TIMELINE

Green revolution: the way forward

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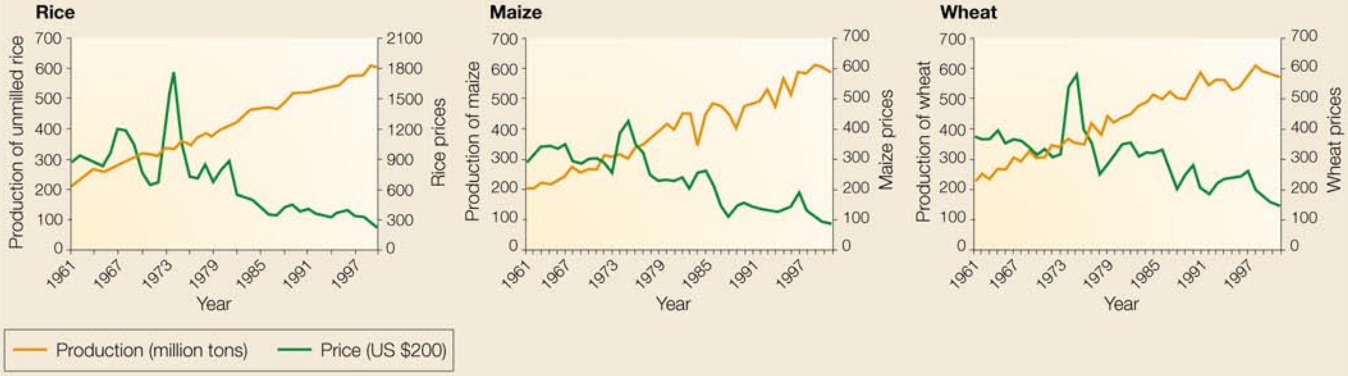
The origin of agriculture led to the domestication of many plant species and to the exploitation of natural resources. It took almost 10,000 years for food grain production to reach 1 billion tons, in 1960, and only 40 years to reach 2 billion tons, in 2000. This unprecedented increase, which has been named the 'green revolution', resulted from the creation of genetically improved crop varieties, combined with the application of improved agronomic practices.

The 1960s was a decade of despair with regard to the world's ability to cope with the food–population balance, particularly in developing countries. Most of the lands suitable for agriculture in Asian countries had been cultivated while population growth rates were accelerating, owing to the rapidly declining mortality rates that have resulted from advances in modern medicine and health care. International organizations and concerned professionals hosted seminars and conferences to raise awareness of the ensuing food crisis and to mobilize global resources to tackle the problem on an emergency basis. In their famous book, *Famine 1975!*, published in 1967, the Paddock brothers[1] predicted that "Ten years from now, parts of the underdeveloped world will be suffering from famine. In 15 years, the famines will be catastrophic, and revolutions and social turmoil and economic upheavals will sweep areas of Asia, Africa and Latin America".

Fortunately, large-scale famines, and social and economic upheavals, were averted, thanks to the marked increase in cereal-grain yields in many developing countries that began in the late 1960s. This phenomenon — known as the 'green revolution' — was due largely to the widespread adoption of technology that was developed to generate genetically improved varieties of crops with increased yields.

The green revolution has had a tremendous impact on food production, socio-economic conditions and environmental sustainability (BOX 1). Between 1966 and 2000, the population of densely populated low-income countries almost doubled, but food production increased by 125%. The marked achievements in world food production were caused by applying advanced technology to the development of high-yielding varieties of cereals. These varieties, in particular those of rice, maize and wheat, were first developed at the International Rice Research Institute (IRRI) in the Philippines and at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico, respectively. Since then, national programmes have developed many improved varieties of cereals that have become widely grown. Because rice,

Box 1 | The impact of the green revolution



Impact on food production

The gradual replacement of traditional varieties of rice, maize and wheat by improved varieties, and the associated improvement in farm-management practices, has had a marked effect on the growth of rice, wheat and maize output, particularly in Asia. For example, since the first high-yielding variety of rice was released in 1966, the rice area harvested has increased only marginally by 20%, whereas the average rice yield has doubled. Total rice production increased by 132% from 1966 to 1999. During the same period, world wheat production increased by 91%, to 576 million tons.

In many Asian countries, the growth in cereal production has outstripped the rise in population, leading to a substantial increase in cereal consumption. During 1965–1990, the daily caloric intake in relation to requirement improved by ~150% in several Asian countries.

