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CENTENARY REVIEW

Applying innovations and new technologies for international collaborative wheat improvement

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SUMMARY

Despite the successes of the Green Revolution, about a billion people are still undernourished and food security in the developing world faces new challenges in terms of population growth, reduced water resources, climate change and decreased public sector investment. It is also becoming widely recognized that poverty is a cause of environmental degradation, conflict and civil unrest. Internationally coordinated agricultural research can play a significant role in improving food security by deploying promising new technologies as well as adapting those with well-established impact.

In addition to the genetic challenges of crop improvement, agriculturalists must also embrace the problems associated with a highly heterogeneous and unpredictable environment. Not only are new genetic tools becoming more accessible, but a new generation of quantitative tools are available to enable better definition of agro-ecosystems, of cultivar by environment interactions, and of socio-economic issues, while satellite imagery can help predict crop yields on large scales. Identifying areas of low genetic diversity – for example as found in large tracts of South Asia – is an important aspect of reducing vulnerability to disease epidemics. Global strategies for incorporating durable disease resistance genes into a wider genetic background, as well as participatory approaches that deliver a fuller range of options to farmers, are being implemented to increase cultivar diversity.

The unpredictable effects of environment on productivity can be buffered somewhat by crop management practices that maintain healthy soils, while reversing the consequences of rapid agricultural intensification on soil degradation. Conservation agriculture is an alternative strategy that is especially pertinent for resource-poor farmers.

The potential synergy between genetic improvement and innovative crop management practices has been referred to as the Doubly Green Revolution. The unique benefits and efficiency of the international collaborative platform are indisputable when considering the duplications that otherwise would have been required to achieve the same impacts through unilateral or even bilateral programmes. Furthermore, while the West takes for granted public support for crucial economic and social issues, this is not the case in a number of less-developed countries where the activities of International Agricultural Research Centres (IARCs) and other development assistance organizations can provide continuity in agricultural research and infrastructure.

INTRODUCTION

In spite of the documented impacts of the so-called 'Green Revolution', 2 billion people still lack reliable access to safe, nutritious food, and 800 million of them are chronically malnourished (Fresco & Baudoin 2002). Over the next half century it is predicted that the global demand for cereals will increase by approximately 60% (Rosegrant & Cline 2003). In other words, food security is still an issue today. This has other implications.

In their examination of post-Cold War patterns of conflict with a focus on the role of agriculture, de Soysa & Gleditsch (1999) conclude that the rehabilitation of agriculture is a central condition for reducing poverty, preventing environmental destruction and

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reducing violence. The Norwegian-based International Peace Research Institute in Oslo also concludes that conflicts around the world are increasingly the result of poverty, rather than ideology or politics.

Ironically, trends in foreign assistance for agricultural and rural development have been declining in many other donor countries and institutions. In 2000, the World Bank reported its lowest level of support to agriculture and rural development in its history – though this trend has recently started to reverse (J. Dixon, personal communication). To give some perspective, in 2004 the USA spent 40 times more money on the military than it did on overseas development assistance, and farm subsidies in developed countries in 2000 amounted to a figure (US $327 billion) ten times more than the total cost of world agricultural research (Evans 2005).

Support for agricultural research in developed and developing countries, in both national and international research centres, has dropped precipitously. If these trends continue, we risk losing the broad continuum of agricultural research organizations (from the more basic to the more applied and practical) needed to keep agriculture moving forward. Strong public sector research programmes are also needed to provide dynamic research environments to train new generations of scientists. In addition, they play a role as 'honest scientific brokers' so that farmers and consumers do not become hostages to private sector research monopolies.

Thirty-five years ago in his Nobel Peace Prize acceptance speech, Borlaug (1971) said that the Green Revolution had won a temporary success in man's war against hunger, which, if fully implemented, could provide sufficient food for humankind through to the end of the 20th century. However, hunger still stalks far too many poor people today. The world has the technology, either available or well advanced in the research pipeline, to feed a population of 10 billion people. Whether or not farmers will be permitted to use this new technology rests partly on the support and funding for agricultural research.

Despite the successes of the international wheat improvement effort described in the first paper of this series (Reynolds & Borlaug 2006), the issue of food security in the developing world faces ever greater challenges caused by increasing population, dwindling water resources (Rosegrant 1997; WMO 1997), ever more unpredictable climates (Fischer *et al*. 2002), and decreased public sector investment in agriculture and rural affairs (Falcon & Naylor 2005). The present review discusses new approaches that the international network of wheat scientists can employ in order to continue making impacts on agricultural productivity in the developing world. The need to underpin the genetic basis of durable disease resistance is addressed first because without it, hard won increases in genetic yield potential and adaptation may be ephemeral. While conventional plant breeding has relied heavily on empirical approaches to increase yield in the past, there is a broad consensus that strategic approaches based on sound physiological and genetic understanding of yield will also be required if further yield gains are to be achieved (Jackson *et al*. 1996; Miflin 2000; Slafer 2003; Snape 2004). However, no matter how sophisticated our ability to manipulate genes becomes, applied scientists face at least as great a challenge in tailoring cropping systems to an environment that is still incompletely quantified, highly heterogeneous, and most challenging of all, unpredictable in time scales of days, crop seasons and decades.

MAINTAINING AND IMPROVING CROP PRODUCTIVITY THROUGH BREEDING

Overcoming the threat of global disease epidemics: the Global Rust Initiative

The rusts (*Puccinia* spp.) were referred to by Classical writers such as Aristotle, Ovid and Pliny. Many epidemics have been recorded over the past 150 years in the Near and Far East, Europe and the Americas. Several devastating rust epidemics resulted in major famines in Asia and grain losses on a massive scale in North America in 1903, 1905 and 1950–54. The most effective way to prevent such epidemics is through global disease monitoring. For 30 years, international testing operated freely around the world, largely unfettered by plant quarantine restrictions or those imposed by intellectual property rights. However, over the past 10–15 years, the system of public nurseries (including CIMMYT's international wheat disease screening nurseries) has broken down to a considerable extent due to reduced public sector investment (CIMMYT 2004). In consequence, disease surveillance and early warning systems have suffered, and rust diseases are on the rise. A perfect example is the recently documented spread of yellow rust caused by a *Yr9*-virulent race of *Puccinia striiformis* that first evolved in eastern Africa and migrated to South Asia through Middle East and West Asia in about 10 years, causing severe epidemics in its migration path (Singh *et al*. 2004).

