was established during the late 1970s. At that time, the main goals were intergeneric hybridization and subsequent introgression of agronomically important traits into modern high-yielding strains, and *Aegilops*, *Hordeum*, *Secale* and *Thinopyrum* spp. received the most attention. Major achievements to date include the registration of Karnal bunt and *Helminthosporium sativum* resistant stocks and the release in Mexico and Pakistan of Karnal bunt-resistant and salt-tolerant cultivars, respectively (Mujeeb-Kazi and Hettel 1995).

During the late 1980s, the wide crosses section expanded to include interspecific hybridization and started exploiting the variability locked in the three genome donors of modern wheat. As a result, more than 500 synthetic wheats having exotic A, B or D genomes were produced and are being maintained at CIMMYT. These synthetics are proving to be extremely valuable sources of resistance to various biotic and abiotic stresses, as well as of yield-related traits (Mujeeb-Kazi and Hettel 1995).

## Properties and Uses

Today wheat is grown as an autumn/early winter-sown cool season crop in latitudes from 45° to 55° to as close to the equator as latitude 12° at low altitudes (<1500 m asl). Further from the equator, winters are too cold to permit overwintering but commercial spring-sown spring wheat takes over, being found up to latitude 62°N in Europe. Spring-type wheat also occurs from latitude 20° right to the equator at high altitudes (>1500 m) in cool tropical highlands, where it is usually grown during the wet summer season.

Daylength sensitivity (wheat is a long-day plant) and temperature-conditioned vernalization requirements, both genetically determined traits, are principal determinants of adaptation. A major phenological separation exists between spring-habit wheats, with no vernalization response and marked daylength sensitivity, and winter-habit wheats, which almost always show a strong or obligate requirement for vernalizing temperatures to induce timely floral initiation, as well as daylength sensitivity. There are also intermediate or facultative habit wheats. Traditionally, spring wheats were sown at high latitudes in the spring, and winter or facultative wheats at middle latitudes in the autumn. As wheat growing has shifted to lower latitudes and with hybridization and selection, these distinctions have become less

clear. In particular, autumn-sown spring wheats with reduced daylength sensitivity have come to dominate at lower latitudes (less than 35°S and N).

Wheat is relatively tolerant to drought, requiring as little as 200-250 mm average evapotranspiration for commercial production. It is moderately tolerant to frost, except during the period from stem elongation through anthesis. Wheat is also quite tolerant of heat, at least under irrigated cultivation in locations with low atmospheric humidity (e.g. in the Sudan). It is not well adapted to strongly acid or saline soils, but genetic differences exist, especially for tolerance to acid soils with aluminium toxicity problems. The widely varied environments where wheat is grown, however, are solid testimonial to its genetic diversity for adaptation. It is interesting to speculate that the hexaploid nature of bread wheat may explain a significant part of this broad adaptation.

Rain-fed wheat production is found from where average growing season rainfall is close to nil (growth on stored residual summer moisture in moisture-retentive soils of low latitude environments like central India) to up to 1000 mm. On less favoured soils and without fallow, the minimum average growing season rainfall is about 200 mm, meaning an average annual rainfall of 250 mm in winter rainfall mid-latitude environments like North Africa. One year of fallow to conserve moisture if soils are retentive improves yield, greatly reduces risk in such environments, and is essential for commercial production in more continental locations (e.g. Great Plains of the USA, prairies of Canada, steppes of Siberia, Central Anatolian Plateau) if annual precipitation falls below about 350 mm. In the last 30 years, supplemental and full irrigation have permitted the expansion of wheat into many arid and semi-arid environments.

Cereal grains, although low in protein content and deficient in protein nutritional quality (low levels of the essential amino acid lysine), constitute the major source of energy and nutrients in the world (Roderick and Fox 1987). Wheat accounts for the largest proportion of global cereal production (USDA 1995) and, chiefly in the form of bread, is the principal food item in most developing countries, for it provides the population with more energy and nutrients than any other single food source (Pomeranz 1987). The chemical composition and nutritional value of wheat and wheat-based products have been extensively reviewed elsewhere (Roderick and Fox 1987; Ranhotra 1991).