Impact on socio-economic conditions

The increase in *per capita* availability of cereals, and a proportional decline in the cost of production, contributed to a decline in the real price of rice, wheat and maize, in international and domestic markets. The unit cost of production is about 20–30% lower for high-yielding varieties than for traditional varieties of rice, and the price of rice, wheat and maize (adjusted for inflation) is 40% lower now than in the mid-1960s (see figure). The decline in food prices has benefited both the urban poor and the rural landless.

Impact on environmental sustainability

The widespread adoption of high-yielding varieties has helped most Asian countries to meet their growing food needs from productive lands and so has reduced the pressure to open up more fragile lands. Had 1961 yields still prevailed today, three times more land in China and two times more land in India would be needed to equal 1992 cereal production. If the Asian countries had attempted to produce a 1990 harvest at the yield levels of the 1960s, most of the forests, woodlands, pastures and range lands would have disappeared, and mountain sides would have been eroded, with disastrous consequences for the land and wildlife habitats.

The availability of cereal varieties with multiple resistance to diseases and insects has reduced agrochemical use, so improving the human health of farming communities, making pesticide-free food more available, and protecting useful fauna and flora.

maize and wheat account for almost 50% of calories in the human diet, the focus has been on increasing the production of these three species.

In this article, I provide a historical perspective on the green revolution. I discuss the genetic modification made to cereal varieties to raise their productivity, the impact of improved varieties on food grain production and the strategies for further improvement, to meet the demand of a growing human population.

Genetic improvement strategies

Several genetic traits were selected to increase the yield, YIELD STABILITY and wide-scale adaptability of rice, maize and wheat varieties. These include selection for higher yield potential (productivity); wide adaptation (adaptability to diverse environments); short growth duration; resistance to biotic stresses (diseases and insects); tolerance to abiotic stresses (such as drought and flooding); and superior grain quality.

Conventional hybridization and selection was and still is widely used for improving yield potential (BOX 2). This strategy creates variability by hybridizing the elite genotype (the breeding lines that have the most sought-after characteristics) with other improved varieties, endemic varieties and even wild species, followed by selection of the desirable recombinants. It has been estimated that, on average, ~1% increase has occurred per year in the yield potential of rice and wheat in the past 30 years after the development of dwarf (short stature) varieties, which is discussed below.

Another approach for increasing the yield potential — one that has been very successful in rice and wheat — is ideotype breeding or modification of plant architecture (morphology). For example, plants were selected for reduced height, increased tiller (shoot) number and for erect instead of droopy leaves. The yield potential of maize was also increased by reducing the plant height and by selecting for erect leaves[2].

To further increase the yield potential of rice, a new plant type was conceptualized[3]. The proposed modifications to the plant architecture included a reduction in tiller number, an increase in the number of grains per PANICLE and increased stem stiffness (FIG. 1). Numerous breeding lines with desired characteristics have been developed and several have outyielded the modern high-yielding varieties by 15–20%. Wheat breeders are using a similar approach for increasing the yield potential of wheat[4].

Heterosis breeding — which exploits the increased vigour (improved growth rates) of F_1 hybrid plants — has been used to improve the yield potential of maize (BOX 2). In fact, most maize growers in developed countries grow maize hybrids, and the area planted to maize hybrids in developing countries is also increasing. Rice hybrids with a yield advantage of 10–15% were introduced in China in the 1970s[5] and are now planted in about 50% of the rice area in that country. The rice hybrids suitable for planting in the tropics and subtropics that have been developed at the IRRI and by National Agricultural Research Systems (NARS) outyield the best-improved cultivars by 12–15%; it is hoped that, when adopted widely, they will have an impact on rice production. Research on wheat hybrids is also underway, but wheat hybrids are not grown commercially as yet[6].

A further method for selecting individuals that are adapted to diverse environments is the shuttle breeding approach used by Norman Borlaug[7]. This method, which allows selection of individuals adapted to diverse environments by breeding alternate generations of segregating populations at different locations, has been very successful in wheat (BOX 2).

Varietal improvement

Yield potential. The varieties of rice and wheat that were cultivated before the green revolution were tall and leafy with weak stems, and had a harvest index of 0.3. When high doses of nitrogenous fertilizer were applied, traditional varieties tillered profusely, grew excessively tall, lodged early and yielded less than when lower fertilizer levels were used. To increase the yield potential, it was necessary to improve the harvest index and nitrogen responsiveness by increasing lodging resistance. This was accomplished through reducing plant height by incorporating a recessive gene, *sd1*, for short stature in rice[8] from a Chinese variety, Dee-geo-woo-gen, and one of the recessive genes,

Box 2 | Crop breeding strategies

Conventional breeding

In a conventional breeding programme (see figure part **a**), two parents are crossed and the segregating populations are screened for the trait under transfer (disease resistance in the example shown), as well as for many agronomic traits, such as lodging resistance, growth duration, plant height, panicle characteristics and percentage of empty grains. Even in the observational and yield trials, data on all these traits are obtained.

