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An invited paper from the 12th Australasian Plant Breeding Conference

History and past achievements of plant breeding

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> *'The disappearance of wheat or rice or corn... would be a catastrophe as devastating and annihilating as a nuclear holocaust.'*
>
> *Kahn* (*1985*)

Abstract. Developments in improving the world's three most important staple food crops—maize, wheat, and rice—are reviewed. A discussion of the origins and diffusion of maize and wheat and farmers' early plant breeding efforts is followed by an overview of the rise of the private sector in maize breeding, the development of international agricultural research, the Green Revolution in wheat and rice, the development of hybrid rice, and recent (1960–2000) achievements in international maize breeding research. Promising new tools for breeding improved food crops in developing countries are reviewed, including genomics and genetic engineering. Issues that will concern plant breeders—especially those focusing on the needs of developing countries—in years to come are discussed, including the rise of the private sector, intellectual property protection, and globalisation. The paper concludes with some thoughts on how plant breeding has changed in the course of the past century and must adapt to the needs of the present century.

Additional keywords: CIMMYT, maize, wheat, rice, developing countries.

Introduction

Plant breeding has been variously described as an art, a science, and a defining element of culture. Duvick (1996) succinctly observes that 'plant breeding and plant culture have always been essential agents of change in human society.' The origins of plant domestication and breeding are largely unknown to us, although it is clear that people and plants have co-evolved for millennia and that humans have shaped a great number of plant species to their growing need for food, feed, and fiber. Anyone who has ever had the opportunity to observe the great variety in colour in present-day rice, wheat, and maize varieties is actually observing evidence of the carefully nurtured genetic diversity that has sustained people throughout history. In these few pages, we attempt to give some idea of the changes that plant breeding has brought to human beings, especially in more recent times in developing countries. Although we certainly cannot cover the entire panorama of plant breeding, we focus on developments in the world's three most important staple food crops—maize, wheat, and (to a much lesser extent) rice.

We begin by discussing the diffusion of maize worldwide and the transition from breeding on farms to breeding by commercial hybrid maize enterprises. Next, we look at the history of wheat and wheat breeding, focusing attention on the rise of international agricultural research and the Green Revolution in wheat and rice. Turning our attention back to maize, we describe some of the gains that have been made in maize research through the kind of international collaboration that yielded the Green Revolution in wheat and rice. A review of promising new tools for breeding improved food crops in developing countries is followed by a discussion of the issues with which plant breeders—especially those focusing on the needs of developing countries—can expect to contend in years to come, including the rise of the private sector, intellectual property protection, and globalisation. We conclude with some thoughts on how plant breeding has changed in the course of the past century and must adapt to the needs of the present century.

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Maize from antiquity to the rise of the farmer-breeders

It is instructive to remember just how recently plant breeding became a vocation for scientists. Mendel's work was rediscovered and its potential applications widely appreciated only a little over a century ago. Before then, for thousands of years, plant breeding was almost entirely the domain of rural people.

The improvement of maize, described as 'a species that does not exist naturally in the wild and can only survive if sown and protected by humans...', is strongly correlated with the development of cultural complexity and rise of the high civilisations of pre-hispanic Mesoamerica (Salvador 1997). Maize is likely to have been first domesticated in south-central or south-western Mexico (Goodman 1988); by the mid-1600s it was grown throughout the Americas, from southern Canada to central Chile. Troyer (1999) describes maize as 'a short-day crop of tropical origin', which, as it moved out of its Mexican center of origin, adapted to a tremendous range of new environments. As Salvador (1997) points out, after the Spanish arrived in Mesoamerica in the 16th century, 'maize spread quickly wherever Spaniards traveled, in large part because of its broad adaptability and high productivity.'

Throughout its history in Mesoamerica, maize has remained largely a subsistence crop. The maize populations that survive on the holdings of small-scale farmers are 'under constant selection pressure for adaptation to the microclimates of the myriad mountain valleys where these farmers subsist… Consequently, there is high genetic biodiversity in the Mexican maize pool, a factor of great importance for the breeding of current and future maize cultivars' (Salvador 1997). The importance of this diversity and its preservation cannot be underestimated.

Nor can the importance of farmers' knowledge be underestimated in the continued evolution of maize. Although it would be some time before the scientific basis of maize breeding was well understood, the 'close planting of diverse strains [of maize by native American peoples] indicates that a recognition of the positive benefits of heterosis was firmly in place many thousands of years ago in the Americas... many years before the modern scientific era would indicate' (Goldman 1999).

The flint and dent maize that made its way north to what is now the USA became the basis for noted advances in maize breeding. Flint maize cultivars arrived in the south-western USA about 1000 BCE and continued to move north; dent corn arrived in the south-eastern USA much later, about 1500 CE (Troyer 1999). The crop valued by Native Americans became essential to the subsistence and expansion of colonial settlers and others in North America, and they also contributed to its improvement. By 1916, it was estimated that 1000 maize cultivars were grown in the USA, 250 of which had been grown before 1840 (Troyer 1999). One of the most popular cultivars by the turn of the century was Reid's Yellow Dent. The product of crosses between seed corn brought by Robert Reid to Illinois late in 1846 and an early native Indian flint corn, it was improved by Reid and his son James for decades and became widely known after winning first prise in the corn show at the Columbia Exposition in Chicago in 1893 (Kahn 1985; Troyer 1999). The variety (the best ears of which, according to legend, were kept under the mattresses of the Reid family over the winter) became the basis for the family seed business and dominated the maize area in the USA for 50 years. Troyer (1999) concludes that 'Reid Yellow Dent obviously received a superior combination of genes for adaptedness from its two differently adapted parents as evidenced from its popularity over such an enormous area.'

Reid Yellow Dent contributed to the development of many other successful maize cultivars over the years and is but one example of the foundation laid by farmer-breeders for future maize breeding. As Duvick (1996) indicates, over the course of the 19th century, 'new settlers in the old Northwest Territory transformed an amalgam of unadapted eastern and southern open-pollinated varieties of corn into a productive group of related varieties known as Corn Belt Dents... Corn in the future Corn Belt States was changed from a risky crop, either too early, too late, or too drought prone, into a crop so dependable and productive that it pushed wheat out of Illinois and Iowa, over to dry Kansas and Nebraska and up to short-season Minnesota and the Dakotas.'