The baking industry's principal reason for preferring wheat over other cereals as an essential raw material is its unique ability to form an insoluble and viscoelastic protein complex, known as gluten, that confers viscoelasticity to flour doughs. Wheat varieties may vary significantly in gluten quality. Although genetically controlled, gluten quality can be greatly influenced by grain productivity factors such as soil fertility and crop management practices (grain yield is negatively correlated to protein content), and by environmental conditions such as frost, heat and rainfall during grain development (Sander *et al.* 1987). For these reasons, wheat quality improvement has been a task for breeders in NARS and international agricultural research centres (IARCs) around the world.

Selecting for specific genes is accompanied by a decrease in genetic diversity. This is demonstrated by the regional predominance of a few glutenin subunits controlled by genes situated on the long arm of wheat group 1 chromosomes, most likely as a function of selection pressure (Morgunov *et al.* 1993; Peña 1995). Fortunately, NARS and CGIAR centres in particular are taking action to maintain and enhance biodiversity while breeding for quality. Genes for increased protein content from *T. dicoccoides* and for novel, quality-desirable glutenins from *T. tauschii* can be transferred into durum wheat and/or bread wheat (Grama *et al.* 1984; Lagudah and Halloran 1988; Khan *et al.* 1989; William *et al.* 1993; Peña *et al.* 1995). They are being exploited at CIMMYT and ICARDA to improve the nutritional

and/or industrial qualities of wheat (Nachit 1992; William *et al.* 1993; R.J. Peña, unpublished data). Finally, landraces and other alien diploid (*T. monococcum, T. boeoticum, T. urartu*) and tetraploid (*T. dicoccon*) species are being examined with the aim of finding additional novel genes that could improve wheat's end-use qualities and enhance its genetic endowment.

Aiming to provide NARS with high-yielding germplasm possessing acceptable quality attributes, CIMMYT and ICARDA have included quality improvement as part of their breeding activities. Traditionally, quality improvement has involved crossing a high-quality wheat parent with a parent possessing other desirable attributes; only offspring carrying the desired traits are selected and advanced throughout the segregating stages. Although somewhat slow and expensive, this breeding approach has succeeded in generating many wheat varieties of acceptable quality around the world.

## Breeding

In their efforts to meet the increasing worldwide demand for food, plant breeders everywhere are finding very little germplasm of cultivated crops having the desired traits with which to make needed improvements in those crops. In conventional bread wheat improvement, breeders have normally made crosses between varieties. Such crosses have few constraints, and all associations of parental traits and segregation are invariably based on genetic recombination. Fortunately, useful genetic resources (i.e. useful in crop improvement) are being found among uncultivated plants in the wild. The challenge is to be able to exploit and incorporate this 'new' germplasm routinely into existing food crops.

Most efforts to transfer alien germplasm from wild plants into cultivated crops have involved the *Triticum* grass species, with the greatest emphasis being placed on improving bread wheat. Introgressing alien variability into bread wheat involves working in two distinct areas: long-term intergeneric and short-term interspecific hybridization. This separation is essentially based on wheat/alien genomic similarity and level of genetic recombination. Because it is short term, interspecific hybridization is the favoured approach for genetic introgression.

In interspecific crosses, the most useful materials are the numerous alien accessions of Triticeae species having genomes similar to the A, B or D genomes of bread wheat. Crosses with these materials allow relatively easy alien gene transfers, are compatible with normal field research and set the stage for simultaneous introgression of several genes.