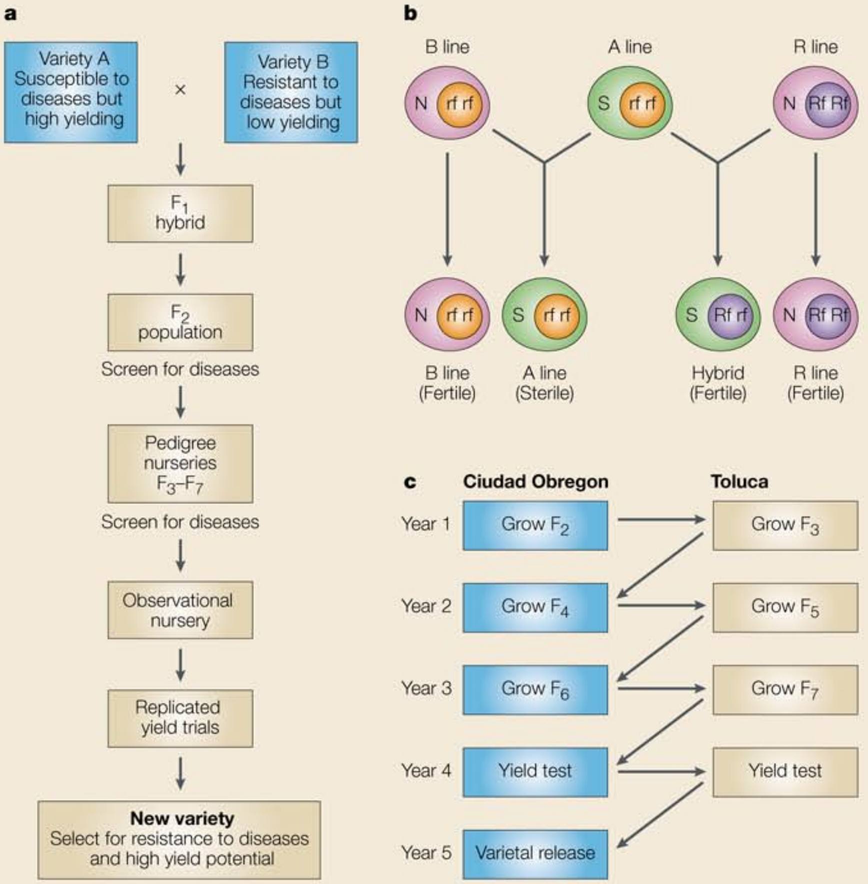
Hybrid breeding

Hybrid breeding (see figure part **b**) exploits the increased vigour (heterosis) seen when crossbreeding plants of different lines. In rice hybrid breeding, three lines that differ in cytoplasmic and nuclear genes required for male fertility are used (A, B and R). The two sterility loci involved are the cytoplasmic gene for sterility, S (N indicates a normal cytoplasm), and the nuclear gene, *rf* (for lack of fertility restoration). To generate fertile F_1 hybrid seeds on a large scale for commercial plantings, a male sterile line, A (which is homozygous for the nuclear *rf* gene), is mated to the 'restorer' line R, which is fertile as it has an 'N' cytoplasm as well as the dominant nuclear *Rf* gene for fertility restoration. The resulting hybrid seeds are fertile because they are heterozygous at the *Rf* locus. Because the male sterile A line is unable to reproduce by selfing, this line must be maintained by crossing it with another line, B (left), which, owing to its 'N' cytoplasm, is male fertile. The resulting hybrid is sterile because cytoplasm is mainly inherited from the mother (line A), which is 'S'. Both the B and the R lines are fertile and can be maintained by the breeder by selfing.

In maize, male flowers (tussels) are at the top and female flowers (cob) are lower down the plant. To produce hybrid seed, the tussels of the plants that are to act as females are mechanically removed and seed is produced by fertilization with the pollen of male parents.

Hybrid wheat breeders use a chemical gametocide to sterilize the plants that are to act as females. These chemically sterilized plants produce hybrid seed when fertilized by pollen from non-treated plants of the male parent.

The hybrid breeding strategy in rice is quite labour-intensive as breeders need to construct the three types of line (A, B and R) for each new hybrid. However, this method has the advantage over chemical gametocide of having no secondary phytotoxic effects on the plants, which would reduce hybrid seed production.