Toward hybrid maize: plant breeding in the public and private sector

While farmers in temperate and tropical environments alike continued to shape maize varieties to their needs, a handful of naturalists, botanists, and eventually scientifically trained plant breeders began to identify and exploit the phenomenon of heterosis to develop hybrid maize. George Harrison Shull, the Princeton Professor of Botany and Genetics who founded the journal *Genetics* in 1916, produced some of the first hybrids, along with his well-known contemporaries Edward East and Donald Jones (Kahn 1985). In 1908, Shull published '*Composition of a Field of Maize*,' in which he 'clearly states that a maize variety is a complex mixture of genotypes... Shull was able to bring together the key aspects of inbreeding and outbreeding theory and show how they are related in a coherent heterosis concept' (Goldman 1999). Around 1919, Henry Agard Wallace, whose family published an influential farming magazine and was to found Pioneer Hi-Bred, possibly the world's most successful maize seed company, started to produce his own hybrids, with a firm emphasis on yield ('Looks mean nothing to a hog,' he was fond of saying) (Kahn 1985). All of these breeders started with cultivars that had been developed either on farms or (later) on university or state experiment stations.

The first hybrids available in the 1920s yielded about 15% better than open-pollinated maize varieties (Duvick 1999). In 1933, farmers grew hybrids on less than 1% of the maize area in the US Corn Belt, but 10 years later, persuaded by higher yields and the advantages conferred by growing a more uniform crop, they planted hybrids on 78% of the area (Kahn 1985), and private companies like Pioneer were on the way to dominating the maize seed industry. Universities would increasingly concentrate on more basic research in maize genetics, such as the research on maize cytogenetics and transposable genes that won Barbara McClintock a belated Nobel Prize in 1983, and the research that would engender the biotechnology industry in the 1980s and 1990s.

Plant breeding research in the developing world: setting the stage for the green revolution in wheat and rice

Henry Wallace not only contributed to transforming the way that maize research and development (R&D) occurred in the USA, he also initiated a research program that would change the way that R&D would be done for food crops in developing countries by giving scientific plant breeding an international focus.

A number of developing countries had established plant breeding programs early in the 20th century. Although many of these programs were conducted under the aegis of colonial regimes and dedicated to profitable export crops such as cocoa, tea, and coffee, work was done on some food crops; for example, wheat was already being bred for rust resistance at Pusa, India, in 1906 (Howard 1953), and Mexico founded a national school of agriculture in the 1850s (G. Martinez, pers. comm.).

In 1940, in his capacity as US Vice President, Wallace attended the inauguration of a new Mexican president and subsequently toured the country at the behest of Mexico's Secretary of Agriculture. He observed the potential for scientific plant breeding and extension to improve Mexican agriculture much as the university research and extension system had fostered change in US agriculture and agribusiness. Upon returning to Washington, Wallace enlisted the help of the Rockefeller Foundation, which set up a research program on maize, wheat, and beans with the government of Mexico in 1943—'the pioneering cooperative effort in international agricultural research' (Baum 1986).

The progress made through this program encouraged the Rockefeller and Ford Foundations to marshal support on a wider scale to establish a consortium called the Consultative Group on International Agricultural Research (CGIAR). The CGIAR would sustain a network of international agricultural research centers. The first centers, such as the International Rice Research Institute (IRRI) and the International Maize and Wheat Improvement Center (CIMMYT, which was based on the original Mexico–Rockefeller Foundation program), conducted research on crop improvement and agronomy, collected genetic resources, trained developing country researchers, and established local research facilities, among many other activities[*].

Together, IRRI and CIMMYT demonstrated the effectiveness of an international approach to breeding improved varieties of staple food crops by laying the groundwork for what became known as the Green Revolution. The Asian subcontinent was on the brink of famine in the mid-1960s. No one had forgotten how terrible such a famine could be; the Bengal Famine of 1943–44, though arising more from geopolitical than agricultural causes, had led to protracted hunger and death for at least 4 million people. In an exceptional international effort, CIMMYT, IRRI, and researchers in national plant breeding programs developed new wheat and rice varieties that yielded much more than the wheat and rice varieties Asian farmers already grew. When these new varieties were grown in India, Pakistan, and Bangladesh, they produced enough grain to prevent millions of people from dying. The scale of this achievement, occurring slightly earlier in wheat than in rice, was so widely recognised that Norman E. Borlaug, the CIMMYT plant breeder who had first developed the wheat varieties, was awarded the Nobel Peace Prize in 1970.

Wheat: from farmer-breeders to international breeding programs

Like maize, wheat started its travels early, and its great diversity can be attributed partially to its extended cultivation and conservation in many parts of the world over a long time. Perhaps as early as 6000 BCE, wheat moved from West to East Asia. By 4000 BCE, Neolithic farmers were growing and improving wheat across large areas from North Africa and the Near East, to South Asia and onwards to China. Wheat came to be grown in Europe and as far north as Scandinavia, as well as in present-day Russia. Part of the famous 'Colombian Exchange,' wheat arrived in the New World when Spaniards took it to Mexico in 1529[†], and then it spread to southern Africa, Australia, and beyond (Feldman 1976; Cassaday *et al.* 2001).

Farmers developed the wheat varieties that became the lifeblood of rural communities as well as scientific breeding programs. For example, wheat became firmly established in Ontario, Canada, in the 1840s when David Fife, a Scots

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[*] The first centers focused on staple food crops (later ones had mandates related to livestock, trees, fish, food policy, and strengthening national research; see www.cgiar.org for more information).

