Proceedings of the

WARREN E. KRONSTAD

Symposium

J. Reeves, A. McNab, and S. Rajaram, editors

CIMMYT

Proceedings of the Warren E. Kronstad Symposium

Held in Ciudad Obregón, Sonora, Mexico

15-17 March 2001

J. Reeves, A. McNab, and S. Rajaram, editors

Sponsored by the CIMMYT Wheat Program, Oregon State University,
USAID, and AgriPro

CIMMYT MR

CIMMYT® (www.cimmyt.org) is an internationally funded, nonprofit, scientific research and training organization. Headquartered in Mexico, CIMMYT works with agricultural research institutions worldwide to improve the productivity, profitability, and sustainability of maize and wheat systems for poor farmers in developing countries. It is one of 16 food and environmental organizations known as the Future Harvest Centers. Located around the world, the Future Harvest Centers conduct research in partnership with farmers, scientists, and policymakers to help alleviate poverty and increase food security while protecting natural resources. The centers are supported by the Consultative Group on International Agricultural Research (CGIAR) (www.cgiar.org), whose members include nearly 60 countries, private foundations, and regional and international organizations. Financial support for CIMMYT's research agenda also comes from many other sources, including foundations, development banks, and public and private agencies.

Future Harvest® builds awareness and support for food and environmental research for a world with less poverty, a healthier human family, well-nourished children, and a better environment. It supports research, promotes partnerships, and sponsors projects that bring the results of research to rural communities, farmers, and families in Africa, Asia, and Latin America (www.futureharvest.org).

Correct citation: Reeves, J., A. McNab, and S. Rajaram (eds.). 2001. *Proceedings of the Warren E. Kronstad Symposium.* Mexico, D.F.: CIMMYT.

AGROVOC Descriptors: Wheats; Triticum aestivum; Biotechnology; Genetic resistance; Septoria; Rusts; Yield components; Environmental factors; Fusarium; Plant breeding; Disease resistance; Germplasm conservation; Developing countries

Additional Keywords: CIMMYT

AGRIS Category Codes: F30 Plant Genetics and Breeding H20 Plant Diseases
Dewey Decimal Classif.: 641.3311

ISBN: 970-648-084-6

Printed in Mexico.

Design and layout: Miguel Mellado E., and Marcelo Ortiz S.

Contents

Posters

Preface

On 15-17 of March 2001, CIMMYT held a special symposium in Ciudad Obregón, Sonora, Mexico, in memory of Dr. Warren E. Kronstad, Distinguished Professor at Oregon State University, who died on 21 May 2000, after a two-year battle with pancreatic cancer.

Dr. Kronstad was a good friend and an esteemed collaborator of the CIMMYT Wheat Program for many years. Starting in the early 1970s, he collaborated with Dr. Norman Borlaug and this author on making crosses between the winter wheat and spring wheat gene pools. He was also a founder and active participant in the CIMMYT/OSU wheat shuttle breeding program that has so successfully bred wheats for different environments all over the world.

I met Warren in the 1970s, and from the beginning I was struck by his dedication to wheat breeding research and plain old hard work. One of the top breeders in the USA, Warren was very successful, as evidenced by the impact of his breeding efforts, not only in the USA, but also in developing countries. Nonetheless, I'm convinced that his biggest contribution was the graduate training program he initiated at Oregon State University. More than 80 MSc and PhD students and visiting scientists, many from developing nations, studied at OSU during Dr. Kronstad's tenure.

He was one of a few agricultural scientists in the USA who had a vision of the developing world. He was deeply committed to eliminating hunger through the increase of the food supply and by mentoring young scientists in sound plant breeding. His contributions to improving wheat production not only in the US, but also in the developing world, will be long remembered.

Sanjaya Rajaram
Director
CIMMYT Wheat Program

Foreword

The challenge to alleviate hunger and poverty in developing countries remains one of humanity's most serious problems. Nearly 20% of the world's population remains food-insecure (more than 40% in South Asia and sub-Saharan Africa). One-third of pre-school children in developing countries are malnourished and therefore at risk of impaired mental and physical development as well as continued poor health, productivity, and food security. Over the next 20 years, population and income growth will increase the demand for food by 50% or more. Cereal demand in the developing world will increase by 50% and account for two-thirds of total global demand by 2020. At the current rate of increase in cereal yields in the developing world (1.2% per annum), this increased demand will not be met, and the situation will be even worse in marginal environments where progress has generally been much slower.

The challenge the world confronts today would be far more serious in the absence of a global network of research partners dedicated to the genetic improvement of staple food crops in developing countries. These partnerships, involving the Future Harvest Centers of the CGIAR, national research organizations in developing countries, and advanced research institutions, have dramatically increased the development and adoption of improved higher yield crop varieties, increasing the availability of food worldwide. In the absence of these research partnerships, 1.5-2.0% more of the world's children would be malnourished, food imports would be about 9% higher, and consumers, urban as well as rural, would expend a greater percentage of their income on staple foods. Instead, daily per capita calorie availability has risen from about 2,100 to about 2,700, and staple foods have become progressively cheaper.

The papers in this volume reflect the successes that have been obtained in improving wheat—the world's most important food crop—and the contributions of the many partners involved. In particular, they emphasize the key role that Warren Kronstad played in these global partnerships and his outstanding contributions to global food security and human development.

At CIMMYT we know that there is still much more to be done if we are to lift people from the daily misery of abject poverty and hunger. A global war on terrorism will have little lasting-effect unless the world also unites to improve the livelihoods of people in all regions of the developing world. At CIMMYT we deeply care about the people we are trying to help, about our partners, and about impacts on hunger and poverty. Warren Kronstad would have expected nothing less.

Timothy G. Reeves
Director General
CIMMYT

Global Public Goods for Poor Farmers: Myth or Reality?

T.G. Reeves and K.A. Cassaday

Are Global Public Goods a Vanishing Commodity?

At the start of a new century, the international agricultural research and development community is undergoing a transformation. Powerful forces are acting to expand research opportunities as never before, but at the same time they seem to have raised barriers to research that are greater than any that have been seen in the past. For many years, international agricultural research organizations have worked very effectively to improve the lives of poor people in developing countries. Now, as research funding diminishes and quiet scientific controversies have become incendiary public debates over patenting life forms, rights to genetic resources, and the predominance of the private sector in biotechnology research, many are questioning how much longer international agricultural research can continue to help poor people. International agricultural research has provided improved seed, better agricultural practices, and information that have helped poor people immeasurably, but the rules of research are changing. Will the new rules transform these so-called "global public goods" into vanishing commodities, or into commodities that poor people cannot hope to access? That is the central question explored in this paper.

The vast majority of the world's poorest farmers still produce crops using farm-saved seed and traditional crop management practices that have been passed down from generation to generation. These can be regarded as a form of "global public goods." Before we discuss why global public goods are important for the world's poor people, and whether developing countries will have access to them ten or twenty years from now, it is useful to explain what we mean by "public goods" and describe some of the problems associated with providing them.

The Potential and Problems of Public Goods

Economists have strict definitions of public goods, but for our purposes it is probably sufficient to describe a public good as a product or service that is easily accessible to all people (it is difficult to exclude anyone from using it) and that can be used by many people at the same time (its use by one person does not preclude its use by any other person). Because the degree of accessibility and the degree of nonrivalry can vary, some public goods are more "pure" than others, but for simplicity we will ignore this distinction. In agriculture, examples of public goods include a high-yielding wheat variety, a labor-saving conservation tillage practice, a market information program broadcast over the radio, and public research in general (Winkelmann 1994)—in fact any nonproprietary technology that is freely available to large numbers of people at little or no cost.

Although they may be highly desirable, public goods are not readily produced by profit-oriented private firms, because it is difficult for the producer of a public good to capture enough benefits to compensate the cost of production. To avert so-called "market failure," governments usually provide public goods because it is agreed to be in the interest of society. The Government of India has invested heavily in agricultural research and extension, for example, to improve agricultural production and eliminate the famines that once ravaged the subcontinent. The government stepped in for a number of reasons, including the fact that private companies lack incentives to invest in a large research and development system to produce improved crop varieties that many farmers are too poor to buy. Even if most Indian farmers could afford to buy improved seed, many may choose not to, since they can easily acquire a small supply from a friend or neighbor and multiply it up on their own. Private firms are understandably reluctant to invest in the provision of products or services from which many individuals can be expected to benefit without helping to pay for the cost (a problem that economists term "free riding").