Shuttle breeding

The focus of the shuttle-breeding approach in Mexico, shown here in figure part c, was to develop wheat varieties with wide adaptation. Segregating populations were grown during winter — the normal wheat-growing season — at Ciudad Obregon, located at 28° latitude and near sea level. The second generation was obtained by planting during May at Toluca, at 18° latitude and an elevation of 2,600 m. The Toluca site is characterized by heavy rainfall and cool temperatures; severe epidemics of both stem rust and stripe rust develop there every year. This shuttling of breeding materials allowed selection for rust resistance and adaptation to diverse growing conditions.

Figure 1 | **Sketches of different plant types of rice.** Left, tall conventional plant type. Centre, improved high-yielding, high-tillering plant type. Right, new plant type ('Super Rice') with low tillering but sturdier stems, and with a larger number of grains per panicle. (Reproduced with permission from REF. 36.)

Rht1 or *Rht2*, for reduced height in wheat[4], from a Japanese variety Norin 10. Because plants with these so-called 'dwarfing' genes put less resources into straw production, they put more into the developing grain, so increasing the harvest index by over 60%. The short-statured varieties of rice and wheat also had a combination of other desirable traits, such as high TILLERING, dark green and erect leaves for better use of solar energy, as well as sturdy stems. Short stature and stem sturdiness resulted in higher responsiveness to nitrogenous fertilizer. So, with the application of fertilizer, the yield potential doubled to about 9 tons ha^{-1}, constituting an important breakthrough in the history of crop improvement. The gains in yield obtained through genetic manipulation in commercial hybrids of temperate maize (in the United States and Canada) were accompanied by large and consistent improvements in resistance to root lodging, stalk lodging, premature plant death and barrenness (plants without cobs). The increase in yield potential has mainly come from the plants being able to withstand increased planting densities, and not from any marked reduction in plant height or rise in harvest index[9]. In tropical maize, however, harvest index was improved through reduction in plant height[2]. Reduction in height was based on selection for polygenic variation as compared with rice and wheat, in which major genes were used to decrease height.

Wide adaptation. Many of the traditional varieties of rice were PHOTOPERIOD SENSITIVE and, because they had been selected for adaptation to specific environments, their cultivation was restricted to one season. However, most of the improved varieties have been made insensitive to photoperiod by the introduction of the *se1* (photoperiod-insensitivity) gene, and can be grown during any season and in most tropical and subtropical countries provided the temperatures are favourable. For example, the IR8 variety of rice, which was released in 1966 by the IRRI, gave double the yield of previous rice varieties when grown in irrigated conditions, as it was more responsive to fertilizers. IR8 also had wide adaptation (features that earned it the name of 'Miracle Rice'): it was grown in most of the rice-growing countries of Asia, Africa and Latin America. Most of the subsequent releases have similar wide adaptation. Wide adaptation was also incorporated into improved varieties of wheat by using the shuttle breeding approach, as discussed in BOX 2.

Short growth duration. The availability of short-duration varieties has led to large increases in cropping intensity, greater on-farm employment, increased food supplies and higher food security in many countries. Most traditional varieties of rice in tropical and subtropical Asia matured in 160–170 days and many were photoperiod sensitive. These were suitable for growing one crop of rice a year during the rainy season but not for multiple cropping systems. Even IR8 and subsequent varieties, which matured in 130 days[10], did not leave sufficient time in one rainy season to grow another crop of rice. Therefore, improved varieties were developed that had even shorter growth duration by incorporating ef (early flowering) genes for early maturity. So, varieties with a duration of 110 days or even 105 days were developed. However, yield is a primary consideration in developing new varieties and, therefore, during the selection process, only those short-duration lines with yield potentials that match those of medium-duration varieties are saved. The key to the success of this programme was the selection of plants with rapid vegetative vigour at earlier growth stages[11]. Because they have higher growth rates at early stages, short-duration varieties are able to produce about the same biomass in 110–115 days as the medium-duration varieties do in 130–135 days. Under most situations, the yields of early- and medium-growth duration varieties are similar. However, because the short-duration varieties produce the same amount of grain in fewer days than medium-duration varieties, their per-day productivity is much higher.

The growth duration of wheat varieties was similarly reduced by incorporating the *Pdp1* and *Pdp2* genes that cause photoperiod insensitivity[4]. Short-duration varieties grow rapidly during the VEGETATIVE PHASE and, because they compete better with weeds, weed-control costs are reduced and, as they use less irrigation water, production costs fall.