The latest threat is a new strain of stem rust, UG 99, detected in Uganda in 1999 and now reported throughout East Africa (CIMMYT 2005*a*). Stem rust, caused by *Puccinia graminis*, has historically caused the most severe losses to wheat production. However, until very recently it has been controlled effectively through the use of genetic resistance in cultivars associated with the Green Revolution during the 1960s and 1970s. For more than 30 years, a major proportion of the CIMMYT wheat germplasm has remained resistant to stem rust. The disease is often not considered important any more, and in

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many countries wheat cultivars are selected in the absence of stem rust pressure. However, in 1998, high susceptibility of CIMMYT germplasm was noted in Uganda and the pathogen race was later identified as carrying a combined virulence for several genes present in CIMMYT germplasm including two genes, *Sr31* and *Sr38*, of alien origin (Pretorius *et al*. 2000). Gene *Sr31*, located in the 1B.1R translocation from rye, occurs at high frequency in CIMMYT's spring wheat germplasm and is also common in several winter wheat cultivars grown in Asia, Europe and the USA. Several important cultivars grown in the Middle East and Asia are susceptible to stem rust race UG 99 and could suffer severe losses if the *Sr31*-virulent *P. graminis* race follows a migration pattern similar to that of *P. striiformis* (Singh *et al*. 2004). Rust spores can travel long distances in the atmospheric jet stream and on the clothing of world travellers (Watson & de Sousa 1983). The UG 99 race is capable of attacking much of the spring and winter wheat germplasm around the world (as much as 50 million ha globally). A major stem rust epidemic is capable of reducing world wheat production by at least 10%, if not in one year, at least over several years. A 60 million metric ton wheat loss would deny 600 million people 0·65 of their daily calorie intake, and represent a direct economic loss of US$ 10 billion at current prices. Plant breeders and pathologists still have time to screen for resistant genotypes, and to multiply these and introduce them into farmers' fields. Fortunately, CIMMYT does have germplasm resistant to UG 99, although not widely represented in commercial cultivars. Stem rust resistance sources have been identified in Kenya (CIMMYT 2005*a*). For these reasons, CIMMYT scientists have launched the Global Rust Initiative with the express purpose of pre-empting epidemics by monitoring new outbreaks of rust all around the world, and rapidly deploying resistant germplasm (CIMMYT 2005*a*).

Pushing back the frontiers of yield potential

Increasing wheat yield is still an important challenge because demand is increasing faster than the rate of yield increase (Reynolds *et al*. 1999). In addition to increasing input use efficiency, increased yield potential will reduce the likelihood of natural ecosystems being converted to agro-ecosystems, especially in the developing world. Increased genetic yield potential (best expressed in high-yielding environments) is also associated with increased yield under abiotic stress such as drought (Trethowan *et al*. 2002), nitrogen limitation (Ortiz-Monasterio *et al*. 1997) and heat stress (Reynolds *et al*. 1994). Traditionally, breeders have achieved yield increases by inter-crossing elite lines and selecting the highest and most stable yielding offspring that also express disease resistance and appropriate end-use characteristics. While this approach is strategic in terms of such traits, it remains empirical in terms of raising yield, since its genetic basis is quite poorly understood (Reynolds *et al*. 1999). For this reason, new and more strategic approaches must be explored if wheat yields are to keep pace with demand. However, studies with sets of wheat cultivars that have been released over the last few decades indicate that improvement in yield is more often associated with increased partitioning of biomass to the grain than it is with biomass (Austin *et al*. 1980; Waddington *et al*. 1986; Sayre *et al*. 1997; Calderini *et al*. 1999; Shearman *et al*. 2005). However, this may not always be the case in barley (Naylor *et al*. 1998). Since harvest index is estimated to have an upper limit of just over 0·6 (Austin *et al*. 1980), which is already being approached (Shearman *et al*. 2005), it is becoming more important than ever to understand the physiological and genetic basis of radiation use efficiency (RUE) and biomass determination if yields are to go on increasing.

Loomis & Amthor (1996) revised the theoretical limits to RUE and, using these calculations, a value of potential productivity for irrigated wheat can be calculated for any given environment. At CIMMYT's main breeding station in NW Mexico, incident radiation for the crop season is approximately 2300 MJ/m². Allowing for incomplete (0·78) light interception by the crop (Reynolds *et al*. 2000), a biomass of up to 4500 g/m² would be attainable in this environment using the most favourable value of quantum efficiency reported for a C3 crop at 25 °C and ambient CO_2 concentration (McCree 1971). Above-ground biomass in this environment is currently a little over 2000 g/m² (Reynolds *et al*. 1999), suggesting improvement in RUE to be theoretically possible.

Genetic approaches for raising RUE in crop species was reviewed by Reynolds *et al*. (2000). At the cellular level, increasing the affinity of Rubisco for CO_2, thereby decreasing its oxygenase activity, could increase RUE. Work in this area was recently reviewed by Parry *et al*. (2003). At the level of leaf photosynthesis, wide crossing with species such as *Triticum urartu* and *T. dicoccoides*, which show higher rates of maximum leaf photosynthesis than cultivated wheat, have been suggested (Austin *et al*. 1982; Carver & Nevo 1990). At the canopy level, modification of leaf architecture may improve RUE by permitting a more optimal light distribution profile, although this may already be optimized in modern cultivars because more erect leaf canopy types are characteristic of many of CIMMYT's best yielding wheat lines (Fischer 1996). Another way of improving canopy photosynthesis may be to optimize the composition of the photosynthetic apparatus and N distribution throughout the canopy, so that leaf photosynthesis is equally efficient at different light intensities (Evans 1993). However, the fact remains that these

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approaches have not generally been applied strategically to improve yield potential (Rajaram & van Ginkel 1996), with the exception of more erectophile leaf canopies (Fischer 1996).