In summary, public goods are goods from which the supplier has difficulty in directly recovering investment costs and earning profits. Difficulty in recovering investment costs and earning profits does not mean that the benefits generated by investing in public goods are small, however. On the contrary, the benefits of public goods may be enormous, even though this may not be readily apparent when they are spread across a large number of beneficiaries. In India, for example, hundreds of millions of people now have access to more food at lower prices, and a major famine has not occurred in many years.

The issues of who pays the costs of public goods and what quantity of public goods is appropriate are contentious ones. In the case of agricultural research that is targeted at the poorest of the poor, those who pay the cost—typically taxpayers in medium- and high-income brackets—often receive a relatively small portion of the benefits. At the same time, the main beneficiaries—peasant farmers and the urban poor who spend a large proportion of their incomes on food—may not have a say in deciding how government priorities are established. For these reasons, agricultural research is often funded at socially suboptimal levels.

The provision of public goods, including agricultural research, becomes more complex as the number of supplying organizations increases and as their constituencies become more diverse. In many countries, including the United States, every state or province has its own agricultural research organization, which is funded by local taxes and responsive to local needs—and therefore more likely to place local interests above national interests. Although certain types of research can be expected to produce large benefits at the national level, individual states lack incentives to carry out this research, because a large portion of the benefits can be expected to "spill over" to other states that are not sharing the costs. Recognizing that this is the case, national governments generally establish national research organizations to provide goods and services that are deemed necessary for all, but which will not necessarily be provided at the local level (for example, national standards for grading agricultural products).

Compared to the provision of national public goods, the provision of international (or global) public goods is an even more daunting prospect. As Kindleberger (1986) observes, "The tendency for public goods to be underproduced is serious enough within a nation bound by some sort of social contract, and directed in public matters by a government with the power to impose and collect taxes. It is…a more serious problem in international political and economic relations in the absence of international government." Peterson (2000) agrees that it is problematic for institutions to provide global public goods in optimal amounts because no international authority exists to support agreements, but he points out that "international regimes" may compensate to some extent. These regimes can be thought of as "institutional structures designed to solve particular public goods problems in the absence of a world government" (Peterson 2000).

In this paper we propose to examine one particular global public goods problem: the provision of international research on improved maize and wheat technology to poor farmers in developing countries. In particular, we focus on how changes in the international environment are transforming the legal and social conventions (the "regime") governing international agricultural research and affecting the flow of improved maize and wheat technology to developing countries. We begin by describing the international research system that develops and delivers improved maize and wheat technology for poor farmers. We then address several issues that will influence whether and how this system continues to operate. Aside from the public goods problems described earlier, these include such divisive issues as the rights to genetic resources and intellectual property protection. We describe strategies that the International Maize and Wheat Improvement Center (CIMMYT) has used to continue delivering global public goods to poor people, and conclude with a brief statement of why, despite the present uncertainty in the global research outlook, there will still be a place for international agricultural research and its products.

Research and Development for Global Public Goods: Origins and Achievements

In the two decades after the Second World War, changing perceptions about the potential socioeconomic effects of applied science led to a realization of the crucial role that research could play in hastening the economic development of poor countries. As noted by Press and Washburn (2000), the role of university research in developing technologies that altered the course of the war (penicillin and streptomycin as well as nuclear weapons) heightened government awareness that “academics were uniquely capable of undertaking crucial research initiatives,” and public funding for research grew rapidly.

During the same period, European nations divested themselves of their colonies and protectorates, leaving a number of newly independent nations to make their way toward economic development with limited resources. By the mid 1960s, a number of these new nations seemed to be faltering on the path to prosperity. The prospect of famine and unrest in developing countries, especially in Asia, underscored the need for a new kind of development assistance. As it became increasingly clear that industrial development did not necessarily lead to sustained economic growth, “agriculture was gaining ascendancy in the economic strategies of developing countries” (Baum 1986). Confidence in the efficacy of publicly sponsored research began to merge with the conviction that agricultural research could stabilize and strengthen the economies of developing nations.

The case for agricultural research as a means of fostering economic growth in the developing world was compelling. The Asian subcontinent had been on the brink of famine in the mid 1960s, but in an exceptional international effort, researchers had developed new wheat and rice varieties that yielded much more than the wheat and rice varieties Asian farmers already grew. When these new varieties were grown in India, Pakistan, and Bangladesh, they produced enough grain to make the difference between life and death for millions of people. The scale of this achievement, termed the “Green Revolution,” was so widely recognized that Norman E. Borlaug, the plant breeder who had developed the wheat varieties, was awarded the Nobel Peace Prize in 1970. Governments, development banks, international organizations, and private foundations became convinced that funding international agricultural research—which efficiently produced technology that could be used in a wide number of developing countries—could have enormous international benefits, both economic and social. These organizations established a consortium, the Consultative Group on International Agricultural Research (CGIAR), to support agricultural research in developing countries. This consortium funded what have come to be called the Future Harvest Centers of the CGIAR.[1] One of the first research centers in this consortium was the institute in which Norman Borlaug had conducted most of his research. Established in 1966, the International Maize and Wheat Improvement Center (better known as “CIMMYT,” its acronym in Spanish), remains committed to improving the productivity, profitability, and sustainability of maize- and wheat-based cropping systems in developing countries. To a great extent, CIMMYT and the other Future Harvest Centers were modeled on the plant science departments of US universities, especially the publicly funded land-grant universities, which had been highly successful in employing science to improve agriculture. The difference was that CIMMYT’s mission was international, and to meet the needs of developing countries the Center emphasized applied rather than basic research. Like many land-grant universities, the Center also had a role in educating researchers by providing highly specialized training to thousands of scientists from developing countries.

As it completes its 35th year, CIMMYT has many achievements to its credit. CIMMYT-related wheat varieties are planted on more than 64 million hectares in developing countries (more than three-quarters of the area planted to modern wheat varieties in those countries). CIMMYT-related maize varieties cover nearly 15 million hectares in non-temperate environments of developing countries (almost half of the area planted to modern maize varieties in those environments). Genetic diversity and the conservation of maize and wheat genetic resources have greatly improved. Innovative crop management practices designed to reduce environmental degradation and conserve resources have been developed.

All of these products and services originated in an extensive, international, collaborative research network that relied on the open exchange of knowledge and technology in the public domain. This network presently involves research and development organizations in more than 100 developing nations as well as similar institutions in numerous industrialized nations.[2] The benefits of collaboration between CIMMYT and national research organizations in developing countries have been impressive. Depending on several economic and technical assumptions, estimates of the value of the additional grain

---

[1] See www.cgiar.org and www.futureharvest.org.

[2] For an idea of institutions with which CIMMYT collaborates, and for information on who funds our research, see our Annual Report (CIMMYT 2000a) (www.cimmyt.org/whatiscimmyt/AR99_2000/content.htm).

production attributable to international wheat breeding range from US$ 2 billion to US$ 4 billion per year (Cassaday et al., forthcoming). In the case of maize, the calculations are more complicated, mainly because of the large size of the private maize breeding industry, but the economic value of the additional grain production attributable to public international maize breeding efforts is likely to exceed US$ 2 billion per year (Morris, personal communication).

The social benefits of this research, though difficult to measure, are also likely to be large. Additional maize and wheat production alone certainly cannot be credited with reducing malnutrition in the developing world, but the prevalence of malnutrition in developing countries declined from 46.5% in 1970 to 31% in 1995 (Smith and Haddad 2000), partly because more food was available to more people. Food has certainly become more affordable for consumers. Between 1982 and 1995, real world wheat prices fell by 28%, and world maize prices dropped by 43% (Pinstrup-Andersen et al. 1999). Cheaper food is important for poor people in developing countries, who spend 50-80% of their disposable income on food compared to the 10-15% spent in Europe and the US (Pinstrup-Andersen and Cohen 2001).

International agricultural research has also benefited the environment. By breeding plant varieties with genetic resistance to pests and diseases, public research organizations made farmers' use of harmful, expensive agrochemicals unnecessary.[3] It has been argued that by increasing agricultural productivity per unit of land, research has prevented farmers from cropping more ecologically fragile land and from invading forested areas. Recent calculations (Grace et al. 2000) indicate that if the developing world had attempted to meet its food requirements in 1995 without the improved varieties of food crops[4] developed since the Green Revolution, an additional 426 million hectares of cropped area would be needed (a five-fold increase over cropped area in 1965). An even more important finding is that this land savings helped to reduce greenhouse gas emissions by 35%. Grace et al. (2000) conclude that, "without the Green Revolution…the atmospheric concentration of greenhouse gases would be significantly higher than they are at present and the actual onset of climate change may have hastened."