Resistance to biotic stresses. The varietal composition and cultivation practices for rice and wheat changed markedly with the introduction of high-yielding varieties. A relatively small number of varieties replaced literally thousands of traditional varieties, thereby reducing the genetic diversity of these crops[12]. Farmers started using improved cultivation practices, such as applying higher doses of fertilizers and establishing higher plant populations per unit area. The development of irrigation facilities and the availability of short-duration, photoperiod-insensitive varieties enabled the farmers in tropical Asia to grow successive crops of rice throughout the year — practices that led to an increase in disease incidence and insect numbers.

Because the chemical control of diseases and insects for prolonged periods in tropical climates is impractical, the use of host-plant resistance to disease and insect control is the logical approach to overcome these production constraints. A major emphasis was placed on developing GERMPLASM that can provide resistance to multiple diseases and insects[13]. Large germplasm collections of rice were screened for resistance at the IRRI, and parents (donors) with resistance to the main diseases — blast, bacterial blight, tungro and grassy stunt — and to four insects — brown planthopper, green leafhopper, stemborer and gall midge — were identified. Some of the germplasm donors were genetically analysed to identify the genes that provide resistance[14], which were then incorporated into improved germplasm to develop multiple-resistant varieties. The first variety of rice with multiple resistance was IR26. Since then, many varieties with multiple resistance have been developed by the IRRI, and by other national programmes. For example, IR36 carried *Xa4* for resistance to bacterial (*Xanthomonas campestris*) blight; *Pita*, *Piz*, *Pib1* and *Pib2*, and *Pik-S* for resistance to blast; *Gs* for resistance to grassy stunt; *bph2* for resistance to brown planthopper; and *glh10* for resistance to green leafhopper. The multiple-resistant varieties have as many as 20 different parents in their ancestry. So, in essence, the plant-breeding process has incorporated useful genes from many traditional varieties into modern varieties.

Large-scale adoption of varieties with multiple resistance has helped to stabilize world rice production, and varieties with multiple resistance show only minor fluctuations in yield from year to year. By comparison, the yield of susceptible IR8 does fluctuate from year to year, as disease or insect attack can drastically reduce it.

However, resistant varieties do not remain resistant forever, as they become susceptible to new races or biotypes of diseases and insects. Therefore, many different genes that confer resistance to each of the diseases and insects have been identified in rice so that when a variety with a particular gene becomes susceptible, a new one with a different gene is introduced[14]. Germplasm with more durable resistance to diseases and insects is also being developed, and strategies for deploying varieties with specific genes during different years and in specific countries are being investigated[15].

Wide-scale adoption of rice varieties with multiple resistance has reduced the need for harmful pesticides and has allowed the implementation of integrated pest management programmes. In field trials conducted in the Philippines, yields of a multiple-resistant variety (IR64) in the plots with and without insecticide treatments were similar[16].

Wheat and maize breeders have similarly incorporated multiple resistance to diseases and insects in improved varieties. For example, modern wheat varieties are resistant to stem rust, leaf rust, stripe rust, septoria, leaf blotch and fusarium head scab[17], and maize breeders have incorporated resistance to several diseases, such as downy mildew, turcicum blight, maize streak virus, grey leaf spot and corn stunt, and to insects, such as armyworms, earworms and stemborers[18].

Tolerance to abiotic stresses. Vast tracts of land in Asia, Africa and Latin America that are suitable for crop production remain unplanted because the soil is nutritionally deficient or contains toxins. Even well-managed ricelands suffer from mild nutritional deficiencies and toxicities. For example, large tracts of rice soils have different levels of salinity and alkalinity, and zinc deficiency in them is becoming a concern. Several improved varieties have been developed through selective breeding to have moderate-to-high levels of tolerance for several nutritional deficiencies and toxicities. IR36, for example, has tolerance to salinity, alkalinity, peatiness, and iron and boron toxicities. Similarly, IR42 has a broad spectrum of tolerance for many soil deficiencies and toxicities. Varieties that are tolerant of these soil conditions have a more stable yield performance, and have been helpful for reclaiming degraded and marginal lands and in extending the coverage with high-yielding varieties.

Rain-fed rice is planted on ~40 million ha worldwide. Vast areas suffer from drought at some stage of the growth cycle of a rice crop. In some areas, crops suffer from floods, which submerge the crop for up to 10 days. As rice varieties cannot survive such prolonged submergence, a few rice varieties have been identified that survive submergence for up to 10 days. A dominant gene, *Sub1* (*submergence tolerance 1*), and several quantitative trait loci (QTL) that improve submergence tolerance have been identified in the FR13A variety of rice from India. Using FR13A as the donor, improved rice varieties with submergence tolerance have been developed[19].