[†] Where the Catholic Church and Spanish government mandated its cultivation, even under unsuitable circumstances, to produce the hosts needed to celebrate the Mass.

farmer, requested a friend in Glasgow to send him some wheat seed. The friend '…took a dockside stroll one evening and espied a few grains of wheat that had been spilled during the unloading of a ship. He had a hole in the lining of his tam-o'-shanter. He picked up the wheat, carried it off in his cap, and sent it to Fife, who duly planted it. Only five spikes ripened. A wandering cow had eaten two of them and was about to devour the other three when Fife's wife came running out of her kitchen, flapping her apron, and routed the invader. Thus was Red Fife wheat, destined in the years ahead to become the progenitor of many celebrated varieties, saved from death at birth' (Khan 1985). Canadian farmers began to cross Red Fife—which supposedly originated in Polish Galicia (Smale and McBride 1996)—with varieties from South Asia around 1892 (Kahn 1985). When Arthur and Charles Saunders crossed Hard Red Calcutta with Red Fife, they produced Marquis, which yielded so well that it made a considerable difference to the wheat economy of Canada and later the USA. Still other famous wheats would be derived from the hard, red, drought-resistant winter wheat called Turkey Red, brought to Kansas with Mennonites emigrating from Russia (Kahn 1985).

Farmer-breeding was further encouraged by the collection and distribution of wheat seed from throughout the world. Beginning in the 1860s in the USA, for example, an official effort was made to collect wheats worldwide and make them available to anyone who might be interested in crossing them with local wheats (Witt 1985).

By the time that Norman Borlaug began working with wheat in the Rockefeller–Mexico program in 1945, scientific breeding programs had been established to ensure that profitable wheat production would not be threatened by disease and other problems. It was fortunate that Borlaug had a network of scientific breeding contacts to draw upon, for the wheat varieties grown in Mexico had changed little since the 16th century (Khan 1985)[*]. Borlaug took advantage of the Mexican climate to accelerate his breeding work: he planted trials in northern Mexico from November to April, and set to work again in central Mexico from May to October. His first focus was on disease resistance (the rusts limited wheat yields throughout the world); later he sought to reduce lodging and began to work with Norin 10, a Japanese wheat that was developed partly from Daruma (a wheat of Japanese or Korean origin) and was sent to the US after the Second World War. Borlaug obtained seed of Norin 10 from Orville Vogel at Washington State University; the shorter wheats that he bred became known as 'semidwarf wheats' and yielded far better than the taller wheats grown in most parts of the world at that time. Their resistance to rust was an additional yield-protecting asset. Wheat production in Mexico began to grow in an unprecedented way, and the potential of the semidwarf wheats in other parts of the developing world, especially South Asia, was not lost on Borlaug. By 1965, through Borlaug's links with Asian researchers and government officials who were greatly concerned about the prospects of another famine, India was importing 250 t of Mexican semidwarf wheat seed and Pakistan imported 350 t. This seed produced so well that farmers in large numbers switched to the semidwarf wheats. Famine did not return to South Asia. Heisey et al. (2002) estimate that in 1997, CIMMYT-related wheat varieties were planted on more than 64 million hectares in developing countries, representing more than 75% of the area planted to modern wheat varieties in those countries.

The Green Revolution in rice

Not everyone in South Asia consumed wheat, however; in most of Asia, in fact, 'food' and 'rice' continue to be synonymous. The projected Asian famine could not be stopped by higher wheat yields alone, a fact recognised by the foundations and governments that initiated rice research by IRRI. Researchers at IRRI worked rapidly to produce IR8, the first of the high-yielding semidwarf rice varieties, which yielded more than twice as much as any other rice variety. This variety was widely grown throughout Asia in the 1970s and was instrumental, with its successors IR36 and IR64, in restoring food security throughout Asia. IR36 had resistance to multiple pests of rice, and IR64 was a powerhouse combining high yield, good grain quality, and pest resistance (CGIAR 2001). Adoption of these and other improved rice varieties was assisted by favorable government policies, especially by policies that encouraged the expansion of irrigation infrastructure. Evenson (1998) estimated that more than 90% of Asia's irrigated area was sown to improved, high-yielding rice varieties by 1998.

Fischer and Cordova (1998) point out that rice breeders successfully reduced the time it took for modern varieties of rice to become ready to harvest from 140 to 100 days. This reduction increased yield per day of the growing season from 70 kg for IR8 to 90 kg for IR64 and IR72. Because the new rice varieties could be harvested sooner, land became available for growing other crops (including wheat; South Asia's rice–wheat cropping systems now support more than 150 million people). The improved grain quality of varieties such as IR64 helped farmers obtain higher prices for their output.

Hybrid rice

Studies described by Huang *et al.* (1998) indicate that 60% of the increase in rice yields in China between 1975 and 1990

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[*] This was not surprising; wheat was introduced to Mexico as a tribute crop to be grown by indigenous people for export to Spain, where it was a staple; Mexico's indigenous population continued to rely upon, and to breed, maize and beans.

could be attributed to new technology, especially the adoption of hybrid rice. Heterosis in rice was first reported by Jones in 1926 (Virmani 1999). The real breakthrough in hybrid rice research occurred in China in 1970, when plant breeder Yuan Longping and an assistant discovered an indica rice in Hunan Province that exhibited male sterility (Huang *et al.* 1998). More than 20 research institutes in several provinces started to seek the 'maintainer' and 'restorer' lines that could be used to breed hybrid rice. The first maintainer variety was discovered by Yuan and another researcher in Jiangxi Province in 1972, and the first restorer by a breeder in Guangxi Province in 1973. By 1974, a hybrid combination 'with marked heterosis' was developed. The potential 15–20% yield advantage of hybrid rice over conventional high-yielding rice varieties caused the hybrid rice area to expand from 135 000 ha (0.4% of rice area) in 1976 to 15.9 million hectares in 1990 (41.2% of rice area). Japonica hybrids adapted to northern Chinese conditions were developed by 1975, but yield advantage over conventional varieties was 'negligible' and adoption has been limited.

Virmani (1999) comments that studies have shown that hybrid rice can offer an economically viable yield advantage over semidwarf rice, but for many farmers the cost and availability of seed are still an issue. Breeders are seeking to develop apomictic rice (see section below) as a way around this problem.

Impact of international agricultural research beyond the Green Revolution

Long after the initial Green Revolution achievements were celebrated, IRRI, CIMMYT, and the other international research centers of the CGIAR have continued to have a large impact in developing countries. Much (though certainly not all) of this impact is related to plant breeding research. A recent study (Evenson 2000; final results forthcoming 2002) considers what might have occurred if the CGIAR Centers had not created extensive, international collaborative research programs for agricultural research with developing countries. Although some collaboration would eventually have been established, it would probably have occurred later, on a lesser scale, and would probably have been less efficient. Evenson concludes that today, in the absence of the CGIAR, wheat prices would be 34% higher, maize prices 29% higher, and rice prices 41% higher. Numbers of malnourished children in developing countries would be 2.2% higher (translating into many millions of children). In other words, a considerable amount of additional land would have to be dedicated to producing staple foods, an even larger portion of consumers' incomes would have to be used to purchase staple foods (a serious consideration, because poor consumers can spend as much as 70% of their income on food), and more children would either die or lead less productive lives as a result of chronic hunger.