Many people would agree that those benefits are impressive and that it is a good thing that public sector research delivers them, but even so it is becoming increasingly challenging to provide international agricultural research to poor countries. The environment in which CIMMYT seeks to fulfill its mission is changing radically. The international community faces several choices that will greatly influence support for international agricultural research and the conditions under which that research will take place. In the following sections we explore those choices. Some of them are related to issues that typically surround the provision of public goods, whereas others reflect concerns over the mission and responsibilities of public institutions dedicated to development.

Global Public Research for Poor People: The Changing Context

Development strategies must adapt to a new constellation of circumstances that influence how international agricultural research will be conducted and how research products will be delivered in the future. These include: declining investment in public research and international aid for agriculture; increasing complexity of the agricultural problems that science is being asked to solve; growing dissent over the conservation, exchange, and use of genetic resources; the proliferation of intellectual property rights and proprietary agricultural technologies; the rise of biotechnology and the associated controversy over genetically modified organisms; increasing economic and political power of the private sector; rising pressure for public-sector institutions to behave like private institutions; and growing concerns over scientific and social equity. Because these issues are so closely related it is difficult to treat them separately, but we shall discuss each of them in turn, emphasizing the choices and dilemmas that they present to the international community.

Declining investment in international agricultural research

Between 1991 and 1996, development assistance fell by nearly 15%. From 1986 to 1996, development assistance directed specifically at agriculture fell almost 50% in real terms (Pinstrup-Andersen and

---

[3] Morris and Ekasingh (forthcoming) point out that, unlike public breeding programs, private companies may not have placed much emphasis on breeding for resistance to diseases and pests, especially if the companies included an agrochemicals division.

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

Cohen 1998).[5] Much of the reduction occurred as the seven wealthiest countries that provided development assistance reduced their contributions. At the same time, many developing countries have reduced their own public spending on agriculture, partly under pressure from donor and lending institutions. The results of public under investment in agriculture may already be apparent. Pinstrup-Andersen and Cohen (1998) have found that, with the exception of China and India, in most low-income countries agriculture grew by less than 3% per year over 1990-96—not enough to keep pace with population growth.

Increasing complexity of research challenges

At the same time that the international community's growing disenchantment with development aid is affecting low-income countries, those same countries are facing agricultural challenges that most wealthy nations would find difficult to overcome.

Twenty years from now, the world's farmers will have to produce 40% more grain to meet demand for cereals, including wheat and maize (Pinstrup-Andersen et al. 1999). In developing countries, the demand for wheat and maize will rise faster than demand for rice, the other major food staple.[6] In two decades, 67% of the world's wheat consumption and 57% of the world's maize consumption will occur in developing countries. Even with projected production increases, by 2020 wheat will constitute more than 50% of the developing world's net cereal imports. Maize will constitute 33% (Rosegrant et al. 1997).

Nearly everyone is aware that the world produces enough food to feed all of its people, but the challenge of supplying food to those who need it most is not as simple as it would appear. Simply increasing the "pile of food," observes Falcon (2000), "is by no means sufficient to assure food security among the poor. If developing countries with a large percentage of undernourished people are to solve employment, income, and food-access problems, most of the increased agricultural output must be grown within the borders of these nations."

That is where the challenge becomes acute, because the agricultural problems of developing nations are extreme. They range from numerous physical problems (such as diseases and pests, drought, floods, severe environmental degradation, and infertile soils) to institutional problems (such as weak extension programs, research organizations literally immobilized by a lack of funding, limited access to agricultural inputs and credit, poor infrastructure, and poorly developed markets), to larger deficiencies in human and financial capital.

These challenges to agriculture are further complicated by the fact that agriculture itself is more complex. In the 1970s, agricultural research, whether it was international, national, or local, tended to be organized along commodity lines, focusing on specific, well-defined problems (e.g., breeding for higher yield, disease resistance, pest resistance; or determining optimal fertilizer application levels). During the 1980s, the focus of research shifted gradually to cropping systems, which tend to be characterized by problems involving interactions between large numbers of on-farm and off-farm enterprises. To respond to these problems, research organizations shifted from mono-disciplinary research to multi-disciplinary research. By the 1990s, more researchers recognized that they needed to give greater attention to environmental and sustainability issues alongside the more traditional emphasis on productivity. At the beginning of the new century, research organizations are also being asked to demonstrate the linkages between technology development and poverty alleviation, which implies focusing more attention on the role of policies and institutions in fostering positive agricultural change.

Clearly, no single institution or technology will meet all of these research goals. Partnerships and consortia are essential for assembling the human expertise, technology, and often the financial capacity needed to make a difference for poor farmers. The complexity of the institutional arrangements supporting international research is growing. Organizations need time to explore, access, and assemble promising research tools and technology. They need time to assess which organizations would be effective research partners. The large number of partners in international research efforts—including funding agencies, nongovernmental organizations (NGOs), private companies, and farmers (through participatory research)—makes it harder to

---

[5] Paarlberg (2000), cited in RAFI (2000), reports that foreign aid to developing country agriculture fell by 57% between 1988 and 1996 (a drop from US$ 9.24 billion to US$ 4 billion, in 1990 dollars). He also reports that World Bank loans for agricultural and rural development fell 47% between 1986 and 1998 (from US$ 6 billion to US$ 3.2 billion, in 1996 dollars).

[6] Demand for wheat will grow by 1.58% per year; demand for maize will grow by 2.35% per year.

reach agreement on how best to operate. Transactions costs increase, and partners have to establish clear guidelines and decision rules to govern their collaboration. The large effort to secure international collaboration may certainly be worthwhile, however (witness the results of CIMMYT's maize and wheat research). As Peterson (2000) points out:

> *In addition to the benefits of international public goods that would not be supplied in the absence of international cooperation, international organizations may generate other benefits for participants. Efficiency gains due to scale economies in the provision of the public good, the greater amount of information made available through the supranational structures, and increased political prestige for those who participate in the agreement are examples. As with costs, these benefits increase with the number of participants and the degree of integration.*

Dissent over genetic resources

Herdt (1999) describes the controversy over the exchange, use, and control of plant genetic resources as the enclosing of the "global genetic commons." He notes that "changing technology and institutions have interacted throughout history to create property rights from what had previously been public goods," and that the ability to manipulate DNA has "generated a new class of asset whose ownership is now being contested by multi-billion dollar companies." As private companies have increasingly obtained intellectual property rights to plant traits, genes, and very small genetic components, many agencies in developing countries have come to believe that their genetic resources may prove potentially valuable to the emerging biotechnology industry. Angered by what they consider "bio-piracy," and concerned that they may one day be denied access to what they consider their own resources, many countries in which genetic resources have been collected are demonstrating less willingness to make genetic resources freely available for use by others.

Many issues related to the conservation, ownership, and exchange of genetic resources remain to be resolved at the national and international levels.[7] The net effect of the trends we have just described, however, has been to reduce the flow of genetic resources for research and create a great deal of uncertainty in the public sector about how to work in an environment where the rules of the game are changing, perhaps beyond recognition. Cassaday et al. (forthcoming) observe that the rules established through the international negotiations on plant genetic resources for food and agriculture, which are underway at the Food and Agriculture Organization (FAO), "could dramatically affect the origins, i.e., the genetic content" of all crops "vital to food security and economic development." These researchers conclude that if the negotiations fail to develop a system that is conducive to international public plant breeding, "governments will have to be prepared to devote considerably greater financial and human resources to plant breeding and acquisition of materials than they seem prepared to provide today." In other words, the commitment to provide a particular set of public goods previously provided through international channels will shift to national governments working individually, which is likely to be a less efficient alternative.

The rise of intellectual property rights and proprietary technology

Preston (2000), reviewing trends and achievements at the US Patent and Trademark Office during the Clinton administration, reported that since 1993:

> *…patent and trademark filings have increased more than 70%. Patent filings have gone from 174,000 in 1993 to just under 300,000 this year, and trademark applications have increased from 140,000 to over 370,000. The sheer volume of all of this data has won the USPTO the distinction of having more data storage than the combined contents of every book in the Library of Congress.*

Obviously not all of these patent filings were related to agricultural research, but it is certain that applied agricultural research in biotechnology generated a good number of them. The proliferation of patents and other forms of intellectual property protection could possibly spread beyond the United States, because many countries are required to adopt intellectual property regimes as part of world trade agreements (Morris and Ekasingh, forthcoming).