Acidic soils are a worldwide phenomenon. Agricultural production on acidic soils is severely limited by several nutritional deficiencies (for example, nitrogen, phosphorus and molybdenum) or toxicities (for example, aluminum and manganese). Aluminum toxicity, however, is considered to be the most common cause of decreased plant growth in acidic soils. Several wheat varieties grown on the acidic soils of Brazil during the 1960s and 1970s had tolerance to aluminum but had low yield potential. Conversely, the CIMMYT wheat varieties had high yield potential but were susceptible to aluminum toxicity. In a collaborative effort between an organization of Pirana State Cooperative (Brazil) and the CIMMYT, high-yielding wheat varieties with aluminum toxicity resistance were developed in the 1980s[20] that have 30% higher yield than old varieties under acidic conditions.

Drought stress is a principal and ubiquitous constraint to maize production in developing countries. Drought might be responsible for an ~15% loss in production. During the past 30 years, considerable progress has been made towards partially alleviating the effects of drought stress through technological advances in crop management and development of germplasm with greater drought tolerance. Several strategies are being followed at the CIMMYT to develop maize germplasm with even higher levels of drought tolerance[21].

Grain quality. Grain quality in rice means different things to different people. Most consumers in the tropics and subtropics prefer long to medium-long and slender grains. However, in temperate areas, short, bold and roundish grains are preferred. Cooking quality is determined largely by the amylose content and gelatinization temperature of starch in the rice grain. In South Asia, consumers prefer rice varieties with high amylose content and low gelatinization temperature. High amylose rices cook dry and fluffy. In South-East Asia, the preference is for rices

Glossary

GERMPLASM
Term used by breeders to refer to the collection of varieties and breeding lines.

HARVEST INDEX
Ratio of dry grain weight to total dry matter.

LANDRACE
A locally adapted strain of a species selected and adapted by farmers.

LODGING
The collapse of top-heavy plants, particularly grain crops.

PANICLE
The terminal shoot of a rice plant that produces grain.

PHOTOPERIOD-SENSITIVE PLANTS
Those that do not flower unless exposed to a day-length that is longer or shorter than a crucial period (in this case, plants that flower only during the short day-length of about 8 hours).

TILLERING
Production of shoots from the lower part of the plant.

VEGETATIVE PHASE
Non-reproductive phase of the life cycle of a plant.

YIELD STABILITY
A measure of consistency or reliability of performance.

Box 3 | **Intellectual property rights**

Through the efforts of the International Rice Genome Sequencing Project (IRGSP), the complete genome sequence of rice will become available in the next 3–4 years. Because of the conservation of gene sequences in cereals[34], the complete genome sequence of rice has broad practical implications for many other economically important species. There is a growing concern, however, that the poor will not be adequately served by the new science. In the past, almost all rice research was done by the public sector through national and international agricultural research centres. However, private-sector investment in rice research is increasing, particularly in the area of gene discovery. This research depends on a proprietary position to enable recovery of research costs and earn profits. By contrast, public-sector institutions have diverse genetic resources and expertise in phenotyping.

Therefore, the International Rice Research Institute (IRRI) proposed the formation of an international working group on functional genomics. It was agreed that the following activities are of high priority: first, create an information node to deposit and disseminate information on rice functional genomics; second, build a public platform to promote access to genetic stocks and phenotypic information; third, develop databases on phenotypes and mutants with linkage to sequencing laboratories; and finally, initiate partnerships to develop resources for microarray analysis[35].

The pattern of rights proposed is that genetic resources for functional genomics will be made available to the public and private sectors under a material transfer agreement (MTA). This agreement allows recipients to obtain patents on genes discovered through the use of materials, but requires them to make available rights under those patents at a reasonable royalty for application in commercial markets of the developing world, and at zero royalty application in non-commercial subsistence farming. The proposed MTA will have provisions that allow free use for research purposes of any patents, as well as provisions that recipients cannot obtain any form of intellectual property protection on the genetic stocks themselves. Public institutions that are engaged in developing and studying these genetic resources must agree among themselves to supply materials, and to exchange all information developed and maintained in a common database. They must also follow the same rules as those imposed on the private sector through the MTA. The IRRI has created a website where progress on rice functional genomics can be communicated (see link to the International rice functional genomics working group). This will act as the entry point for finding and sharing information, and provide a link to individual laboratories and organizations. The site will also act as a clearing house of information on genetic resources and their availability. Similar models might be considered for other crops.

with intermediate amylose content and intermediate gelatinization temperature. Such rices cook soft and remain tender on cooling. In temperate areas of China, Japan and Korea, consumers prefer rices with low amylose content and low gelatinization temperature, which give a moist and sticky cooked product.