International agricultural research has benefited not only people but the environment as well. By breeding plant varieties with genetic resistance to pests and diseases, public research organisations made farmers' use of harmful, expensive agrochemicals unnecessary. It has been argued that by increasing agricultural productivity per unit of land, research has prevented farmers from cropping more ecologically fragile land and from invading forested areas. Evenson (2000) concludes that in the absence of the work of the CGIAR Centers, the area planted to crops would be significantly higher (4% for wheat, 2% for maize, and 5% for rice). Recent calculations by Grace *et al.* (2000) indicate that if the developing world had attempted to meet its food requirements in 1995 without the improved varieties of food crops[*] developed since the Green Revolution, an additional 426 million hectares of cropped area would be needed (a 5-fold increase over cropped area in 1965). An even more important finding is that this land savings helped to reduce greenhouse gas emissions by 35%. Grace *et al.* conclude that, 'without the Green Revolution... the atmospheric concentration of greenhouse gases would be significantly higher than they are at present and the actual onset of climate change may have hastened.'

For a comprehensive summary of studies on the impact of CGIAR research, see Pingali (2001).

Achievements in breeding maize for developing countries

The plant breeding achievements that occurred during and after the Green Revolution in wheat and rice are well known, but concurrent achievements in maize breeding research are less familiar. Here we would like to focus on two major achievements in maize breeding research at CIMMYT from the 1960s to the end of the century: the development of maize tolerant to drought and low soil nitrogen levels, and the development of maize with superior protein quality.

Maize for African smallholders' risky farming conditions

In sub-Saharan Africa, the great majority of maize farmers have holdings of 0.5–3.0 ha (Byerlee and Heisey 1997)[†] and depend on extremely low-input, low-risk cropping systems. Because they must produce enough maize to feed the family, even in drought years, they dedicate scarce land and labour to producing maize before any other crop, including crops that could improve human nutrition and soil fertility.

Highly erratic rainfall and drought cause great variability in maize production across the region and on individual

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[*] Chiefly wheat, rice, barley, maize, sorghum, millet, rye, and oats.

[†] Only 5% of farmers grow maize commercially on holdings that exceed 50 ha (Byerlee and Heisey 1997).

farms. The effects of insufficient rainfall are made worse by infertile soils. At the regional and national level, below-average maize production and associated cash constraints of farmers discourage the development of the agricultural input sector, especially in remote areas, and in some cases have caused the credit systems of entire countries to collapse. At the farm level, below-average maize production means lower incomes for farmers and an inability to invest in crop improvement technology such as fertiliser (Reeves *et al.* 2002).

CIMMYT considers the development of maize that can cope with drought and low soil fertility to be an important means of helping African smallholders remove the barriers to maize production. If resource-poor farmers can grow maize with higher and more stable yields under their typical conditions (in other words, at the 1.2 t/ha yield level), they will have more income to invest in fertilizers. If household food security can be maintained on a smaller amount of land area, crop production is likely to become more diverse and include a larger proportion of legumes and cash crops (Reeves *et al.* 2002).

Conventional breeding efforts usually focused on raising yields under optimal, agronomically well-managed conditions. In 1996, however, CIMMYT introduced a very different breeding approach, based on more than 12 years of strategic research, to sub-Saharan Africa. In this approach, maize genotypes are evaluated under carefully managed drought and N stress, and the best ones are selected, provided they respond similarly well to optimal conditions (Bänziger and Cooper 2001). This approach is now delivering results.

Among cultivars that had already been released and were available on the market, several cultivars of potential value to smallholders were identified. New cultivars have recently been released in the region (CIMMYT 2002). These include ZM521, an open-pollinated variety. In trials from Ethiopia to South Africa, ZM521 yielded on average 34% better than current releases and showed impressive yield stability. In trials averaging 1–2 t/ha, ZM521 yielded 2.2 t/ha compared with the local check cultivars, which yielded 1.4 t/ha on average, surpassing them by 50% at yield levels typical for smallholder farmers (Bänziger *et al.* 2000).

Several studies have shown that these drought- and N-stress tolerant varieties and hybrids do not take up more water or nutrients (Bänziger *et al.* 1999; Bolaños and Edmeades 1993*a*, 1993*b*; Bolaños *et al.* 1993; Lafitte and Edmeades 1994*a*, 1994*b*, 1994*c*). They use water and nutrients more efficiently for producing grain because they have a higher grain harvest index under conditions that usually reduce the harvest index to less than 0.2–0.3. For this reason, the new cultivars meet all the requirements for sustainably increasing maize yields and improving food and income security. They give smallholder farmers, for the first time, incentives to use improved management practices and diversify crop production.

Quality protein maize for nutritional security

Quality protein maize (QPM), which has been introduced into more than a dozen developing countries through the efforts of CIMMYT, national programs, and Sasakawa–Global 2000, can increase protein availability in regions where maize consumption is high and better sources of protein are unobtainable—often because people cannot afford them. Because it contains nearly twice the lysine and tryptophan—amino acids essential for human nutrition—of normal maize, QPM delivers better quality protein to consumers than they would obtain simply by consuming normal maize. CIMMYT and its partners have developed stable, high-yielding, and disease- and storage-pest resistant QPM hybrids and varieties for diverse settings. New QPM synthetics—superior open-pollinated varieties formed from inbred lines—feature special characteristics such as low and uniform ear placement, resistance to ear rot and root lodging, and (most notably) levels of tryptophan (0.11% of the whole grain), lysine (0.475% of the whole grain), and protein (11.0% of the whole grain) all far beyond those contained in normal maize (CIMMYT 2001). Molecular markers and other advanced laboratory techniques are being harnessed to transfer and maintain the quality protein genes, which are the product of a natural mutation in maize. As a result, in recent years 14 developing countries released dozens of new QPM hybrids and varieties for farmers, and several have launched major QPM promotion programs. Two CIMMYT researchers won the 2000 World Food Prize for their pioneering work on QPM.