As noted, the private sector traditionally did not invest in developing new plant varieties, mainly owing to the nonappropriability of benefits. Private investment in

---

[7] It is hoped that international agreements such as the Convention on Biodiversity and the Food and Agriculture Organization's International Undertaking on Plant Genetic Resources for Food and Agriculture will contribute to their resolution.

agricultural research and development (R&D) increased in the 1930s and 1940s with the advent of hybrid maize seed companies (since the nature of hybrids is that the benefits become appropriable). In the 1990s, as the potential of biotechnology became clear, the "business of breeding" really began. Private companies poured money into R&D. Some observers believe that in the US the private sector's expenditure on research now exceeds expenditures by the public sector.

What motivated the rise in private-sector investment in plant breeding? Without a doubt, the potential for claiming intellectual property rights to plant varieties, genes, alleles, and other genetic components has driven this investment. Because the techniques of molecular genetics made it possible to identify the developer of a plant variety without question, it became far easier to claim intellectual property over plant varieties (Herdt 1999). In other words, plant variety protection (PVP), patents, and other types of intellectual property rights have made it possible for companies to appropriate benefits from investments in plant breeding, thereby converting what was once a public good into a private good.

Not everybody is comfortable with this development. As genetic resources in their many forms—plant varieties, the genetic components of plants, and the information associated with them—have gained in value, they are increasingly perceived to be strategic assets, and many observers are disturbed to see that the private sector is appropriating the rights to these assets. Critics are especially concerned by what they see as a fairness issue—many of the genetic resources used as inputs into modern breeding programs were improved by farmers over thousands of years of on-farm selection, and it is not obvious that these farmers (or their descendents) are being compensated.

Even though the new appropriability of genetic resources provides an incentive for private companies to invest in research, another fairness issue emerges when one considers that private companies develop products only for commercial markets. They rarely develop products for the many poor farmers, especially subsistence farmers, who cannot afford to pay for them. The drive towards intellectual property rights has obviously changed the ethos of plant breeding in the public sector, which relied on "a willingness to share discoveries and materials for the common good" (Herdt 1999). In other words, public goods (information, seed) were used to produce other public goods (international agricultural research and its products), but this is no longer the case. Public-sector scientists developing research products for poor people find it increasingly difficult and costly to access the products and processes required for their research. Because researchers may have to work with a number of patented "enabling technologies" to achieve their goals (these technologies can include molecular constructs, transformation processes, genes, and traits), the amount of time spent negotiating access to technology is likely to erode the time and money spent developing and delivering it.[8] Furthermore, one of the most difficult choices facing public organizations is whether to seek intellectual property protection over their own products. Their motivation is not so much to profit from this action as to prevent other agencies from appropriating rights to their research materials and making them difficult and/or expensive for others to access. Falcon (2000) concludes that "the fear that 'outsiders' will patent existing products…has left national agricultural research systems and the international agricultural research centers in a quandary as to whether or not to employ patenting as a defensive strategy against bio-piracy."

Finally, another implication of the rise of proprietary agricultural technology is that researchers in the public arena no longer face a simple decision about *which technology* to use in their research. Because property rights link a technology with its owner, researchers more often than not are also deciding *which corporate entity* they must partner with—or pay—to achieve their goals. Although many observers worry that alliances with private organizations are nothing less than exploitative, others believe that the only realistic strategy is to build alliances that achieve public goals even if they also benefit private bank accounts.

Dissent over biotechnology

Widely differing perceptions about the potential benefits and drawbacks of biotechnology have colored

---

[8] The development of "golden rice," which contains higher levels of beta-carotene, a vitamin A precursor, was heralded as a major achievement on behalf of poor people. It took some time for the public to realize that poor people could not immediately gain access to golden rice because researchers had developed the rice using proprietary technology, and a host of licensing and other issues would have to be resolved before the nutritional promise of golden rice became a reality (see "New mechanisms for accessing and providing research products," later in this paper).

an active and very public debate that covers a range of scientific, political, and ethical issues. Tripp (2000) observes that proponents of biotechnology "argue for the need to increase food production and point to the possibility of addressing the problems of marginalized farmers," whereas opponents "question the safety, relevance, and equity of the new technology." Some have gone so far as to mandate a moratorium on the release of genetically modified organisms (GMOs) and a complete cessation of research. Others have sought to ensure that the views of developing countries are represented in this debate, fearing that the most food-secure nations will take decisions with repercussions for the least food-secure nations. Organizations concerned with agricultural research are now deciding where they stand on these issues.

For international research organizations such as CIMMYT, one problem resulting from this dissent—which is fuelled in part by incomplete knowledge and false information—is that it threatens to close off many avenues of potentially productive research for developing countries. Pinstrup-Andersen and Cohen (2001), in an extensive review of this problem, observe that "positions for or against the use of genetic engineering in food and agriculture in industrialized countries are frequently extrapolated directly to developing countries," even though the perspectives and interests of groups in industrialized and developing nations differ greatly with respect to the technology. For example, rich nations can afford to worry about the health consequences of GM food and determine that it is better to abandon research and commercialization of GM food crops, whereas many poor nations may find it in their interest to explore GMOs' potential for increasing food production and agricultural export earnings. Research on GM food crops may diminish if industrialized nations decide that it is safer to use GM technology to develop pharmaceuticals, with the result that many technologies of potential use for agriculture in developing countries are not developed. Falcon (2000) comments that developing countries "express concern that key research initiatives with biotechnology will not be pursued because of what they perceive to be the private sector's focus on the wrong products, for the wrong reasons, at the wrong time." Pinstrup-Andersen and Cohen (2001) note that these divergent views are likely to lead rich and poor nations to adopt different policies and standards that "may conflict with the current globalization trends," and that "for globalization to continue in the area of food and agriculture, certain policies and standards need to be synchronized, and the biggest threat is that low-income countries will have to adopt policies and standards that are appropriate only for high-income situations."

The predominance of the private sector

As noted, private organizations have marshaled an impressive array of financial and human resources to support their agricultural R&D goals. Heisey et al. (2000) have assessed investments by the public and private sector in plant breeding research in several settings (Australia, Canada, the UK, and US). They found that "across industrialized countries and across crops, the general trend has been towards relatively greater private sector investment in plant breeding, and greater use of private sector varieties in farmers' fields." In the US, "it is likely that for field crops alone private plant breeding expenditures now surpass public expenditures by a considerable margin."[9] In developing countries, Morris (forthcoming) documents that the private sector now invests more in maize breeding than the public sector.

Biotechnology research especially highlights the contrast between public and private investments in agricultural R&D. According to Sandburg (1999), the National Science Foundation provided US$ 30 million for plant genomics research in 1998 and US$ 50 million in 1999, whereas private companies spent US$ 1.5-2.0 billion. When the Novartis Agricultural Discovery Institute, Inc. (NADII, now known as the Torrey Mesa Research Institute) was established in California in 1998, funding for the first 10 years was anticipated to be US$ 600 million. (Funding for all 17 Future Harvest Centers of the CGIAR, by comparison, was US$ 340 million in 1998.) The financial clout of the multi-billion-dollar biotechnology industry, which had its origins in technology developed in the public sector, has come to have implications for how the public sector—including organizations such as CIMMYT—chooses to do its work. Some of these implications are discussed in the next section.

Pressures for the public sector to act like the private sector

The private sector traditionally has supported public-sector research in many ways, including direct research grants, donations, endowed chairs, and scholarships.

---

[9] See also C.E. Pray (1999) "Role of the private sector in linking the US agricultural, scientific, and technological community with the global scientific and technological community," unpublished paper, Rutgers University.

More recently, however, private organizations seem to be financing a greater share of the research in universities[10] and public organizations under arrangements that have called the independence of the public sector into question.