Many of the improved rice varieties have high amylose content because the donors for disease and insect resistance typically used in the breeding process had high amylose content. However, recent releases have intermediate amylose content and gelatinization temperature, which are better accepted in South-East Asia. IR64, for example, is the most widely grown variety of rice in the world. Because amylose content is controlled by a series of alleles at the *wx* (waxy) locus[22], these alleles can be manipulated to breed plants with a specific amylose content.

Development of 'quality protein maize' (QPM) has been another breakthrough in maize breeding. QPM looks, grows and tastes like normal maize, but contains nearly double its lysine and tryptophan content, and has a balanced amino-acid content that greatly enhances its nutritive value. QPM can contribute to reducing protein deficiencies, particularly in young children. In studies conducted in Colombia, Guatemala, Peru and more recently in Ghana, malnourished children were restored to health on controlled diets using QPM. Nutritional studies with pigs, poultry and other animals have all shown a significant advantage from the use of QPM in animal feeds[23].

The way forward

The world population continues to increase at an annual growth rate of 1.3%, with 83% of this increase occurring in the developing countries of Asia, Africa and Latin America. Providing for population growth requires an expansion in world grain production of 26 million tons per year. Moreover, owing to rising living standards, food habits are changing in many countries, particularly in Asia, and people are consuming more livestock products, such as meat, eggs and milk. This is driving the demand for feed grains at a rapid rate.

Based on population projections and improved consumption patterns in developing countries, world food production must increase by 50%. This increase will have to be achieved from less land, with less water, less labour and fewer chemicals.

Strategies to meet the challenge. To feed a world population that is predicted to reach 8 billion by 2025, we have to develop food crop varieties with higher yield potential and yield stability. Traditional breeding methods (BOX 2) will continue to be used, supplemented by genetic engineering and genomic techniques, which are offering new opportunities for identifying the genetic basis of desirable traits and have facilitated the development of new crop varieties.

Improving the yield potential. Several biotechnological approaches for increasing the crop yield potential are being investigated. These include the introduction of cloned novel genes through transformation and the use of molecular marker technology.

Most yield traits are polygenically inherited and are strongly influenced by the environment. Therefore, determination of genotypic values from phenotypic expression is not precise and selection strategies must take into account low heritabilities. Breeders generally select for yield when uniform breeding lines are obtained. Until now it has not been possible to select for individual QTL with a positive effect on yield in segregating populations. Recently, QTL for yield have been tagged with molecular markers in rice and introgressed into elite germplasm[24]. Such molecular approaches would be helpful in selecting for yield-enhancing QTL in early generations and contribute to selection efficiency for yield.

Increasing the yield stability. As discussed above, host-plant resistance to insects and environmental stress is important in reducing crop yield losses. Recent breakthroughs in cellular and molecular biology have opened new vistas for developing crop varieties with novel genes for resistance, which will be used alongside conventional approaches. For example, good sources of resistance to rice stemborers are not available in the rice and maize germplasm. Therefore, the *Bt* gene from *Bacillus thuringiensis* was introduced into maize[25] and rice[26] through transformation, and transgenic plants show high levels of resistance to stemborers. *Bt* maize was planted on 6.8 million ha primarily in the United States, Canada and Argentina in 2000 (REF. 27) and showed excellent resistance to stemborers; its cultivation has resulted in a drastic reduction of insecticide use for stemborer control. Techniques aided by molecular markers are helpful in developing varieties with complex resistance, as resistance that is governed by polygenes is generally more durable. For example, we combined three and even four genes for bacterial blight resistance of rice through selection aided by molecular markers[28]. The rice germplasm with combined genes showed a broader spectrum of resistance to several races of bacterial pathogen. Resistance governed by several genes is likely to be more durable.

Progress in developing crop cultivars for tolerance to abiotic stresses has been slow, because of our lack of knowledge about the mechanism of tolerance, a poor understanding of the inheritance of tolerance, low heritability, and a lack of efficient techniques for screening the germplasm and the breeding materials. Genetic engineering techniques hold great promise for developing crop cultivars with higher levels of tolerance to abiotic stresses. For example, the accumulation of plant sugar alcohols, such as mannitol, is a widespread response that might protect plants against environmental stress through osmoregulation. In mannitol-deficient tobacco plants that were transformed with a bacterial gene, *mtlD*, which encodes mannitol[29], the sugar alcohol concentrations exceeded 6 mmol g^{-1} fresh weight in the leaves and roots of some transformants, whereas it was not detected in these organs in wild-type plants. Furthermore, these plants had an increased ability to tolerate salinity. The *mtlD* gene is being introduced into rice to increase the level of salinity tolerance.