Some new applications in plant breeding for developing countries

Plant breeding still depends on genetic resources, on the information that is available about them, and the skill used to apply that information to achieve breeding objectives, but much has changed since keen observational skills provided most of the information needed for farmers and breeders to improve a crop. Contemporary plant breeders are taking advantage of the vastly expanding potential for new information technologies, linked with new molecular and genetic research tools, to provide information for crop improvement. Genetic resources can be understood, evaluated, and used as never before. Here we provide a few general comments and some examples of how new and emerging plant breeding technology has changed the way that crops are improved for developing country farmers.

Molecular markers, genomics, and genetic engineering

New plant breeding approaches involving molecular markers, candidate genes identified through functional genomics, and genetic engineering will allow more efficient improvement of traits that have been difficult to handle through earlier breeding approaches.

By now it is well known that molecular markers hold great promise for increasing efficiency (e.g. by making advances more rapidly than under traditional breeding schemes) and effectiveness (e.g. through making it increasingly possible to pyramid useful genes) in plant breeding. At IRRI, multiple genes for resistance to rice bacterial blight and blast have been pyramided through molecular marker technology to provide durable resistance to these pests. Researchers are also using marker-assisted selection (MAS) to increase drought tolerance (research that is linked to worldwide efforts in structural and functional genomics).

In wheat, CIMMYT researchers use MAS to screen for resistance to barley yellow dwarf virus; in maize, MAS is used to screen for resistance to maize streak virus, for the presence of the quality protein trait, and for drought tolerance. Breeders have used MAS to develop maize for drought environments, and CIMMYT is working with national programs in Kenya and Zimbabwe in an innovative experiment aimed at using a single MAS selection step at an early stage of recombination to further speed the development of drought-tolerant materials.

Despite this progress, the application of markers for complex traits remains challenging. Although geneticists can accelerate breeders' work in the field by identifying plants that carry the useful gene(s) or sets of alleles called quantitative trait loci (QTLs), QTLs identified for resistance to abiotic stresses such as drought usually have a small effect. The resolution of QTL mapping for such traits is generally low. Within the CGIAR, researchers are currently taking advantage of (and seeking) new opportunities for partnerships to speed the identification of gene sequences underlying genetic differences between cultivars. Allelic variants of candidate genes can be identified through comparative mapping and allele mining of the Centers' collections of genetic resources. Based on the sequence differences, superior markers can be developed for wide-scale use in breeding programs. CGIAR breeding programs will benefit from greater access to new high-throughput methods for genotyping, such as those based on microarray technology.

By identifying gene sequences associated with agronomic function, breeders will gain access to genes available in crops other than the ones with which they are working. For example, by identifying genes in a model crop such as rice, breeders may discover homologues in other crops. Tools designed to assist breeders in using these genes across species will be especially useful for combining traits such as yield, nutritional quality, stress tolerance, and specialty traits of value for commercialisation.

Finally, immediate one-stop availability of all aspects of crop information (farming system/crop/molecular), from multiple databases in a user-friendly, real-time format, will enable breeders and other agricultural scientists to identify sources of useful genes for various traits and increase their efficiency in developing superior varieties. The International Crop Information System (ICIS), under development by several CGIAR Centers, national research programs, and advanced research institutes, is just one example of the sort of database that contemporary plant breeders require to improve the efficiency of their research.

Apomixis

Apomictic plants reproduce asexually, rendering seed that will produce plants that are exact clones of the mother plant, regardless of the genetic make-up of available pollen. If this ability could be transferred to non-apomictic species, including maize, wheat, and rice, poor farmers would be able to save seed with improved traits (including hybrid seed) from one crop cycle to the next. They would not lose those traits through the normal process of cross fertilisation; nor would they have to purchase seed every year to benefit from the higher yields conferred by hybrids. In 1999, CIMMYT, France's Institut de Recherche pour le Développement, Pioneer Hi-Bred International, Inc., Limagrain, and Novartis Seeds AG (now Syngenta) reached a 5-year research agreement for the development of apomictic plant varieties. The objective of the agreement is to understand the biology and genetics of this phenomenon for possible use in certain crop plants.

Wide hybridisation: *recent advances in wheat and maize*

The hybridisation of crop species with distant relatives (wild species) has clear advantages: it broadens the genepool and permits the transfer of alien genes that confer positive benefits, such as stress tolerance, which lead to higher yields. By crossing durum wheat with some of wheat's wild relatives, researchers have created synthetic wheats that allow them to tap into the desirable genes present in wild species.

Synthetic wheats developed at CIMMYT have been found to possess resistance to many diseases (e.g. Karnal bunt, fusarium head scab, helminthosporium spot blotch) as well as tolerance to environmental stresses such as heat and drought. Though not adequate for farm production, the synthetic wheats can be crossed readily with high-yielding wheats, thereby acting as a genetic bridge that allows useful traits to be transferred to improved wheat. Disease resistance can be extremely valuable for preserving yields; for example, scab alone has been reported to cause losses of billions of dollars and millions of tons of grain in the US and China. To date, CIMMYT has formed about 800 synthetics. Several have shown very high levels of resistance to scab (e.g. infection rates of only 5–10%, compared with 45–60% in susceptible checks) (Rajaram 2001).

The potential of synthetic wheats was further highlighted in 2001, when CIMMYT reported on the development of wheats that tolerated very dry conditions. These lines are descended from crosses between different types of wheat and goat grass (*Aegilops tauschii*), one of wheat's wild relatives. Though still under development, the new wheats have produced up to 30% more grain for 2 years running in tests comparing them to one of their parents under tough dryland conditions (Rajaram 2001). Drought tolerance genes inherited from their wild ancestor have made all the difference.