### Interspecific hybridization

*Triticum tauschii,* which has the D genome, could be very useful for transferring unique multiple diversity to wheat. At CIMMYT we are using *T. tauschii* accessions in the following ways:

- Producing synthetic hexaploids by crossing durum cultivars with *T. tauschii* accessions and using synthetic hexaploid wheats for crosses onto wheat (Fig. 21.1). This permits exchanges across all three genomes.
- Crossing elite, but susceptible, bread wheat cultivars with resistant *T. tauschii* accessions and backcrossing the ABDD $F_1$ hybrids with the elite bread wheat cultivar used in the initial cross. The progenies will reflect D genome exchanges only.
- Extracting the AABB genomes from commercial bread wheat cultivars and then developing hexaploids through crosses with desired *T. tauschii* accessions. This partitions the D genome very precisely.
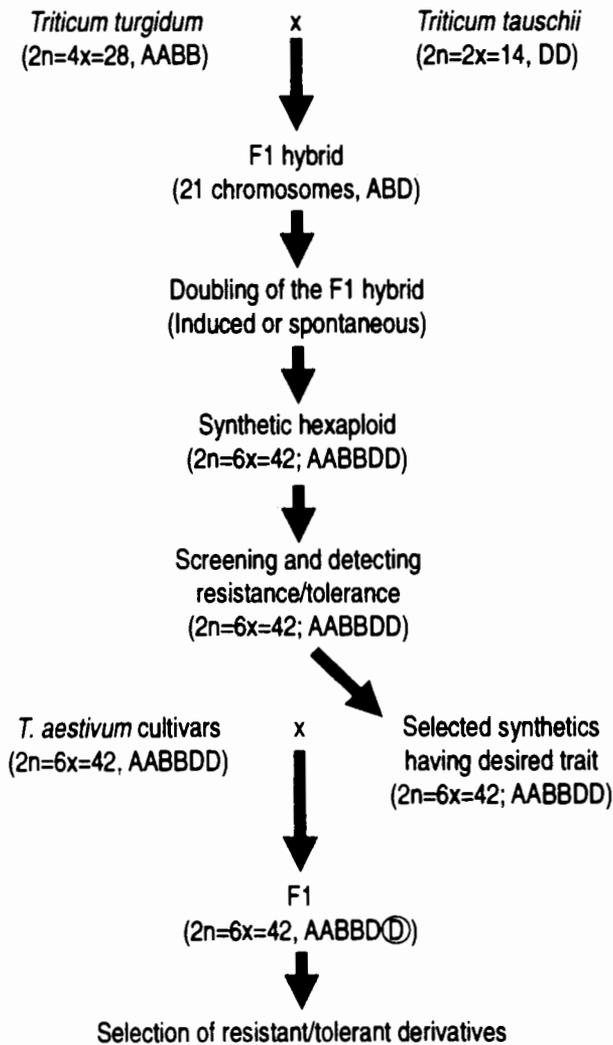
*Triticum turgidum*            x        *Triticum tauschii*
(2n=4x=28, AABB)                        (2n=2x=14, DD)

F1 hybrid
(21 chromosomes, ABD)

Doubling of the F1 hybrid
(Induced or spontaneous)

Synthetic hexaploid
(2n=6x=42; AABBDD)

Screening and detecting
resistance/tolerance
(2n=6x=42; AABBDD)

*T. aestivum* cultivars      x        Selected synthetics
(2n=6x=42, AABBDD)                    having desired trait
                                      (2n=6x=42; AABBDD)

F1
(2n=6x=42, AABBD(D))

Selection of resistant/tolerant derivatives

Fig. 21.1.  Schematic showing the production of synthetic hexaploids derived from crossing *Triticum turgidum* x *T. tauschii* and their utilization.

*Intergeneric hybridization*

A few new hybrids have been obtained since Wang (1989) reviewed intergeneric crosses involving perennial Triticeae. All genomes of the perennial Triticeae have been combined, either singly or in combination, with the A, B and D bread wheat genomes (Wang 1989; Mujeeb-Kazi *et al.* 1994). To date, there are at least 89 different combinations involving the three wheat genomes and the eight genomes of the perennial species. Of these, 52 involve hexaploid wheats, 30 involve tetraploid wheats and 7 involve diploid primitive wheats.