In 1998, NADII reached a still-controversial agreement with the University of California-Berkeley in which NADII agreed to provide US$ 25 million over five years to the university's Department of Plant and Microbial Biology to conduct basic research on plant genomics. Under the conditions of the grant, department researchers do not work on specific products for Novartis (now re-named Syngenta), but Syngenta receives the first right to negotiate licenses on about one-third of the department's discoveries—discoveries from research funded by NADII/Torrey Mesa as well as by state and federal organizations. Syngenta benefits from gaining access to research that could yield commercial products, and the university gains access to Syngenta's proprietary gene sequencing database, an immensely valuable resource otherwise unavailable to the university. A committee formed by three professors from the department and two Syngenta representatives decides which research projects to fund through the Torrey Mesa grant. The decision to award Syngenta the right to negotiate for 30-40% of the department's inventions was based on the fact that the Torrey Mesa grant would fund 30-40% of the department's annual research budget (Sandburg 1999).[11]

Many observers of events at UC-Berkeley felt that this arrangement blatantly challenged the university's mission as a public institution committed to preserving academic freedom—particularly the freedom to ensure that its research agenda remained independent of commercial interests. Others wondered how much longer the university could claim to serve the public good in any case, given that state funding for UC-Berkeley had fallen to 34% in 2000 compared to 50% twelve years previously (Press and Washburn 2000).

Similar doubts have been expressed in response to the trend among universities and other public organizations to patent their inventions. Universities that once regarded patents as "fundamentally at odds with their obligation to disseminate knowledge as widely as possible" have altered their way of doing business, so that "nearly every research university in the [US]…has a technology-licensing office" (Press and Washburn 2000). Many university campuses are now surrounded by clutches of start-up companies formed on the basis of university discoveries. Despite a handful of lucrative successes,[12] however, most licensing offices have yet to become a major source of funds for the universities they serve (Press and Washburn 2000).

Strategies such as these have raised questions that have echoed throughout the public sector. Some of these questions are related to the future of public-sector research itself, whereas others are related to the increasingly blurry distinction between public and private research. If the public sector is unwilling to increase funding for research, will public research organizations continue to achieve their goals? Many fear that if public institutions cannot compete with the resources offered by the private sector, they will no longer attract and retain the best researchers. Others worry that public organizations will not conduct the kind of basic research that truly inspires innovation. Still others have expressed great concern that the public research agenda, which often addresses issues and meets needs of little importance to the private sector, will become distorted by the private sector's goals. Can intellectual freedom be protected if private rather than public funding increasingly supports public institutions? Finally, what really defines a "public" institution? Public institutions may profess to serve the public good, but will their financial statements and research portfolios give the lie to that assertion? We will return to some of these questions, and to how CIMMYT and other international research organizations are attempting to deal with them, later in this paper.[13]

---

[10] Corporations provided US$ 850 million to US universities in 1985 and US$ 4.25 billion less than a decade later (Press and Washburn 2000).

[11] An even more controversial arrangement had been established—and challenged—earlier between Scripps Research Institute and Sandoz (Sandburg 1999), in which Sandoz was first awarded the right to license *all* of Scripps' inventions over the course of ten years. This arrangement proved so controversial that, following US congressional hearings, the terms of the agreement were altered to give Sandoz first rights to license 46% of Scripps' discoveries over five years, with an option to renew the agreement for another five years.

[12] For example, Stanford University earned US$ 61 million from its technology transfer efforts in 1999 (Press and Washburn 2000).

[13] For a clear and thorough discussion of these questions, see Morris and Ekasingh (forthcoming).

The struggle for equity in science

Diverging investment in agricultural R&D by the public and private sectors, diverging perspectives in wealthy and poor nations about potential applications of biotechnology, concerns over the ability of public organizations to access new technologies and processes for research, and the complexity of the new technology itself have raised the twin specters of “scientific imperialism” and “scientific apartheid.” We have already discussed fears that wealthy nations will dictate the scientific limits of poor nations, not only through the kinds of research they choose to undertake but through the positions advocated by civil society organizations and development assistance agencies. Pinstrup-Anderson and Cohen (2001), for example, have shown how opposition to biotechnology in developing countries by civil society organizations in industrialized nations has elicited the response from developing nations that they would prefer to determine for themselves, on the basis of their needs and values, whether and how they will use GMOs and other products of biotechnology. Herdt (1999) cautions that the increasing use of intellectual property rights could “raise costs or discourage innovations in the developing world, or shift power unfairly to industrialized country firms away from developing country organizations.”

A parallel concern is that results of research undertaken in industrialized nations will be increasingly beyond the reach of most developing nations, and that the technology gap will only become wider over time. With some notable exceptions,[14] most developing nations lack the financial and human resources to mount ambitious biotechnology research programs, either publicly or privately funded. Nor do many nations have the resources to access technology that has already been developed (including GMOs) and monitor its use. Serageldin and Persley (2000) state the problem simply: “The economic concentration of investment, science, and infrastructure in industrial countries and the lack of access to the resulting technologies are major impediments to the successful applications of modern biotechnology to the needs of global food security and to create wealth for the presently poor people and countries.”

The struggle for social equity

If international research organizations such as CIMMYT are preoccupied by the prospect of growing inequity in science, it is because they are even more preoccupied by the prospect of growing inequity in society. One of the arguments in favor of international agricultural research is that its benefits are felt by the poorest members of society. Who are these people whose lives will be affected if agricultural research fails to help them? They include the nearly three billion individuals who survive on less than US$ 2 per day—two dollars for food, clothing, shelter, education, medical treatment, and other needs. They include the world’s 160 million malnourished children. They include the people who live in rural areas in developing countries and depend on agriculture to provide income and food security—more than 70% of the population.

Should the interrelated trends discussed previously combine to inhibit international public agricultural research, fewer research organizations may survive to act as “agencies for equity.” Although international agricultural research seems to be hemmed about with a growing number of constraints, at CIMMYT we believe that these constraints are not insurmountable. Our strategies for ensuring that international research empowers poor people and eradicates scientific apartheid—in short, our strategies for keeping public goods *public*—are discussed next.

CIMMYT: Freedom to Achieve a Humanitarian Mission

In adapting its research strategies to a volatile new research environment, CIMMYT is fully aware that “society benefits when the public sector has ‘freedom to operate,’ when it maintains public access to research tools subject to intellectual property protection by the private sector, and when it engages in fruitful collaborative research” (Heisey et al. 2000). Here we outline some of the alternatives that will ensure that CIMMYT remains effective and true to its mission in the midst of great change in the way research is conducted.

Partnerships for a new research environment

Especially as a result of new intellectual property arrangements, public research organizations are entering into a larger variety of research partnerships than in the past. These partnerships range from traditional philanthropic arrangements to purely

---

[14] Argentina, Brazil, China, India, Kenya, Mexico, South Africa, and Thailand, for example, have all dedicated significant resources to biotechnology research.

commercial alliances and include direct support for research, collaborative public sector research, licensing (different agreements for sharing costs and technology), market segmentation, technology grants for research in developing nations, and joint ventures (Falcon 2000). Here we will not discuss CIMMYT's more "traditional" research partnerships (although these, too, are changing as they come to involve a wider range of participants).[15] Instead we will describe 1) alliances between CIMMYT and the private sector and 2) partnerships between CIMMYT and other public research organizations in which processes or products of biotechnology are used.

Partnerships with private research organizations. Private and public research organizations increasingly agree that it is urgent to explore the ways that their interests may intersect for the benefit of society. For example, the development of drugs to combat AIDS and the breakthrough with golden rice have both raised awareness that private corporations may have a moral responsibility to make their products available to poor nations (in other words, under certain conditions the private research sector should further the objectives of the public sector).[16]

With regard to agreements with the private sector, CIMMYT's policy is to enter into such agreements only if they enhance the Center's ability to achieve its mandate of service to the resource-poor and the environment. In simple terms, will an agreement help CIMMYT to more quickly develop new, appropriate technologies and deliver them to farmers' fields in developing countries? If so, the agreement is what we call a "win-win" alliance, and the Center can participate. Within this framework, CIMMYT has established four agreements with private research organizations that provide access to expertise and technologies that otherwise would not be available.[17] Three of the agreements involve research on wheat: a project to evaluate the potential of hybrid wheat; a project with a private company in Spain to improve disease resistance, yield, and quality in durum and bread wheat; and a project with a private company in Mexico to improve the industrial quality of bread wheat.[18]

A fourth project aims to develop apomictic maize plants. Since 1990, a joint project between CIMMYT and France's Institut de Recherche pour le Développement (IRD)—a public research organization—has focused on understanding apomixis (the asexual reproduction of plants through seed) and how the trait might be transferred to maize. To accelerate progress in this potentially revolutionary area, in 1999 CIMMYT and IRD formally entered into an important research collaboration with three private seed companies (Pioneer Hi-Bred International, Groupe Limagrain, and Syngenta). The five-year agreement is aimed at further understanding apomixis, which is the natural ability of some plants to reproduce offspring identical to the mother plant through asexual reproduction. In the plant kingdom, more than 400 species, most with little or no agronomic potential, possess this apomictic characteristic. Greater knowledge about this natural plant mechanism could provide the basis for its transfer to some of the most commonly grown agricultural crops, for instance, hybrid maize. For the agreement's seed-producing partners, enhanced knowledge of apomixis might create new options for improved multiplication and quality of seeds. For CIMMYT and IRD, the transfer of apomixis to maize offers the long-term possibility of delivering superior hybrid crop traits, such as disease resistance and higher yields, to the resource-poor farmers of the world through the inherent reproductive characteristics of apomictic plants.