While increases in biomass have started to be reported in spring wheat (Reynolds *et al*. 1999) and winter wheat (Shearman *et al*. 2005), other research revealed serendipitous increases in biomass of about 10% in spring wheat, specifically associated with the introduction of the long arm of chromosome 7D (containing a gene for leaf rust resistance *Lr19*) from a distant relative of wheat, *Lophopyrum elongatum*, into a number of wheat backgrounds (Reynolds *et al*. 2001). Detailed physiological investigation revealed that the basis of this increase in biomass was associated with a small increase in assimilation rate during the spike growth stage, and a much larger increase in photosynthetic rate during grain filling associated with an increased number of grains/spike (Reynolds *et al*. 2005*b*). Further experiments, in which grain number was increased artificially in elite lines with a brief light treatment during rapid spike growth stage, showed that even the highest yielding lines possess a photosynthetic capacity in excess of that needed to fill the grains they would normally set (Reynolds *et al*. 2005*b*). These results are consistent with a review of data from wheat experiments indicating sink to be more yield limiting than source (Slafer & Savin 1994). While excess photosynthetic capacity may have survival value in the wild, it is wasteful in agronomic situations where factors that could reduce photosynthetic capacity (herbivores, disease, weeds, etc.) are largely controlled. As such, it is surprising that while significant research effort is invested in trying to increase photosynthetic capacity (Parry *et al*. 2003), very little aims to increase spike fertility and thus sink strength so that RUE can be optimized. Nonetheless, very recently the role of *Gn1a*, a gene that determines grain set in rice via regulation of cytokinin levels, has been shown as a major QTL for yield potential (Ashikari *et al*. 2005).

One way to exploit this excess photosynthetic capacity would be to increase spike fertility and therefore grain number. A number of traits are being explored including increasing spikelet number per spike (large spike trait), as well as the so-called multi-ovary trait, which causes a single floret to set up to four kernels instead of just the usual one (Reynolds *et al*. 2005*b*). Currently, both approaches suffer from the problem of low kernel weight, but pre-breeding is under way with different spike architectures to try to accommodate better the large number of grains in terms of space and vascular connections. Traits that have shown association with improved yield in populations of random sister lines include above-ground biomass at flowering, spike mass at flowering, and to a lesser extent duration of rapid spike growth phase (Reynolds *et al*. 2005*b*).

The many candidate traits for increasing yield of wheat under abiotic stress such as drought have also been reviewed (Loss & Siddique 1994; Araus *et al*. 2002; Richards *et al*. 2002). Traits can be grouped together such that physiological effects among groups are likely to be relatively independent genetically (Fig. 1*a*). Grouping traits in this way, while admittedly based on an incomplete knowledge of drought adaptation and its genetic basis, does help to establish a broad conceptual platform for research as well as permitting a strategic approach to breeding, whereby drought-adaptive genes are more likely to be accumulated when parents with contrasting drought adaptive mechanisms are crossed (Reynolds *et al*. 2005*a*). Conceptual frameworks such as this, based on evidence from the literature, help focus research on issues such as whether there may be common physiological and/or genetic bases between drought and other abiotic stresses such as high temperature (Fig. 1*b*), and will permit more targeted exploration of genetic resources for candidate genes. In the meantime, new allelic variation is being exploited through wide crossing (Trethowan *et al*., in press), as well as utilization of selected wheat landraces that show good expression of drought-adaptive traits with a novel genetic base, as indicated by DNA fingerprinting assays (Reynolds *et al*. 2005*b*).

The process of incorporating new genetic diversity can be accelerated with suitable early generation selection tools that enable the best progeny to be identified before costly yield trials. For example, canopy temperature (CT) is now used in drought breeding at CIMMYT to select lines having greater access to water (Reynolds *et al*. 2005*b*; Trethowan *et al*., in press) and CT has been shown to be an effective complement to visual selection in breeding for irrigated wheat (van Ginkel *et al*. 2004).

However, knowledge of performance traits is incomplete without an understanding of genotype by environment interaction (G × E). With reliable phenotypic data and appropriate statistical techniques, variance associated with G × E can be partitioned to discrete environmental variables in time, and interpreted in terms of the unique response of a genotype, at a given phenological stage, to year to year variation in weather patterns (Reynolds *et al*. 2002; Brancourt-Hulmel *et al*. 2003; Crossa *et al*. 2004).

Applying biotechnology to increase genetic gains

As our understanding of the physiological basis of yield and how cultivars interact with environment accumulates, methods for manipulation of DNA such as Marker Assisted Selection (MAS) and genetic transformation with cloned genes will become increasingly powerful. These methods have already shown impact (Reeves & Cassaday 2002; Snape

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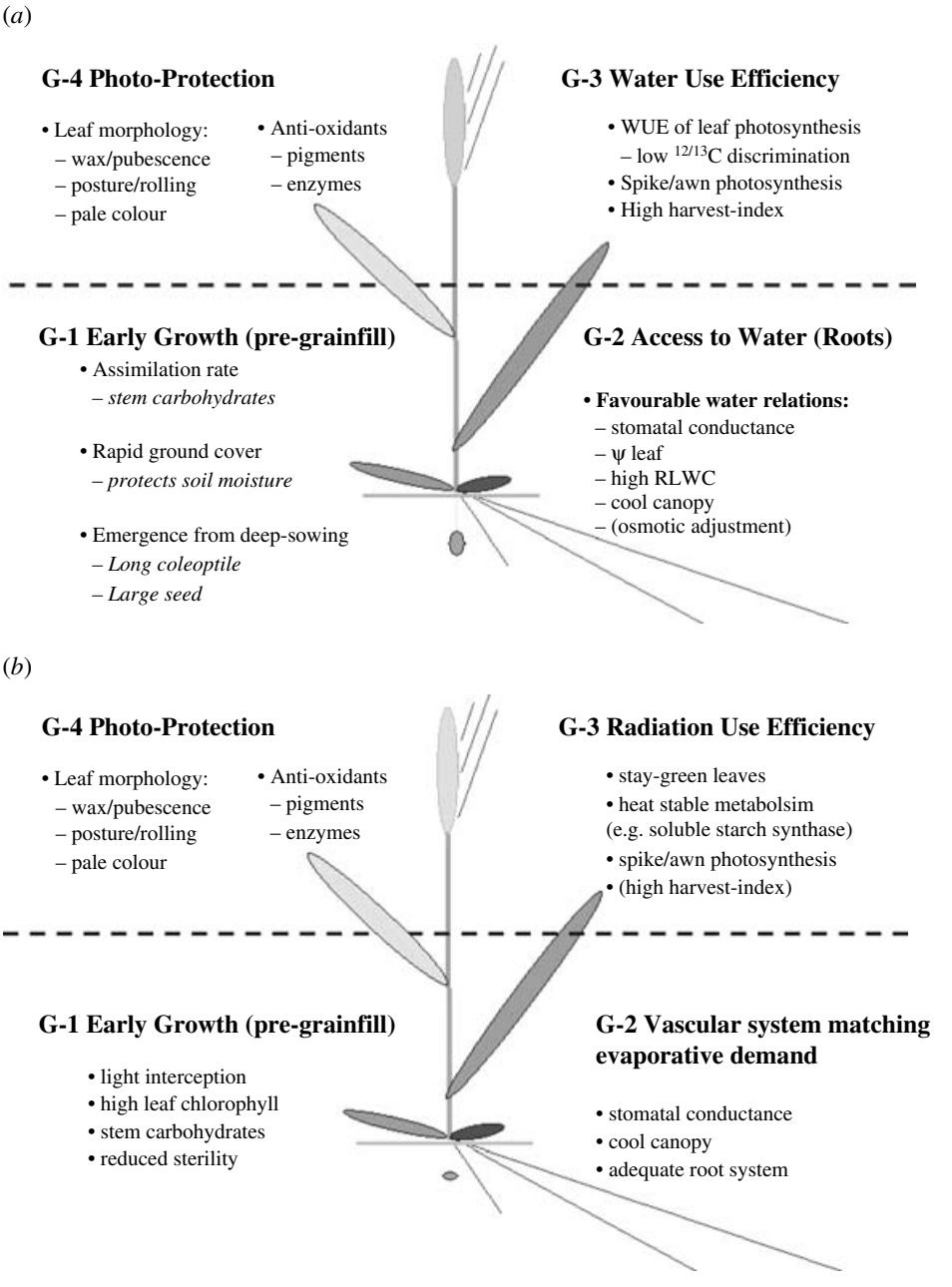