Improved crops in the genomics era

Although genetic improvement through conventional breeding has had a significant role in food production, many limiting physical and biological factors remain, particularly in the less productive agricultural areas. For example, only limited progress has been made through conventional breeding to develop drought-tolerant cultivars. Success in developing crop cultivars with tolerance to such stresses will depend to a large extent on our ability to identify and manipulate the genetic factors that underlie complex traits — a goal that modern methods promise to achieve. Plant genomics is the engine that will drive trait discovery and help solve intractable problems in crop production. The International Rice Genome Sequencing Project (IRGSP) was launched in 1998 under the sponsorship of the Rice Genome Research Program in Tsukuba, Japan, with the aim of sequencing the entire genome in the next 3–4 years.

In addition to its importance as a food source for one-third of the human population, rice has one of the most compact genomes among cereals (450 Mb), and it contains one-fifth as much DNA as maize and only ~3% as much DNA as wheat[30]. The complete rice genome sequence will provide an enormous pool of molecular markers and genes for rice improvement. The wealth of sequence information will be exploited to determine the biological functions encoded by a sequence through detailed genetic and phenotypic analysis. The availability of a large collection of cDNAs or ESTs (expressed sequence tags) will allow reverse genetics to be used to functionally analyse genes by, for example, insertional or deletion mutagenesis[31]. A large number of insertional mutants have been produced in rice by Preira in the Netherlands and Hirochica in Japan (see link to the Rice Insertion Mutant Database), and Hei Leung has produced a large collection of chemical- and irradiation-induced mutants of rice variety IR64 at the IRRI. By using high-throughput technologies, such as DNA microarrays or gene chips, it is possible to use mutants or isogenic lines to assess gene function on a genomic scale. As a first step, DNA arrays that consist of defence-response genes are being prepared in collaboration with other laboratories to evaluate their expression dynamics in rice[32].

Candidate genes are the primary output of the functional assignment of DNA sequences to mutant phenotypes. Each allele represents a functional state of the gene but its effect might vary depending on the genotypic background. From the perspective of crop improvement, it is essential that beneficial alleles that control a combination of traits can be identified and used to develop elite germplasm. The candidate genes to which functions have been assigned through forward or reverse genetics can be used to examine allelic diversity in the elite germplasm as well as in old LANDRACES or even in wild relatives. This should allow newly discovered genes to be rapidly applied to selecting desirable lines in breeding programmes. The knowledge of gene functions and the breeding methodology for combining multiple genes will have a far-reaching impact on trait synthesis and genetic advance[33].

A concern that has emerged from the considerable private investment in rice functional genomics has been that economically disadvantaged countries will not be adequately served by the benefits of the new advances. Awareness of this potential problem means that regulation can be put into place to ensure that the parties involved — public and private sector investors, as well as researchers — agree on how and under which conditions material should be distributed and used (BOX 3). It is obvious that we will need improved crop varieties for feeding the global population in the future. Traditional and genomic techniques will be used to breed such varieties. Cooperation between the private and public sectors will be important for applying genomic technologies to crop improvement.

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Online links

DATABASES

The following terms in this article are linked online to:

Oryzabase: http://www.shigen.nig.ac.jp/rice/oryzabase/
bph2 | *Gs* | *Pib1* | *Pib2* | *Pita* | *sd1* | *se1* | *Sub1* | *wx* | *Xa4*

FURTHER INFORMATION

Food and Agriculture Organization: http://www.fao.org/
Future Harvest (a charitable and educational organization): http://www.futureharvest.org
Gurdev Khush's website: http://www.cgiar.org/irri
International Maize and Wheat Improvement Center: http://www.cimmyt.cgiar.org/
International rice functional genomics working group: http://www.cgiar.org/irri/genomics/index.htm
International Rice Research Institute: http://www.cgiar.org/irri/
Rice bioinformatics: http://www.cgiar.org/irri/bioinformatics/index.htm
Rice Genome Research Program: http://rgp.dna.affrc.go.jp/
Rice Insertion Mutant Database: http://pc7080.abr.affrc.go.jp/~miyao/pub/tos17/