The wide array of genetic variability residing in the above Triticeae relatives supplies a superb arsenal of new defences against biotic and abiotic stresses in cereals. However, the use of this variation has its constraints, since genomic homoeology does not offer a satisfactory level of chromosomal association in the $F_1$ hybrids to promote alien gene transfers. Use of the *ph1* locus may provide a way to overcome the recombination constraint. Other genetic manipulations progressively

revolve around production of alien disomic chromosome additions or substitutions, which could lead to translocations or subtle genetic exchanges through cytogenetic and novel manipulative procedures. Although the transfer process is slow, the potential benefits of incorporating these diverse genetic resources into wheat are extremely high.

Outputs from intergeneric programmes are long term, and even a 10-year (two cycles per year) span could be considered a short-term involvement because of the research complexity associated with inducing alien introgression, identifying expression and achieving stability. Novel genes have unique potential for contributing to stress resistance in wheat. The release in Pakistan of two wheat varieties (Pasban 90 and Rohtas 90) derived from wheat/*Th. distichum* advanced lines and the registration of five *Helminthosporium sativum* resistant lines from *Th. curvifolium* advanced lines (Mujeeb-Kazi *et al.* 1996) are two successful examples that encourage continuing the pursuit of this long-term procedure.

### Prospects

Variability is needed to further increase wheat's yield potential; provide new sources of disease and pest resistance and maintain the yield levels achieved so far; develop germplasm adapted to more marginal environments, and to improve quality.

Most wheat breeding programmes dedicate a major portion of their efforts to protecting gains in yield potential by incorporating new and better genes or combinations of genes for disease and pest resistance. Collections of adapted and unadapted wheats have been rich sources of resistance to various diseases, and their greatest underlying value is as a reservoir of undetected resistance genes (Williams 1989). For most wheat diseases there is a need to identify more genes for resistance of the hypersensitive type to achieve combinations of genes that confer resistances similar to stem rust resistance, which so far has been very effective. The wild relatives of wheat will most likely be major contributors to this type of resistance.

There is also a need to identify the quantitative type of resistance (partial resistance), characterized by durability and a reduced rate of epidemic build-up (Parlevliet 1988). This type of resistance may be very important in diseases such as yellow rust, where race-specific resistance has not been very long lasting. The most likely sources of quantitative resistance are landraces and obsolete cultivars that have been grown extensively over many years in areas where particular diseases are endemic.

Fungal diseases are the predominant causes of losses of yield and quality in wheat, with nematodes, viruses, insects and bacteria of much less importance. Globally the most important of the fungal diseases are the rusts. All three rusts of wheat are potentially dangerous and research efforts aimed at combating them have developed various control strategies, of which genetic resistance is the most cost-effective and environmentally sound measure. For example, durable resistance to stem rust (*Puccinia graminis* Pers. f.sp. *tritici* Eriks. & Henn.) has kept this traditional pathogen of wheat at bay for the last 40 years. Durable resistance to leaf rust (*P.†recondita* Rob. ex Desm. f.sp. *tritici*), presently the most significant rust, is currently being incorporated into the wheats. Resistance to yellow or stripe rust (*P.†striiformis* West. f.sp. *tritici*), important in the wetter, cooler areas, is still inadequate; however, it appears that good resistance will be incorporated in the near future.

Further details on diseases and others of less widespread importance can be obtained from Wiese (1987), Heyne (1987) and Roelfs *et al.* (1992).

Overall, it is worth noting that growing conditions have generally become more favourable for wheat diseases and pests with time, particularly as irrigated wheat

cropping has spread, N fertilizer levels have increased and cropping intensity has risen. The developed world has tended to respond to this situation by increasing the use of fungicides and pesticides, whereas the developing world, often being unable to afford these chemicals, has had to rely largely on host plant resistance for control of losses. More recently, in view of heightened environmental concerns and diminishing profitability of wheat, the developed world is also turning in this direction. Nevertheless, a huge job remains to incorporate adequate durable resistance to all significant diseases and pests for each wheat environment, and scope also exists for better non-chemical management strategies. Molecular biology is expected to have a significant impact on the former endeavour.