Fig. 1. Conceptual models for abiotic stress adaptation in wheat based on consensus in literature. Traits are placed in four groups such that the genes and/or physiological effects among groups are likely to be relatively independent and when parents with contrasting expression in trait-groups are crossed, stress-adaptive genes are more likely to be combined. (*a*) Adaptation to drought (from Reynolds *et al*. 2005*a*); (*b*) adaptation to high temperature.

2004). Meanwhile, heavy investment in genomics is providing a potent tool to identify the key genes associated with domestication and superior cultivar performance that will enable the targeted exploration and exploitation of germplasm collections for novel and potentially superior alleles. The use of advanced statistical techniques and data modelling are likely to have a significant impact.

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Molecular markers

Biotechnology is already applied in international wheat breeding to screen for a number of genetically simple traits that are of strategic importance. At CIMMYT, 7000 marker assays are performed annually (William *et al.* 2003) and five markers are used routinely. These include two markers for cereal cyst nematode, *Cre1* (located on chromosome 2BL) and *Cre3* (from *T. tauschii* located on chromosome 2DL) developed by CSIRO Plant Industry, Australia (Lagudah *et al.* 1997). Cereal cyst nematode is a problem in many marginal wheat environments throughout the world, and genetic resistance is a key element of root health (Trethowan *et al.* 2005). A microsatellite marker (*Xgwm 37* on chromosome 7DL) for barley yellow dwarf virus was developed at CIMMYT deriving from *Thinopyrum intermedium* (Ayala *et al.* 2001). A marker that is used to facilitate wide crossing is *ph1b* (chromosome 5BL), which was developed at the John Innes Centre UK. It is associated with suppression of homologous chromosome pairing (Qu *et al.* 1998). The fifth marker is a Sequence Tagged Site (STS) marker derived from *Ae. ventricosa* and is used when transferring disease resistance from bread wheat (ABD genomes) to durum wheat (AB genomes). The marker identifies the durum derivatives that have the translocation associated with genes for stripe rust (*Yr17*), leaf rust (*Lr37*) and stem rust (*Sr38*). A marker for high tolerance to boron (*Bo1*) has just been validated (H. M. William, personal communication); boron toxicity is frequently associated with soils in marginal environments worldwide which exacerbates yield loss when water is limited (Ascher-Ellis *et al.* 2001).

Marker assisted selection is expected to become much more widespread in breeding programmes in the future, as new markers for major genes are discovered. A marker for root lesion nematode resistance (*Rlnn1*) has been validated and will be used in conjunction with markers for cereal cyst nematode. Markers for durable rust resistance genes *Lr34/Yr18* and *Lr 46/yr 29* are used to identify genotypes where the presence of the genes is masked by major genes (William *et al.* 2003). Other publicly available markers include ones associated with resistance to powdery mildew, head scab and Russian wheat aphid. In addition, diagnostic markers are being evaluated for alternative (gibberellic acid sensitive) dwarfing genes (Ellis *et al.* 2005), which can improve emergence characteristics due to long coleoptiles when seed is sown in hot and dry environments rather than *Rht-B1b, Rht-D1b* (Rebetzke *et al.* 1999; Trethowan *et al.* 2005).

The achievements described above are all associated with markers for genetically simple or qualitative traits. Despite heavy investment, there has been significantly less success identifying markers for quantitative trait loci (QTLs) such as drought adaptation (Snape 2004). Given that QTL analysis is essentially a statistical rather than a deterministic analysis of genes, the likelihood of identifying all of the genes associated with a complex trait decreases with the number of loci involved and the size of the individual effects. However, as marker technology advances and combines with gene discovery approaches, more QTLs associated with adaptation to complex environments will emerge (Snape 2004). Nonetheless, the main challenge to their application in breeding will be to determine the right combination of alleles to use, since conditions vary significantly from site to site and from year to year and significant QTL × environment interactions exist. A multi-staged approach to identifying molecular markers may be the best approach where QTLs for generic stress-adaptive traits are identified first in the appropriate well-controlled field environments. Generic traits for drought might include capacity of roots to access water deep in the soil, high intrinsic water use efficiency, antioxidant systems for photo-protection, etc. (Reynolds *et al.* 2005*a*). Subsequently, location specific marker populations (already optimized for the appropriate generic traits) would need to be designed to identify QTLs for more locally specific traits such as local soil characteristics, as well as for fine-tuning of QTLs related to rainfall distribution, temperature profiles, and photoperiod etc.