Partnerships between public research organizations to explore the potential of biotechnology. CIMMYT conducts a wide range of biotechnology research and

---

[15] For example, a research consortium to address the challenging environmental and productivity problems in South Asia's rice-wheat systems has, at one time or another, involved national and international research organizations, nongovernmental organizations, farmers, local private machinery companies, and researchers from advanced public research organizations in industrialized countries. This consortium was recently recognized by the CGIAR as one of the most successful research partnerships established by the Future Harvest Centers. Information on the Rice-Wheat Consortium for the Indo-Gangetic Plains is available at www.rwc.cgiar.org.

[16] Representatives of seven of the world's academies of science (the Brazilian, Chinese, Indian, Mexican, UK, US, and Third World academies) recently issued a white paper (Anonymous 2000) on transgenic plants and world agriculture, stating: "Private corporations and research institutions should make arrangements for GM technology, now held under strict patents and licensing agreements, with responsible scientists for use for hunger alleviation and to enhance food security in developing countries. In addition, special exemptions should be given to the world's poor farmers to protect them from inappropriate restrictions in propagating their crops."

[17] In 1999, 3% of CIMMYT's research resources came from agreements with the private sector.

[18] Details of these agreements may be found in CIMMYT's annual report (CIMMYT 2000a).

collaborates with a number of public sector institutions in developing countries. Here we will describe a project recently initiated in Kenya. Scientists from the Kenya Agricultural Research Institute (KARI) and CIMMYT are using conventional as well as biotechnological breeding strategies to develop maize resistant to stem borers, which are estimated to destroy 15-40% of Kenya's maize crop each year. The Insect Resistant Maize for Africa (IRMA) Project is funded by the Novartis Foundation for Sustainable Development. The project was launched through a consultative meeting in which all groups concerned with the outcome met to discuss their views of the project, including representatives from KARI and CIMMYT as well as from farmers', women's, and church associations; extension services; various ministries; the private sector; and a contingent of Kenyan print and broadcast media.

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

The project calls on CIMMYT and KARI expertise in maize breeding, agricultural economics, biotechnology, entomology, and communications. It is important to emphasize that project researchers have agreed to identify and develop gene constructs that contain no herbicide or antibiotic markers. Maize varieties produced by the IRMA Project will carry only "clean" or "purified" Bt genes, circumventing concerns about unforeseen impacts on the environment or human health. While this approach costs more and takes longer, IRMA researchers are committed to addressing all reasonable issues that emerge regarding the technology.

Policies for a new research environment

As the research environment becomes more complex and public research organizations enter into more alliances with the private sector, CIMMYT has sought to develop clear, open policies with respect to intellectual property and new technology. These policies provide a public account of CIMMYT's strategies for making its research products available to the international community and for working with private organizations in ways that are absolutely consistent with its mission to help the poor.

CIMMYT's intellectual property policy and intellectual property management. In 2000, CIMMYT released its policy on intellectual property (CIMMYT 2000b).[19] The preamble emphasizes the Center's concern over preserving public access to its research products:

> *As a publicly funded international research institute, CIMMYT regards its research products as international public goods. Yet, in the current political and legal environment, producing and keeping the products of its research in the public domain, free for use and development both by scientists and farmers, have become increasingly problematic. It is in this context that CIMMYT has examined, and will continue to examine, its policies and practices in regards to intellectual property rights.*

For the most part, the policy spells out procedures for managing intellectual property that were already in place within CIMMYT. One example is the procedure to hold the genetic resources designated under a 1994 FAO/CGIAR agreement in trust for the benefit of the international community, especially developing countries. The new intellectual property policy represents a departure from previous modes of operation, however, by establishing that CIMMYT will take steps to protect its inventions through patents, plant breeders' rights, copyrights, trademarks, statutory invention registrations or their equivalent, and/or trade secrets under the following conditions:

> *To support public and private partnerships which pursue mission-based research or which develop and apply research results; to assure ready access by others to research products developed or funded by CIMMYT; to avoid possible restrictions arising from "blocking" patents and to ensure CIMMYT's ability to pursue its research without undue hindrance; to facilitate the*

---

[19] See www.cimmyt.org/resources/Obtaining_seed/IP_policy/htm/IP-Policy.htm.

> *transfer of technology, research products, and other benefits to the resource poor including, where appropriate, through commercialization or utilization of research products; and/or to facilitate the negotiation and conclusion of agreements for access to proprietary technologies of use to CIMMYT's research and in furtherance of its mission.*

The policy further specifies that, in light of the "evolving legal and political environment," CIMMYT's Board of Trustees will "regularly review this Policy and its implementation in order to ensure that CIMMYT is well positioned to carry out its mission."

CIMMYT was one of the first Future Harvest Centers to release an intellectual property policy, and the press quickly noted the decision. The policy was described in *Nature,* which quoted a CIMMYT Board member as saying that "this is not an effort by the organization to 'get rich' by patenting discoveries, but to ensure broad distribution of plant materials through a flexible policy" (Dalton 2000).

Aside from its new policy, CIMMYT has several organizational avenues for managing intellectual property and related issues. For a number of years, CIMMYT has maintained standing committees on intellectual property, biosafety, and bioethics, and the center has conducted a full intellectual property audit. In 2001, an Intellectual Property Management Unit will be established to provide further guidance and leadership on intellectual property issues.

CIMMYT's genetic engineering strategy. In developing the tenets of its genetic engineering strategy for wheat and maize, CIMMYT has emphasized the needs of its partners in national research organizations and the usefulness and safety of its products for farmers. Five points guide the Center's genetic engineering program:

- Plant varieties that are genetically engineered by CIMMYT are developed in concert with a national program partner to meet a delineated need.
- CIMMYT provides only transformed plants that carry "clean" events, meaning that only the gene of interest is inserted into the final product.
- No transformed plants that carry selectable markers, such as herbicide or antibiotic resistance, are provided to national programs for release.
- CIMMYT's focus on possible genes for transfer is only on plant, bacterial, fungal, and viral genes (i.e., not on animal genes, especially human genes).
- CIMMYT works only in countries that have biosafety legislation and regulations.

New mechanisms for accessing and providing research products

CIMMYT actively seeks new ways of accessing research tools and providing research products. It has been suggested that one potential means of reducing some of the complicated legal arrangements involved in accessing and disseminating new technology is a mechanism known as a "patent pool," which has been used in the US for 150 years, mostly in the manufacturing industry and more recently in the electronics industry (Clark et al. 2000).[20] This mechanism, which is regulated by the Antitrust Division of the US Department of Justice and by the Federal Trade Commission, is thought to offer "one way to address the issue of access to vital patented biotechnology products and processes" (US Patent and Trademark Office 2001).

A patent pool consists of two or more patent owners who agree to license one or more of their patents to one another or third parties. The pool has the advantage of allowing organizations to make all of the components needed to conduct a process or produce a technology available from one source. Ideally, according to Clark et al. (2000:8-9), such arrangements would make it possible to integrate complementary technologies, reduce transactions costs, clear blocking positions, avoid costly infringement legislation, and promote the dissemination of technology. These authors note that "the re-emergence of…patent pools suggests that the social and economic benefits of such arrangements outweigh the costs." They contend that patent pools can encourage "the cooperative efforts needed to realize the true economic and social benefits of genomic inventions. In addition, since each party in a patent pool would benefit from the work of others, the members may focus on their core competencies, thus spurring innovation at a faster rate." Should patent pools become more common in the biotechnology industry, public research institutes may have greater access to technology for their research—if the conditions are acceptable to their goals as public institutions.