Maize, in combination with its wild relatives *Tripsacum* and teosinte, has potential for apomixis research and for developing maize resistant to *Striga*, a parasitic weed of maize that, if left unchecked, severely curtails maize production in eastern and southern Africa. For apomixis, a large step forward was taken at CIMMYT with the development of apomictic, maize-like plants through wide hybridisation; crossing and screening will continue in the hope of producing a true apomictic maize plant. For *Striga*, CIMMYT researchers are evaluating teosinte and *Tripsacum* accessions for resistance; some promising materials have been identified. Maize–*Tripsacum* hybrid derivatives coming from a potentially immune material were also evaluated. Plants backcrossed 3 times to maize were evaluated in the field and showed zero *Striga* emergence. They were further evaluated in the laboratory of Sheffield University's Department of Animal and Plant Sciences, UK, and showed both a reduced level of *Striga* emergence and poor growth of the attached *Striga* plants. One accession has been selected for further analysis, based on field response and the availability of advanced backcross generations to maize.

Issues for plant breeders

In the roughly 100 years since the Mendelian principles of genetics were rediscovered, plant breeding research has moved increasingly out of the field and into the laboratory, out of the public sector and into the private sector, and out of an informal system of exchanging genetic resources and into a more restricted environment of intellectual property regulations. In these circumstances, what issues now confront plant breeders, especially those working for developing countries?

First: *Focus on the traits that matter*

The most immediate issue for plant breeding research directed at conditions in developing countries is to continue focusing on the traits that matter in those countries. Important traits for the future in developing countries (in addition to stress tolerance, already documented) include input-use efficiency (water, nutrients, and other inputs), varieties for new cropping systems (for example, reduced and zero tillage systems or new crop rotations), quality (to enable developing countries to export their production), and nutrition (to combat malnutrition among people who cannot afford to supplement their diets with a wide range of foods or vitamins).

Water

The amount of water available for agriculture in developing countries is likely to decline steadily during the next 50 years as more water is diverted to meet the needs of urban centers and as the effects of global warming become more acute. The need for drought-tolerant maize, especially in eastern and southern Africa, was discussed earlier. In wheat and rice, water shortages will be most severe in developing countries where these crops are grown under irrigation and where urbanisation is proceeding at alarming rates (e.g. India). Water shortages may affect more than 30 million hectares of irrigated wheat land, at a time when demand for wheat will be even higher than it is today. CIMMYT's wheat breeders have crossed promising sources of drought tolerance (synthetic wheats, landraces, related species, and some adapted cultivars) with high-yielding, disease-resistant wheats. Their aim is to improve yield by combining tolerance to drought with responsiveness to improved soil moisture status. Disease resistance is also a key component of the strategy (Rajaram 2001). The progeny of these crosses are evaluated under a combination of gravity basin and drip irrigation schemes. Drip irrigation gives breeders greater flexibility in controlling the timing of drought stress—a critical factor affecting yield in many production systems—and uses up to 50% less water than gravity-fed irrigation to obtain the same yield. Wheats that respond well to water deficits at different stages of growth are identified and advanced in CIMMYT's wheat breeding program (see also the earlier discussion of synthetic wheats). These materials are screened for rust and *Septoria tritici* resistance and further evaluated for yield under full and partial drought stress prior to inclusion in CIMMYT's international yield evaluation network.

As discussed earlier, biotechnology should increasingly contribute to improving drought tolerance in crop species, both through more efficient methods of selection and through the identification and use of a wider range of genes contributing to drought tolerance.

Nitrogen

CIMMYT breeders have developed a method to identify wheats with better nitrogen-use efficiency. They crossed wheats that were good at absorbing nitrogen with others that utilised nitrogen exceptionally well. After 8 years of testing, they confirmed that by alternately applying first high and then low nitrogen levels to successive cycles of offspring, they produced lines that yielded better than all the others (Rajaram 2001). This method, used throughout the breeding process, will ensure that all CIMMYT wheats combine good nitrogen uptake and good nitrogen utilisation.

Wheat quality

During the late 1980s, CIMMYT emphasised raising wheat yields because we were working in countries where increasing wheat production and productivity were more important than improving grain quality. Because there is often a direct, inverse relationship between yield and quality (i.e. the higher the yield, the lower the quality, and *vice versa*), improving end-use quality could not be justified as a major breeding goal. At that time, higher quality wheat did not fetch higher prices than regular wheat in the areas where CIMMYT worked.

In the early 1990s, quality improvement became more important in wheat breeding programs around the world, especially in countries where wheat markets were liberalised and end-use quality traits such as protein content and gluten strength increasingly determined the commercial value of the wheat crop. In 1995 CIMMYT bread wheat breeders gradually increased quality selection pressure and started using genotypes with strong, extensible gluten in new crosses. Selecting for quality parameters is now fully integrated into CIMMYT's wheat breeding research (Rajaram 2001; R. J. Peña, CIMMYT, Senior Scientist, Head, Industrial Quality, pers. comm.).

Applications of biotechnology offer further opportunities for investigating the genetic and biochemical basis of individual protein subunits and other molecules contributing to the end-use quality of wheat. Using genetic transformation, new cultivars with improved quality can be developed through the insertion of genes coding for key grain quality attributes. Molecular marker technology should increase the efficiency of breeding for quality.

Nutrition

The diets of the rural and the urban poor tend to be deficient not only in calories but also in protein quantity and quality (i.e. amino acid balance), vitamins, and micronutrients. Women and children, who make up the vast majority of people living in poverty, usually suffer most from these deficiencies. Nutritionally fortified maize and wheat being developed at CIMMYT could make an enormous difference in nutritional security for these people. This research relies on the complementary tools of conventional breeding and biotechnology, as well as information from nutritional and socioeconomic studies, to ensure that the most appropriate varieties are developed. (We focus here on maize and wheat, given that the story of vitamin A rice ('golden rice'), and IRRI's role in its development, will already be familiar to readers.)

Aside from improving the protein quality of maize (discussed earlier), researchers have examined ways of increasing its micronutrient content[*]. Initially CIMMYT's research on improving micronutrient levels in maize focused on southern and eastern Africa, where white-grained maize is the major staple food and deficiencies of micronutrients and vitamin A are often acute. Researchers systematically evaluated nearly 2000 maize varieties and landraces, representing the entire genetic base of white-grained tropical maize, to identify maize with higher iron and zinc concentrations. This undertaking was not as straightforward as one might think, partly because the environment in which a variety is tested greatly influences the concentration of micronutrients in maize kernels and partly because high micronutrient varieties often showed lower yields. After considerable preliminary work, researchers developed experimental hybrids that could meet an additional 30%, 20%, and 10% of the daily iron demand of men, women, and pregnant women, respectively, without compromising yield, and they are exploring strategies to further boost nutritional value (CIMMYT 2001).