Transformation

Research in comparative biology and genetics (synteny; Devos *et al.* 1995; Gale & Devos 1998) is leading to the discovery of new traits and their genes that have the potential to confer increased crop productivity in a range of environments. The understandable fears associated with moving DNA between taxa have to be balanced against the potential benefits to humanity. For example, genetic transformation using the *Bt* gene from bacteria has transformed the cultivation of cotton from the most insecticide-intensive crop in the world to one that is relatively environmentally friendly, in those countries where the use of transgenics is permitted. A number of studies have demonstrated that using Bt cotton reduces the use of insecticide sprays (James 2002; Bennett *et al.* 2004, 2005). In China, insecticide applications were reduced by an average of 67% and the active ingredient by 80% (Huang *et al.* 2002). There are other benefits to smallholders too. The use of Bt cotton on a typical 1·7 hectare farm in the Makhathini Flats region of South Africa would result in a labour reduction of 12 days of spraying, eliminate 100 km of walking, and save 1000 litres of water, while increasing income (James 2002).

It is unrealistic to expect that natural selection can provide an optimal range of genes within a given taxa to meet the demands of environmental change.

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Humans have intervened heavily with the course of natural selection for millennia. Some crop species not only depend on cultivation for their survival, but also display considerable genetic changes, some natural and others directed by human selection (Duvick 1996). Naturally occurring allelic variation for genes such as *Kr* and *Ph* in wheat (see review by Jauhar 1993), genes originally intended to ensure true breeding, indicate that inter-specific or wide-crossing is a natural strategy. The movement of genes between distinct taxa is not therefore new, and has not proven to be dangerous over history. However, modern technology needs to be applied with appropriate caution and tangible benefits weighed against the sometimes less tangible risks.

Drought is an intractable problem that puts the livelihoods of millions of poor at risk every crop season. While conventional and marker-assisted breeding can permit favourable reshuffling of genes within conventional gene pools, transformation offers the possibility of introducing new traits and regulatory mechanisms that would otherwise be inaccessible. The regulatory gene DREB from Arabidopsis has been introduced into wheat and has shown tentatively promising results associated with drought conditioning (Pellegrineschi *et al*. 2004). The NCED gene, also from *Arabidopsis*, has been shown to increase the expression of abscisic acid (ABA) in tomato and was associated with decreased stomatal conductance and increased water use efficiency (Thompson *et al*. 2004). The result is consistent with work by Davies & Zhang (1991), who have shown that ABA-mediated root signals in response to drying soil also reduce stomatal conductance of leaves. Natural variation in water use efficiency in wheat is known to exist, and has been exploited in Australia to improve drought tolerance (Rebetzke *et al*. 2002). However, the trait is constitutive and may be associated with reduced performance in wetter years (Condon *et al*. 2002). Therefore, new sources of genetic diversity for WUE may be quite valuable especially if they can be combined with stress-inducible promoters.

Using conceptual models of stress adaptation, trait combinations can be devised for specific environments and evaluated more rapidly using multiple transformation approaches than conventional approaches (Daniell & Dhingra 2002). For example, if the mechanism of action of the genes DREB and NCED are independent, their effect on drought adaptation may be additive in terms of genetic gains under drought. Furthermore, many dry environments also suffer from severe heat stress during grain-filling while the enzyme soluble starch synthase (SSS) in wheat has been shown to be rate limiting at high temperatures (Keeling *et al*. 1994). However, rice is able to convert sucrose to starch at high temperature and humidity. The SSS gene from rice has been made available to CIMMYT by JIRCAS, Japan, and lines are now ready for testing at high temperature. If successful, it will be combined with DREB and NCED to provide a broader genetic base for abiotic stress adaptation.

Another area in which transformation could potentially increase food security dramatically is in transferring disease resistance genes among taxa. For example, among all the cereals, rice is unique in its immunity to the rusts (*Puccinia* spp.), while all the other cereals show susceptibility that has led to many famines and economic crises (Harlan 1976). Transferring the genes for rust immunity from rice into wheat and barley could be a major advance.

There is an increasing potential to improve the nutritional quality of food. The development, using conventional plant breeding methods, of high-lysine, high-tryptophan quality protein maize (QPM) varieties and hybrids took some two decades of painstaking research work (Bjarnason & Vasal 1992). Transformation technology can achieve these goals much faster, as has been shown recently with the transfer of genes to increase the quantities of vitamin A, iron and other micronutrients contained in rice, potentially bringing significant benefits for millions of people suffering from deficiencies of these nutritional elements which can cause blindness (vitamin A) and anaemia (iron). Unfortunately, 'Golden rice' is now tied up in complex patent negotiations. In terms of food preferences, bread wheat is and has been a favoured crop for millennia because its dough is superior for making leavened bread and other bakery products, due to the presence of two proteins – gliadin and glutenin. No other cereals have this combination. If the genes for these proteins could be identified and transferred to the other cereals, especially rice and maize, it would help many developing countries in the tropics, where bread wheat flour is often the single largest food import.

Genomics

Genomics and related technologies, proteomics and metabolomics, permit the dissection of traits into their respective genetic, enzymatic and biochemical components. The large amount of information coming from such studies can only be targeted to genetic improvement of crops if experiments are designed with a comprehensive knowledge of the many environmental and developmental factors involved in crop adaptation (Cushman & Bohnert 2000). The probability of identifying candidate genes will be low unless their expression is measured appropriately in terms of which tissue(s) is sampled and when in terms of phenological stage(s) and time(s) of day, and additionally interactions of genetic background with the climatic and agronomic factors need to be well established. In fact much of this background information has yet to be established, especially for complex adaptive mechanisms, and sound judgement and

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the use of multidisciplinary approaches are needed if impact in farmers' fields is the goal (Miflin 2000; Koebner & Summers 2003; Morandini & Salamini 2003; Slafer 2003; Sinclair *et al*. 2004; Snape 2004; Evans 2005).