Increasingly, the international community appears to be seeking a forum for reconciling the objectives of private and public research institutions with respect to

---

[20] The authors are grateful to Victoria Henson-Apollonio, Senior Research Officer, Intellectual Property, with the CGIAR Central Advisory Service on Intellectual Property, for drawing our attention to patent pooling.

developing countries. A white paper issued by seven academies of science in 2000 advocates the establishment of an international advisory committee to "assess the interests of private companies and developing countries in the generation and use of transgenic plants to benefit the poor—not only to help resolve the intellectual property issues involved, but also to identify areas of common interest and opportunity between private sector and public sector institutions" (Anonymous 2000). Such an advisory group could become a valuable resource for international research organizations working in developing nations. The current Central Advisory Service on Intellectual Property of the Future Harvest Centers—an international forum that has already been established—could possibly play this role, at least within the CGIAR.

Meanwhile, private research organizations have become increasingly aware of the importance of collaborating with public research initiatives, especially in developing countries, and this trend could be beneficial for international agricultural research.[21] Nash (2000) reports that the developers of golden rice, Ingo Potrykus and Peter Beyer, "struck a deal with AstraZeneca, which…holds exclusive rights to one of the genes Potrykus and Beyer used to create golden rice. In exchange for commercial marketing rights in the US and other affluent markets, AstraZeneca agreed to lend its financial muscle and legal expertise to the cause of putting the seeds into the hands of poor farmers at no charge." In January 2001, Syngenta, one of the world's largest agrochemical companies, published the first complete genome of a food crop (rice). With this information, Syngenta researchers can achieve highly specific breeding objectives very rapidly, because it enables them to identify particular genes (such as a gene conferring resistance to an important disease) that would be useful to transfer from one variety to others. The value of this information for public breeding research in developing countries is obvious. Syngenta, in a statement issued on 26 January 2001, said that in developing countries, "where rice is a vital crop, Syngenta will work with local research institutes to explore how this information can best be used to find crop improvements to benefit subsistence farmers. It is our policy to provide such information and technology for use in products for subsistence farmers, without royalties or technology fees." Many members of the development community welcomed this effort to channel important technology to the people who arguably have most to benefit from it.

Dialogue, advocacy, and information for research planning

CIMMYT researchers are committed to conducting an open dialogue on many of the scientific, legal, and institutional changes that are transforming the environment in which it seeks to fulfill its mission. For example, CIMMYT convened an international forum in Tlaxcala, Mexico, in late 1999 to initiate a dialogue on key issues related to public/private alliances in agricultural research. The participants were all highly respected, experienced individuals active with the private sector, major public research institutes in the developing world, multilateral donor agencies, academia, and the CGIAR. Participants produced a statement that reflected their consensus on how public and private research organizations could adopt complementary and mutually reinforcing forms of working together (CIMMYT 2000c).[22] CIMMYT also participates in numerous international forums on biotechnology, including the Africa Biotechnology Stakeholders Forum, which addresses the special issues surrounding biotechnology in the African context.

Because it is a well-known research institution with decades of experience in developing countries, CIMMYT can also help educate a wider audience about issues that are important to agricultural development. The IRMA Project has a strong public education and awareness program related to the technology it develops, for example. This program is directed at the general public as well as farmers and other important groups who have an interest in the project's progress and outcomes. In addition, CIMMYT has publicly advocated that national governments—not the governments of industrialized nations—must take their own decisions with respect to GMOs and other products of biotechnology, and that those decisions should emerge from "serious discussion based on credible, science-based information" (Feldmann et al. 2000).

---

[21] Perhaps this awareness builds on the belated realization by many pharmaceutical companies that they should develop more flexible and lenient policies for providing AIDS medication in developing countries.

[22] See www.cimmyt.org/whatiscimmyt/tlaxcala.htm.

Through its own research, CIMMYT is careful to provide sound information for research management decisions related to new technology and the research environment. For example, a CIMMYT researcher and a colleague from a national public research program recently reviewed the ways that public and private plant breeding organizations could reorient their efforts (Morris and Ekasingh, forthcoming). Concluding that "if public breeding programs do not change the way they operate, they will become marginalized," Morris and Ekasingh also caution that public breeding programs should not simply "withdraw completely from areas claimed by the private sector, because a continuing public-sector presence may be desirable for efficiency as well as equity reasons." They identify five "essential functions" for public breeding programs in the future: the conservation of genetic resources, training of plant breeders, varietal testing and evaluation, biosafety regulation, and crop genetic improvement for carefully selected products, traits, and crops (e.g., those that are important for subsistence farmers).

CIMMYT researchers have also published research and review articles on geneflow between GMOs and other crops; the efficiency of conventional breeding methods compared to molecular breeding; economic and social incentives for farmers to preserve genetic resources *in situ*; economic returns to conserving and using genetic resources; flows of wheat and maize genetic resources between developing and developed countries; the implications of providing GM seed to farmers in developing countries; and many other topics.[23]

Global Public Goods for Poor Farmers: Still a Reality

Much of the recent investment in agricultural research has been made by the private sector to meet commercial needs and satisfy stakeholders, but it has not been used directly to generate global public goods. As private interests in agricultural research grow, what will be the fate of international agricultural research and the goods and services it provides? Will centers such as CIMMYT remain active forces for agricultural development, or will they merely represent an outmoded way of doing business?

We do not underestimate the challenges, but we strongly believe that international agricultural research will continue to be an effective force for change in the developing world. To some extent, the current fierce debate over intellectual property and other issues has obscured the fact that much of the history of agriculture, including agricultural research, consists of a series of upheavals and accommodations that occurred as public and private organizations sought to adapt to economic and institutional change (Heisey 2000). Although the research environment has become extremely volatile, it is to be hoped that the international community will mobilize its considerable authority and resources to support international research and ensure that poor people are not excluded from development opportunities through short-sighted policies, agreements, and purely commercial interests.

We know that if less technology is generated to help the poor, and if fewer poor people can access that technology, the cost of social equity will rise for every individual on earth. The consequences for the rural poor will not be small. Some people will pay with their lives; others will take their suffering to overcrowded cities or across borders to wealthy nations. At CIMMYT we believe it is urgent to join actively in the debates surrounding international agricultural research and discover more efficient ways of fulfilling our mission. The penalty for not acting, and for being excluded from new research opportunities, is going up exponentially—each year, and for each person.

References

Anonymous. 2000. *Transgenic Plants and World Agriculture.* Washington, DC: National Academy Press.

Baum, W.C. 1986. *Partners against Hunger: Consultative Group on International Agricultural Research.* Washington, DC: World Bank for the Consultative Group on International Agricultural Research.

Cassaday, K., M. Smale, C. Fowler, and P.W. Heisey. Benefits from giving and receiving genetic resources: The case of wheat. Plant Genetic Resources Newsletter (forthcoming).

CIMMYT (International Maize and Wheat Improvement Center). 2000a. *Science and Sustenance: Annual Report, 1999-2000.* Mexico, D.F.: CIMMYT.

CIMMYT (International Maize and Wheat Improvement Center). 2000b. *International Maize and Wheat Improvement Center Policy on Intellectual Property.* Mexico, D.F.: CIMMYT.

---

[23] See, for example, Serratos et al. (1997) on gene flow among improved maize, landraces, and teosinte; Dreher et al. (2000; 2001) and Ribaut and Poland (2000) on issues related to conventional and molecular breeding; and Smale (1998) on numerous genetic resources issues, including measurements of genetic diversity and the economics of genetic resource conservation.

CIMMYT (International Maize and Wheat Improvement Center). 2000c. *Tlaxcala Statement on Public/Private Sector Alliances in Agricultural Research: Opportunities, Mechanisms, and Limits.* Mexico, D.F.: CIMMYT.

Clark, J., J. Piccolo, B. Stanton, and K. Tyson, with M. Critharis and S. Kunin. 2000. *Patent Pools: A Solution to the Problem of Access in Biotechnology Patents?* Washington, DC: US Patent and Trademark Office.

Dalton, R. 2000. Cereal gene bank accepts need for patents. *Nature* 404 (6 April):534.

Dreher, K., M.L. Morris, M. Khairallah, J.-M. Ribaut, S. Pandey, and S. Srinivasan. 2000. Is marker-assisted selection cost-effective compared to conventional plant breeding methods? The case of Quality Protein Maize. Presented at the Third Annual Conference of the International Consortium for Agricultural Biotechnology Research (ICABR).