The introduction of wheat cropping into marginal areas will present many abiotic stress challenges. Mineral ion deficiencies and toxicities, drought, wind, salinity and temperature extremes are some of the factors that will limit wheat production in these environments. Primitive wheats and wild relatives that originated in such environments can be expected to provide genes for tolerance to these abiotic stresses. The genetic variation that man has exploited in wheat, along with the agronomic modification of the crop environment, has permitted the wheat crop to be pushed into almost all cropping environments of the world, with the major exception of the humid lowland tropics. Here, diseases and high mean temperatures will probably permanently exclude wheat growing, and rice and maize will remain the main cereals.

At the dry and cold limits of wheat adaptation one tends to find that wheat is replaced by barley. Wheat lacks the vigour and frost resistance that give barley an advantage in such marginal environments. Wheat also is not as tolerant of salinity as barley. Introduction and breeding of traits from wheat progenitors and landraces may permit some gains in adaptation of wheat in this respect; certainly breeding for salt tolerance is receiving attention and some progress has been made. Better resistance to waterlogging, lodging and shattering would reduce the not insignificant and recurring losses these problems cause in most environments. Certain soil micro-element deficiencies (e.g. zinc, copper, boron) and toxicities (e.g. aluminium, manganese, boron) limit wheat production in an increasing number of environments (as soils become depleted and/or soils inexorably acidify), yet useful genetic variation for tolerance of these problems exists. This needs to be exploited to lessen soil amelioration costs.

Genetic improvement of wheat is likely to remain a major source of productivity gains. The crop's yield potential has risen about 1% annually over the past 30 years. This trend is expected to continue but may require greater breeding resources, especially as recent gains in efficiency that resulted from computerization and mechanization of breeding begin to dwindle. Innovations in molecular biology appear unlikely to effect an impact on yield progress at any time. Thus it is likely that more resources will need to be invested in other potentially useful improvement strategies such as exploiting heterosis in wheat through the use of $F_1$ hybrids and developing input-saving wheats that compete better against weeds or extract greater amounts of available soil nutrients (e.g. phosphorus and zinc). Despite considerable progress in the last 100 years, huge scope still exists for strengthening and making more durable the resistance of wheat to diseases, viruses and insects. This appears to be the area in which molecular biology will make its first impact on wheat breeding. Molecular biology is also likely to aid conventional breeding in changing the quality of wheat grain by developing it for novel industrial uses and improving its nutritional structure in ways that would clearly benefit consumers (increasing its content of available iron, zinc, vitamin A and certain amino acids).

The last 30 years have witnessed an unprecedented level of international wheat germplasm exchange and the development of a greater degree of genetic relatedness among successful cultivars globally; the concept of broad adaptation has thus been well vindicated. However, this is seen by some as increasing genetic vulnerability to pathogens, although such vulnerability depends more on similarities in resistance genes, which may actually be more diverse now than before. This notwithstanding, various new factors (including the growing strength of national breeding programmes in the developing world and the advent of breeders' rights) should result in increased diversity among cultivars and perhaps lead to the exploitation of hitherto-overlooked specific adaptation in wheat. This would be especially important if climate change accelerates. Just as increasing nitrogen supply and improving weed control have been almost universal driving factors of wheat cultivation in the last 50 years, higher atmospheric concentrations of $CO_2$ and warmer temperatures could significantly influence breeding objectives in the next.

Evans (1993) argued convincingly that agronomic advances and improvements in yield, efficiency or sustainability also create breeding opportunities; this was the case with the improved nitrogen-use efficiency and reduced herbicide use mentioned above. Looking ahead, the global move toward reduced tillage and increased crop residue retention – so important for sustaining the soil resource – will require wheats to possess new traits such as resistance to diseases encouraged by crop residues or adaptation to less than ideal seedbed conditions. Although some scope probably exists for reducing the need for fertilizer applications through breeding for nutrient-use efficiency (e.g. phosphorus and zinc), it may be that the current interest in breeding for low nitrogen input will be overtaken by agronomic solutions to this yield constraint (optimal timing of fertilizer application, rotations with legumes). There will, however, inevitably be other moves toward more sustainable wheat cropping systems and these will undoubtedly place new demands on wheat improvement.

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