Genomics approaches will undoubtedly pay off in the short term by identifying genes for MAS related to relatively simple characteristics such as disease resistance or quality traits in wheat (Snape 2004). However, while micro-array information may be readily interpreted to show that a gene or metabolic pathway is involved in response to, for instance, an abiotic stress, it does not necessarily follow that a perturbation of that gene or pathway will have a large effect on a genotype's adaptive response. According to enzymological theory (Kacser & Burns 1981), the probability of any single gene modification significantly altering the flux of the system is extremely low, since the flux is a systematic property and variation at any single locus is reflected and buffered by the whole system. This theoretical view is borne out by much work in transgenic plants reviewed by Stitt & Sonnewald (1995), where components of metabolism have been modified by insertion of antisense genes. Gene discovery is just the first step in manipulating complex traits. Directed manipulation of the genome to achieve desirable expression of complex traits will require a systematic understanding of gene interactions and regulation. Barring serendipity, this will not come about without painstaking experiments where the effects of individual loci are evaluated using knock-out mutants, transgenic antisense or RNAi technologies, and alternative alleles tested in a series of genetic backgrounds and different environments; a phenomenal task. The relatively new field of gene modelling (Cooper *et al*. 2002; White, in press), as well as advanced statistical approaches for modelling interactions among genes and with environment (Crossa *et al*. 2005), will no doubt provide platforms from which information can be interpreted and new experiments designed.

OVERCOMING THE CHALLENGES OF COMPLEX, CHANGING AND FRAGILE ENVIRONMENTS

While the parameters to genetically improve yield or adaptation to biotic and abiotic stresses can be broadly defined, a greater challenge yet is to maintain productivity in unstable environments where factors like unpredictable climate, fragile soils and poor agricultural infrastructure are among the factors that increase the risk of cultivation. For example, although considerable differences of opinion exist as to the timing, severity and differential effect of climate change associated with global warming, a consensus seems to have emerged about three important aspects (Fischer *et al*. 2002). The first is that catastrophic weather events are likely to increase, taking the form of more severe storms, more flooding and, of most concern for agricultural production, more frequent and severe droughts. Secondly, it appears possible that favoured lands will experience even more favourable growing conditions but that areas which are currently subject to periodic flooding and, more particularly, drought are likely to experience increased devastation. Thirdly, virtually all agricultural research directed at overcoming the effects of heat, drought, and associated biotic and abiotic stresses will be of high potential benefit to ameliorating the likely negative effects of global warming.

To overcome problems associated with the unpredictability of cropping systems, research approaches and technologies must incorporate a degree of buffering capacity. The fact that CIMMYT already has breeding programmes targeted at different abiotically and biotically stressed environments would allow rapid deployment of existing nurseries to regions facing new challenges, while the allocation of breeding resources to emerging climate scenarios are rationalized. The use of crop models in combination with remote sensing techniques will help these decisions to be made. Greater participation of extension services and farmers in varietal selection is an approach that can help reduce genetic vulnerability to diseases while at the same time increasing adaptation of cultivars to local conditions and crop management practices. Finally, a strong conservation agriculture movement is already laying the groundwork whereby potentially fragile agricultural soils are being stabilized and buffered against nutrient and water deficiencies.

MODELLING ENVIRONMENTAL DATA AND USE OF REMOTE SENSING TO REFINE TARGET ENVIRONMENTS

Comprehensive knowledge of target breeding environments is theoretically a pre-requisite to designing selection environments. In practice, they reflect the best compromise between what is known of the target locations and the environments available to breeders. A major factor in the success of the spring wheat breeding programme based in Mexico, in addition to strong international collaboration, is attributable to the range of climates found in the country, enabling agronomic and disease resistance characteristics to be selected in alternative generations under appropriate agro-ecological conditions. Shuttle breeding with other countries such as Brazil for acid soil environments, or Ecuador for yellow rust virulence is also employed, but national phyto-sanitary requirements increase costs and timeframes. In addition, as already outlined, CIMMYT has focused on generic traits and distributed largely unfinished germplasm for local selection and crossing, such that precise knowledge of

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target locations was not required. Nonetheless, a more complete knowledge of target environments is strategically useful in terms of determining which new traits and genes may be useful and the appropriate allocation of resources. In other words, knowledge of agroclimatic factors permits fine tuning of the genetic makeup of nurseries as well as assisting with projections of where wheat may be adopted or decline based on additional socioeconomic factors (Dixon *et al.* 2001).

This is where the new generation of GIS and modelling tools has already contributed to wheat breeding and will continue to do so in the future. For example, White *et al.* (2001) used interpolated climate data from the Ethiopian Country Almanac to predict the potential expansion of wheat production in that country, which currently imports 0·3–0·5 of what is consumed. Essentially, the technique involves modelling meteorological data based on a limited number of sites by taking changes in latitude and altitude into consideration. While it had been assumed that moisture availability limited productivity in Ethiopia, their analysis suggested that high temperature stress was in fact the major limitation, indicating a different germplasm requirement. A similar approach was used by Hodson *et al.* (1998) in Bolivia to determine how crop technologies that had been developed in one agroecological zone might be extended to other countries in the Andean region.

Another new technology that can be used to help validate agroclimatic models is remote sensing of crop yields by satellite using spectral reflectance indices. While climatic data can be interpolated with relatively limited ground-based information, crop productivity information is not easily available at the site level. Satellite images have been used to predict yield, for example in NW Mexico, and have shown to be extremely accurate even when comparing farmers' fields (Lobell *et al.* 2003). Satellite information could be used to estimate yields at strategic locations and then be used to calibrate predictive agroclimatic models such as those described above. In addition, other remotely sensed data such as crop temperature using infra-red sensors could be converted, with appropriate algorithms, to air temperature data to augment ground-based data sets and give better resolution to interpolated climate surfaces. Researchers in the area of remote sensing are trying to develop diagnostic indices for agronomic problems such as micronutrient deficiency and disease incidence as well as to identify weed species in wheat (Girma *et al.* 2005).

In summary, by providing more accurate agroclimatic information target environments will be better defined, enabling breeding objectives to be established more strategically. Along with diagnostic remote sensing techniques, regions of extreme agroecological heterogeneity will be identified as well as areas with dangerously low genetic diversity; thus identifying targets for more focused approaches to variety selection (see below). In addition, existing information about the relationship between productivity and climate can be used to model the consequences of climate change (Jones & Thornton 2003). The time from making a cross to seeing the impact in farmers' fields is currently about 10 years, and so information on the possible changes in size and distribution of current target mega-environments would contribute to the availability of appropriate new varieties.