In wheat, CIMMYT has identified significant variation for iron and zinc, but the lines with the greatest concentration of these elements either yield poorly or consist of wild relatives of wheat (the maize research described earlier produced similar findings). Research has concentrated on understanding the genetic bases of micronutrient concentration. This information will make it possible to transfer the ability to produce higher concentrations of iron and zinc from low-yielding wheats into higher yielding and/or widely adapted wheats.

In addition to simply adding quantities of iron and zinc, it is important to reduce other factors that often limit the availability of these micronutrients. One major negative factor is phytic acid, a powerful chelator of elements such as iron. CIMMYT is introducing low phytic acid mutants into tropical maize varieties to determine the effect on the bioavailability of micronutrients; similar options are being investigated for wheat (CIMMYT 2001).

Iron, zinc, magnesium, and other micronutrients can be enhanced in maize and wheat by engineering new enzymes that control micronutrient uptake, movement, and storage. In addition, by modifying key enzymes, negative factors such as phytic acid can be reduced. Levels of critical vitamins such as vitamin A and folic acid may also be improved. In an effort to improve grain protein quality, scientists from CIMMYT and CINVESTAV (Mexico's Centro de Investigación y de Estudios Avanzados) inserted a gene for a seed protein from amaranth into maize. The protein produced has very high levels of lysine and tryptophan, much like QPM (which is not transgenic). This approach provides an additional boost to the amino acid profile in

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[*] This research was part of a project involving several CGIAR Centers and coordinated by the International Food Policy Research Institute (IFPRI), 'Identifying Agricultural Strategies for Reducing Micronutrient Malnutrition'.

maize and could help to develop wheat (and other cereals) with better protein quality (CIMMYT 2001).

Second: *Find a balance in the roles of the public and private sectors*, *especially in R&D for developing countries*

For a considerable period, publicly funded institutions have conducted much of the plant breeding research for and in developing countries. This situation is changing; the new appropriability of genetic resources has provided an incentive for private companies to invest in research. More than ever, it is essential that public and private research organisations adopt complementary and mutually reinforcing forms of working together.

What are the roles of public and private organisations in such a collaboration? CIMMYT convened an international forum in Tlaxcala, Mexico, in late 1999 to initiate a dialogue on key issues related to public/private alliances in agricultural research (CIMMYT 2000*b*). This group concluded that the private and public sectors each have a role to play in moving agriculture from a subsistence to a commercial basis. Public sector research can help promote private sector involvement in developing countries by reducing the costs of private firms' entry into R&D, but the public sector (and/or public sector funding) has a role to play in serving the needs of farmers where market conditions discourage the private sector from making the investments needed to provide a range of appropriate, affordable technologies. Conditions that discourage private investment include a preponderance of noncommercial farmers in transition to commercial farming, small markets, and marginal environments, as well as situations in which the private sector operates but offers a limited range of technology choices. Even where both private sector and international researchers are active, strong public national programs are still needed to adapt international research to local conditions, and national governments should allocate increased resources for this to occur. Where this strategy is not fully possible in the short term, other institutional arrangements to accomplish this purpose should be devised.

The Tlaxcala forum also emphasised that the relative strengths of the private and public sectors in genomic information and germplasm, respectively, should provide a strong basis for forming alliances. Alliances are critical to ensure that biological and information technologies are adapted to benefit resource-poor farmers. These alliances will probably be based on market segmentation, for example, by country, region, product (e.g. hybrid maize *v.* open-pollinated maize), crop, and/or type of farmer (commercial, subsistence).

At CIMMYT, additional resources have been obtained for biotechnology research as a result of successful negotiations and partnerships with the private sector. CIMMYT's policy is to enter into such agreements only if they enhance the Center's ability to achieve its mandate of service to the resource-poor and the environment (Reeves and Cassaday 2001). The agreements give CIMMYT access to the technologies and resources necessary to meet the demand for improved maize and wheat germplasm for our partners, and they give our partners in the South ready access to these new technologies. As we move forward, these 'win–win' arrangements will become more important, and we will need to add to our expertise in the management of intellectual property and negotiating skills (see below). One example (among several) of research in which these partnerships are of critical importance is the development of apomictic maize, described earlier.

Third: *Develop expertise in managing and accessing intellectual property*

As Pardey and Wright (2001) observe, 'Though nations have sometimes monopolised key genetic resources, until recently agricultural technologies... have otherwise been unencumbered by proprietary claims and freely available to all.' As noted earlier, since the 1980s, genetic resources in their many forms—plant varieties, the genetic components of plants, and the information associated with them—have gained in value, and the private sector has increasingly appropriated the rights to these assets. Public-sector scientists developing research products for poor people find it more difficult and costly to access the genetic resources, products, and processes required for their research. Pardey and Wright (2001) emphasise that reduced funding for agricultural research in developing countries probably hampers the ability to meet food requirements far more than intellectual property issues, but that, nevertheless, '…a problem lies ahead for research on some staple food crops as poorer developing countries move into compliance with their intellectual property commitments to the WTO by the year 2005 and as patent applications are increasingly lodged in developing countries.'

Public organisations themselves are feeling compelled to seek intellectual property protection over their products, not so much to profit from this action as to prevent other agencies from appropriating rights to their research materials and making them difficult and/or expensive for others to access. CIMMYT's policy on intellectual property (CIMMYT 2000*a*), for example, emphasises the Center's concern over preserving public access to its research products.

Fourth: *Seek a balanced*, *interdisciplinary approach*

Success in plant breeding research, especially the kind of applied research conducted at CIMMYT and other CGIAR Centers, depends a great deal on being able to use the most appropriate technology to develop the most appropriate end product. At CIMMYT, we feel strongly that neither tradition nor novelty should dictate the most appropriate means of achieving a breeding objective. Our objective has always been to harness new science effectively, without losing the advantages of traditional approaches, as the research projects discussed in the course of this paper have indicated.