PARTICIPATORY SELECTION TO INCREASE PRODUCTIVITY AND GENETIC DIVERSITY IN FARMERS' FIELDS

One of the major challenges to improving food security in rural resource-poor communities is to develop cultivars that are tailored to specific local environments. Although germplasm can be developed at a national and international level to incorporate a number of generically useful traits, it is a major challenge for scientists with limited public sector resources to test the full range of genetic diversity generated by a breeding programme under all possible environments. There are some very large tracts of wheat in the developing world that are sown to relatively few cultivars (Smale *et al.* 2002). This results in lost productivity because the cultivars sown may not be optimally adapted to their local environment (Witcombe 1999), and many farms could be vulnerable to unpredictable changes in the weather or disease virulence. For example, although there are over 380 named cultivars, just two of these (HD2329 and Inqalab) occupied 0·15 of the total spring wheat area sown in the developing world (estimated at 56 m ha in 1997; Smale *et al.* 2002). This indicates that the problem is not one of a lack of availability of cultivars (CIMMYT alone distributes over 1500 new wheat genotypes each year) but rather their rate of adoption and turnover in farmers' fields. Mechanisms need to be promoted whereby the genetic diversity that is generated is better utilized.

Farmer participatory variety selection (PVS) is one such mechanism that has proven to be effective in increasing genetic diversity and in some cases productivity for several cereals including wheat (Witcombe 1999; Ortiz-Ferrara *et al.* 2001; Witcombe *et al.* 2001), barley (Ceccarelli *et al.* 2001), and maize and rice (Bellon & Reeves 2002). While the consideration of farmers' evaluations of variety characteristics is not new – over 25 years ago the Institute of Agricultural Research in Ethiopia was using farmers' evaluations; farm women rejected high-yielding wheat because of threshing difficulties (Dixon 1978) – over time participatory methods have been refined and fine-tuned.

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Sometimes results are quite surprising. A PVS study in Nepal with wheat showed large gender-based differences in selection criteria, with women giving first priority to disease and insect pests followed by chapatti-making and then yield, while men prioritized late heat tolerance, grain type and shattering tolerance, with yield 7th and chapatti-making quality last (Ortiz-Ferrara *et al*. 2001). Studies conducted by ICARDA in Syria, Morocco and Tunisia showed PVS of barley to be effective at increasing farm yields in comparison with cultivars released through conventional on-station testing by professional breeders. Farmers also put emphasis on traits that breeders ignored, such as straw yield, or vice versa, e.g. disease resistance (Ceccarelli *et al*. 2001).

The challenge is how best to incorporate participatory approaches into the network (Morris & Bellon 2004). A crucial factor is to determine the optimum distribution of effort between developing germplasm with generically valuable traits for distribution to broad mega-environments, breeding cultivars that also encompass local-adaptive traits, and dissemination of a sufficient diversity of cultivars such that more agro-ecological niches are reached and genetic vulnerability to disease and pests is reduced. The more comprehensive the feedback from the international testing network as it encompasses greater participation, the better targeted new germplasm will become in terms of both generic and local-adaptive traits.

SUSTAINABLE CROP MANAGEMENT: BUFFERING YIELDS AGAINST UNPREDICTABLE ENVIRONMENTS

In addition to using locally adapted cultivars, one of the best paths towards maintaining productivity in unstable environments is through well-managed crops and soils, which provide an adequate supply of nutrients and water. However, the demand for staple crops due to population growth has led to more intensive farming in the developing world. One of the most serious consequences of rapid agricultural intensification has been soil degradation, for example, in the rice-wheat systems of the Punjab in South Asia, one of the largest agro-ecosystems in the world (Lal 2004*a*). Left unchecked, this process eventually leads to soil loss through erosion, problems of chemical imbalance such as salinity, and in the worst-cases, desertification (Lal 2004*b*). Water scarcity is intensified in poor soils because of their reduced capacity to absorb and retain moisture. The key is loss of soil organic matter. Although breeding can improve the tolerance of cultivars to salinity and reduced moisture, it is not a sustainable solution if soils continue to degrade. Since soil tillage is a principal cause of declining organic matter, crop management practices that minimize or eliminate tillage while retaining crop residues within judiciously chosen crop rotations comprise a powerful approach for stabilizing and improving soil health (Bradford & Peterson 2000; de Costa & Surenthran 2005). These practices are central to what has become known as Conservation Agriculture (CA) and empirical data from long-term trials are demonstrating clear benefits (Fig. 2; Lal *et al*. 2004; Sayre *et al*. 2005).

Conservation tillage

While conservation tillage (an application of CA) is spreading rapidly its adoption has been largely confined to the Americas, where about 60 million ha of the cropped land is no-till (Lal 2004*a*). However, because of its many benefits, conservation tillage is an alternative strategy that is especially pertinent for resource-poor farmers in developing countries, since tillage is an expensive and time-consuming operation whether achieved by animal traction or machinery. Reducing and/or eliminating tillage operations can significantly reduce turnaround time on lands that are double or triple cropped annually. Cover of crop residues helps to control weed populations and in combination with reduced soil movement reduces water evaporation. In a case study with resource-poor Indian farmers, Hobbs *et al*. (2000) reported 30% lower production costs associated with savings of up to 1000 litres of water and 100 litres of diesel fuel per hectare. It is estimated that zero-tillage has been adopted on 2 million hectares of wheat in South Asia (Ladha *et al*. 2003; Lal *et al*. 2004).

Conservation tillage has significant environmental benefits (Bradford & Peterson 2000). Improved soil health means less erosion and higher productivity, thereby reducing the probability of encroachment of crops into natural ecosystems. Carbon emissions to the atmosphere are reduced, associated with lower use of fossil fuel, less oxidation of soil organic matter and less burning of crop residues. Other environmental impacts over time may include less herbicide and pesticide use due to the suppression of weeds by residues, and more biological control of insects. Dust levels in the atmosphere are also reduced because crop residues protect the soil from wind and there is less soil disturbance during field operations.

A major challenge is that it can take several cycles before the benefits of residue retention are realized in terms of increased productivity of both grain and straw yield (Govaerts *et al*. 2005). This is especially important for resource-poor farmers who may have alternate uses for crop residues.