A growing concern in plant breeding institutions that do not rely solely on biotechnology is the increasingly limited pool of breeders with experience in the field and not solely in the laboratory. The intellectual and economic allure of such biotechnology-related disciplines as molecular genetics has drawn talented researchers away from the more traditional plant improvement disciplines. The experience of CIMMYT has been that the perspectives of researchers from several disciplines, including scientists with experience in the practicalities of taking new crop varieties from the developmental stage to farmers' fields, are needed to ensure that poor farmers have the seed they need to overcome farming constraints, hunger, and poverty.

To foster sustainable food security, CIMMYT supports an integrative research paradigm that brings together the best genotypes (G), in the right environments (E), under appropriate crop management (M), generating appropriate outcomes for people (P). Everyone who seeks to foster sustainable agriculture in developing countries should recognise the interdependence of these factors, because most organisations alone cannot contribute fully to each aspect of G × E × M × P. Partnerships and consortia that assemble the best possible teams to execute the G × E × M × P approach will underpin the timely and successful achievement of sustainable farming systems and future food security (Reeves *et al.* 2000).

One example of this sort of research is a project on Insect Resistant Maize for Africa (IRMA) (Reeves and Cassaday 2001). In this project, scientists from the Kenya Agricultural Research Institute (KARI) and CIMMYT use conventional as well as biotechnological breeding strategies to develop maize resistant to stem borers, which are estimated to destroy 15–40% of Kenya's maize crop each year. The IRMA project was launched through a consultative meeting in which all groups concerned with the outcome met to discuss their views of the project, including representatives from KARI and CIMMYT as well as from farmers', women's, and church associations; extension services; various ministries; the private sector; and a contingent of Kenyan print and broadcast media. The project calls on CIMMYT and KARI expertise in maize breeding, agricultural economics, biotechnology, entomology, and communications.

Over 5 years, researchers participating in the project will develop integrated pest management strategies and use conventional and biotechnological means (including resistance based on Bt genes) to breed insect-resistant maize for major Kenyan production systems and insect pests. The project will also establish procedures to provide insect-resistant maize to resource-poor farmers; assess the impact of insect-resistant maize in Kenyan agricultural systems; transfer skills and technologies to Kenya to develop, evaluate, disseminate, and monitor insect-resistant maize; and plan, monitor, and document the project's processes and achievements for dissemination to other developing countries, particularly in East Africa.

It is important to emphasise that project researchers have agreed to identify and develop gene constructs that contain no herbicide or antibiotic markers. Maize varieties produced by the IRMA Project will carry only 'clean' or 'purified' Bt genes, circumventing concerns about unforeseen impacts on the environment or human health. While this approach costs more and takes longer, IRMA researchers are committed to addressing all reasonable issues that emerge regarding the technology.

Conclusions

The need for plant breeding research will not diminish with time, especially in developing countries. Three-fourths of the world's poor people still depend directly or indirectly on agriculture (Diaz-Bonilla and Robinson 2001). Rosegrant *et al.* (2001) project that between 1997 and 2020 demand for wheat will grow by 45% (about 266 million tons), demand for maize by 30% (about 175 million tons), and demand for rice by 32% (about 122 million tons). Developing countries in Asia will account for half of the projected increase in world demand for cereals over this period; China alone will account for one-fourth of world demand. Unless land currently dedicated to cereal crops becomes more productive, farmers in developing countries will need to bring an additional 41 million hectares under the plow (20 million in Africa alone). The environmental consequences of expanding cultivation will be enormous. If investment in agricultural research continues to decline, and if crop yields grow more slowly as a result, food will become scarce and prices will rise sharply. The price of rice, for example, would be 40% higher than currently projected in the baseline rice price scenario described in Rosegrant *et al.* (2001).

Nearly everyone is aware that the world produces enough food to feed all of its people, but the challenge of supplying food to those who need it most is not as simple as it would appear. Trade alone is not likely to get more food to hungry people. Falcon (2000) observes that 'If developing countries with a large percentage of undernourished people are to solve employment, income, and food-access problems, most of the increased agricultural output must be grown within the borders of these nations.'

In a globalising world, it is more important than ever that rural people, with few resources and little access to information, gain access to the technology that will not only help them overcome food shortages but eventually produce and sell in rapidly evolving markets. The results of plant breeding research, embodied in improved seed, can reach people far more easily than more complex technologies. Wheat seed that produces grain of export quality, for example, will enable more developing country farmers to compete in the market.

Nor is it enough for plant breeding institutions to assume that their job is done once improved seed is developed. The extension systems of many developing countries have collapsed in recent years, leaving hundreds of millions of farmers without links to the research system. Through farmer participatory approaches to plant breeding and alliances with non-governmental and other community development organisations, plant breeders are increasingly communicating with farmers and helping to foster networks for sharing information as well as research products.

What is increasingly clear, at least for public international plant breeding programs, is that a greater diversity of partnerships is needed to produce the products (often referred to, with varying degrees of accuracy, as 'public goods') that will help bridge the gap between the global 'haves' and 'have-nots.' These partnerships range from traditional philanthropic arrangements to purely commercial alliances and include direct support for research, collaborative public sector research, licensing (different agreements for sharing costs and technology), market segmentation, technology grants for research in developing nations, and joint ventures (Falcon 2000). At CIMMYT, these include alliances between CIMMYT and the private sector (e.g. in the research on apomixis, described earlier) and partnerships between CIMMYT and other public research organisations in which processes or products of biotechnology are used (e.g. the IRMA Project).

Finally, plant breeding institutions, especially international institutions such as the CGIAR Centers, also have a strong responsibility to act as advocates on behalf of the rural poor, especially in demonstrating how public policy can ease the burdens and increase the opportunities arising from globalisation. As Babinard and Pinstrup-Andersen (2001) point out, 'Modern science and new technologies in information, biology, and communications can provide the poor and malnourished with a voice in policymaking and the tools to become more effective at facing the competitive forces and risks brought about by globalisation.'

Mendel's successors in the plant breeding community—at least those who wish to improve human and environmental welfare—have a tough row to hoe. They must contribute to solving problems once viewed as lying far outside the realm of plant improvement, but if they succeed, they will fulfill their role as 'agents of change in human society' and leave a valuable legacy (improved incomes, health, and environmental well-being) for generations to come.

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