Raised bed technologies

Cultivation of irrigated wheat and other rotational crops on raised beds provides a number of tangible benefits in addition to yield. Soil movement is reduced, resulting in greater water use efficiency (WUE), while increased accessibility for controlled

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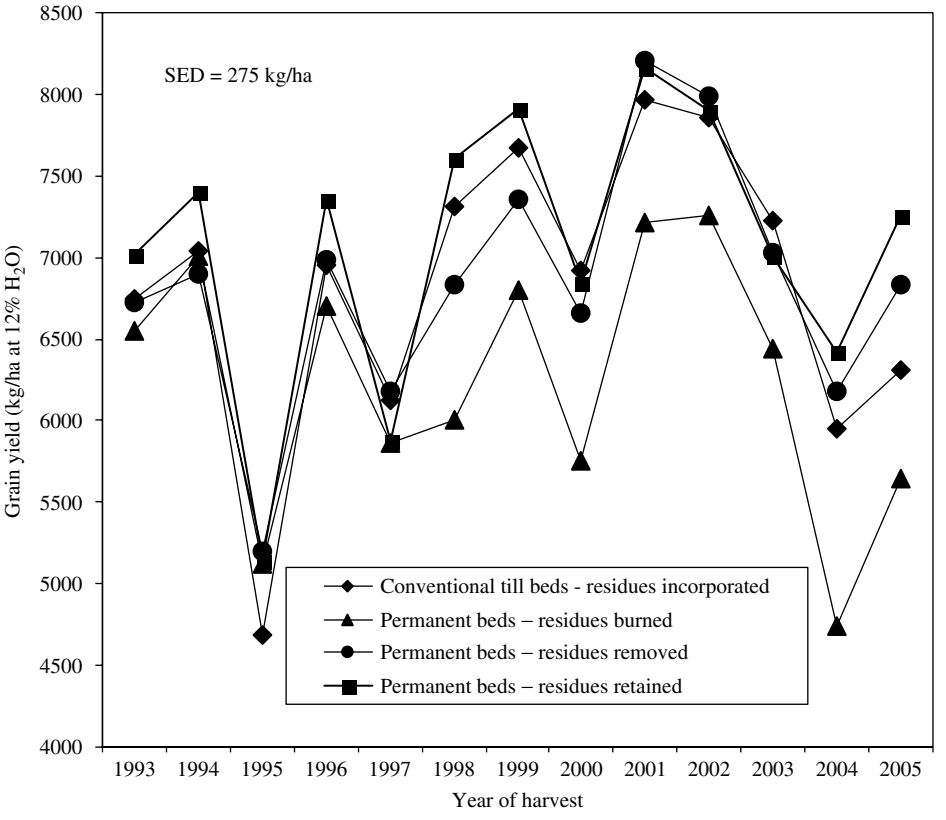


Fig. 2. Effect of different tillage and residue management practices over 13 years on wheat grain yield with optimal management, NW Mexico (see Sayre *et al*. 2005).

traffic of machinery permits delayed N application, increasing nitrogen use efficiency as well as permitting light cultivation, thereby reducing herbicide use (Sayre & Hobbs 2004; Govaerts *et al*. 2005). Sowing on permanent raised beds also makes crop diversification more accessible by providing a fixed platform for developing appropriate small machinery (Tullberg *et al*. 2004). Already adopted in Mexico (Sayre & Hobbs 2004; Sayre *et al*. 2005), it is being adopted in other countries. Future challenges include adapting raised bed technology to all of the crops in the cropping system. In the case of wheat-rice, it will require the direct seeding of rice and furrow irrigation, if the beds are to be made permanent, from season to season.

A technology that can save water and is compatible with raised bed cultivation is alternate furrow irrigation. Plant roots in a drying soil profile send chemical signals to their leaves resulting in a reduction in transpiration rate mediated by reduced stomatal conductance (Davies & Zhang 1991). The result of this response is a decreased growth rate and an increase in WUE. This innate drought-response mechanism can be exploited by a modification in irrigation strategy whereby plants are grown on top of ridges and irrigated first on one side and then on the other at the next irrigation (Davies *et al*. 2002). This has proved to be highly effective in permitting substantially reduced water application while increasing harvest index and thus not significantly reducing yield (Kang *et al*. 2000).

Precision agriculture

Another contribution to more sustainable use of inputs is coming from precision agriculture. For example, agronomists at Oklahoma State University have adapted spectral reflectance sensor technology for use by farmers to calculate precisely the crop requirement for in-season nitrogen application. The technology is based on the fact that certain wavelengths of light reflected by the crop canopy are highly correlated with total crop N content. By measuring an index (NDVI) based on this wavelength and a reference band, early in the crop cycle, crop N needs can be predicted (W. Raun, personal communication: http://www.nue.okstate.edu). The value of this

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technology has already been demonstrated in Mexican and Ecuadorian farmers' fields in collaboration with CIMMYT scientists, enabling them to apply precise amounts of fertilizer for yield optimization while minimizing leaching and gaseous losses of N.

Green Revolutions in crop management

The Tillage Revolution, as it is sometimes referred to, is gaining momentum worldwide (MacIlwain 2004). The adoption of innovative and resource-conserving crop management practices opens up the possibility of a plant breeding specifically targeted not just to macro-environment but also to specific features of crop management. For example, it has been shown that tillage practices influence the composition and intensity of mycorrhizal fungi over a range of soil depths (Oehl *et al*. 2005). New ideotypes may be better adapted to emerge from unploughed soil and grow among the residues of previous crops (Watt *et al*. 2005), as well as to higher levels of organic matter effecting nutrient dynamics and to an increased level and diversity of soil fauna and micro-organisms. This potential synergy between breeding and innovative input-use efficient crop management practices has been referred to as the Doubly Green Revolution (Conway 1997).

CONCLUSIONS

International institutes like CIMMYT and ICARDA and other CGIAR centres, in collaboration with partners in national programmes, and other organizations concerned with agricultural development (CIMMYT 2005*b*) have a key role to play in ensuring that the livelihoods of resource-poor farmers will benefit from new agricultural technologies (Evenson & Gollin 2003). Policy makers need to balance the obvious appeal of high risk investments in the latest technologies with the realities of resource-poor farmers, for whom tried and tested technologies offer immediate and reliable solutions to meeting their daily needs. We recognize the efforts of colleagues worldwide working in agricultural development and look forward to new challenges and partnerships.

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