Dreher, K., M.L. Morris, J.-M. Ribaut, and M. Khairallah. 2001. Potential impacts of biotechnology-assisted selection methods on plant breeding programs in developing countries. Presented at the Pre-Conference Workshop, “Agricultural Biotechnology: Markets and Policies in an International Setting,” at the Annual Conference of the Australian Agricultural and Resource Economics Society, 2001.

Falcon, W.P. 2000. Globalizing germplasm: Barriers, benefits, and boundaries. Presented at the 24th International Conference of Agricultural Economists.

Feldmann, M.P., M.L. Morris, and D. Hoisington. 2000. Genetically modified organisms: Why all the controversy? *Choices: The Magazine of Food, Farm, and Resource Issue* First Quarter 2000:8-12.

Grace, P., P. Sanchez, J. Ingram, C. Palm, Reiner Wassman, M. Fisher, R. Thomas, F. Chandler, W. Bowen, R. Reid, M. Wopereis, and S. Waddington. 2000. The consequences of international agricultural research on greenhouse gas emissions and global climate change. Unpublished report prepared for the Inter-Center Working Group on Climate Change, Consultative Group on International Agricultural Research (CGIAR), Washington, DC.

Heisey, P.W., C.S. Srinivasan, and C. Thirtle. 2000. Privatization of plant breeding in industrialized countries: Causes, consequences, and the public sector response. Presented at the mini-symposium, “Emerging Issues in Agricultural Research Policy and Funding: Lesson from Case Studies,” 24th International Conference of Agricultural Economists.

Herdt, R.W. 1999. Enclosing the global plant genetic commons. Presented at the China Center for Economic Research, 1999, Peking University, Beijing, China.

Kindleberger, C.P. 1986. International public goods without international government. *The American Economic Review* 76(1):1-13.

Morris, M.L. *Impacts of International Maize Breeding Research, 1966-97.* Mexico, D.F.: CIMMYT (forthcoming).

Morris, M.L., and B. Ekasingh. Plant breeding research in developing countries: What roles for the public and private sectors? In: D. Byerlee and R. Echeverría (eds.), *Agricultural Research Policy in an Era of Privatization: Experiences from the Developing World.* Wallingford, UK: CAB International (forthcoming).

Nash, J.M. 2000. Grains of hope. *Time Magazine* 156(5).

Paarlberg, R. 2000. The global food fight. *Foreign Affairs* 79(3):35-36. Cited in RAFI (2000).

Peterson, E.W.F. 2000. The design of supranational organizations for the provision of international public goods: Global environmental protection. *Review of Agricultural Economics* 22(2):355-369.

Pinstrup-Anderson, P., and M.J. Cohen. 1998. *Aid to Developing Country Agriculture: Investing in Poverty Reduction and New Export Opportunities.* 2020 Brief 56. Washington, DC: International Food Policy Research Institute (IFPRI).

Pinstrup-Anderson, P., and M.J. Cohen. 2001. Rich and poor country perspectives on biotechnology. Presented at the Pre-Conference Workshop, “Agricultural Biotechnology: Markets and Policies in an International Setting,” at the Annual Conference of the Australian Agricultural and Resource Economics Society, 2001.

Pinstrup-Andersen, P., R. Pandya-Lorch, and M.W. Rosegrant. 1999. *World Food Prospects: Critical Issues for the Early Twenty-first Century.* Washington, DC: International Food Policy Research Institute (IFPRI).

Press, E., and J. Washburn. 2000. The kept university. Atlantic Monthly (March 2000): www.theatlantic.com/issues/2000/03/press.htm.

Preston, T. 2000. An active eight years for IP. *USPTO Today Online* 1(12): 3-7. Washington, DC: United States Patent and Trademark Office.

RAFI (Rural Advancement Foundation International). 2000. *In Search of Higher Ground: The Intellectual property Challenge to Public Agricultural Research and Human Rights and 28 Alternative Initiatives.* Occasional Papers Series 6(1). Winnipeg, Canada: RAFI.

Ribaut, J.-M., and D. Poland (eds.). 2000. *Molecular Approaches for the Genetic Improvement of Cereals for Stable Production in Water-Limited Environments.* Mexico, D.F.: CIMMYT.

Rosegrant, M.W., M.A. Sombilla, R.V. Gerpacio, and C. Ringler. 1997. Global food markets and US exports in the twenty-first century. Presented at the Illinois World Food and Sustainable Agriculture Program Conference, Meeting the Demand for Food in the 21st Century: Challenges and Opportunities.

Sandburg, B. 1999. The ivory tower IP fix. *IP: The Magazine of Law and Policy for High Technology* (May): www.ipmag.com/monthly/99-may/novartis.html.

Serageldin, I., and G.J. Perlsey. 2000. *Promethean Science: Agricultural Biotechnology, the Environment, and the Poor.* Washington, DC: CGIAR.

Serratos, J.A., M.C. Wilcox, and F. Castillo (eds.). 1997. *Gene Flow among Mexican Landraces, Improved Maize Varieties, and Teosinte.* Mexico, D.F.: CIMMYT, Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP), and CNBA.

Smale, M. (ed.). 1998. *Farmers, Gene Banks, and Crop Breeding: Economic Analyses of Diversity in Wheat, Maize, and Rice.* Dordrecht, the Netherlands: CIMMYT and Kluwer Academic Publishers.

Smith, L., and L. Haddad. 2000. *Overcoming Child Malnutrition in Developing Countries: Past Achievements and Future Choices.* Washington, DC: International Food Policy Research Institute (IFPRI).

Syngenta. 2000. Rice Genome Sequence Fact Sheet. 26 January 2001. Basel, Switzerland: Syngenta International AG.

Tripp, R. 2000. GMOs and NGOs: Biotechnology, the policy process, and the presentation of evidence. *ODI Natural Resource Perspectives* 60. London, UK: Overseas Development Institute (ODI).

US Patent and Trademark Office (USPTO). 2001. Press Release, 19 January 2001. Washington, DC: USPTO.

Winkelmann, D.L. 1994. A view of quintessential agricultural research. In: J. Anderson (ed.), *Technology Policy: Policy Issues for the International Community.* Wallingford, UK: CAB International.

Warren E. Kronstad: An Innovator in Plant Breeding Who Had Worldwide Impacts on Wheat Production

F. Cholick

It is an honor to share my thoughts on Dr. Warren E. Kronstad as a teacher and plant breeder. I consider him my mentor.

Dr. Kronstad was a teacher, first and foremost. I learned this firsthand as an undergraduate student in his plant breeding class of 1971. He cared with equal passion for the subject and his students—an attitude I have attempted to carry over to my roles as plant breeder and Dean of the College of Agriculture and Biological Sciences, South Dakota State University. I believe he taught me well, and I strive to translate his spirit and passion into action 30 years later.

Dr. Kronstad's undergraduate classroom was interactive and highly motivating. He believed that plant breeding was a tool for improving the lot of mankind worldwide, and that global public good was indeed a unique service of plant breeders.

Dr. Kronstad also extended his philosophy to the world through teaching graduate students. Under his tuition, 106 students from 27 countries were awarded MSc and PhD degrees. Each international student was asked to share his or her culture and customs. Those using Oregon-developed wheats were expected to develop a humanitarian understanding of the people they served in developing countries.

Dr. Kronstad's approach was to act as coach and mentor. He took advantage of every opportunity to educate and motivate students, whether in the field, the laboratory, the coffee room, or wherever he could lead a discussion on plant breeding and global public good. Dr. Kronstad treated his graduate students as individuals, at times complimenting, at times pushing. He believed that the human resource was a natural resource, able to be cultivated and nourished.

As a mentor, he saw potential within individuals that was often greater than their own vision, and did everything in his power to develop it. As a coach, he encouraged the development of rock-solid and service-oriented principles and philosophies. He instilled in all of his graduate students the desire to continue their own education and to mentor others in all settings. He always urged his students to think "out of the box" and continually asked "Why?" whether about policies, politics, or science when discussing plant breeding and world food production systems.

Dr. Kronstad's "classroom" was Oregon, the Pacific Northwest, the United States, and the world. He knew that listening was an important part of teaching. He listened to producers, hearing their needs, wants, and desires. He encouraged them to become internationally minded, primarily in wheat breeding research. This was not always a popular message to carry to the people. Some individuals contended that export markets were being lost due to greater productivity in the developing world. A number of the values that he held dear are, I believe, lost today.

Dr. Kronstad believed that varieties were but one component within the production system—he always took a systems approach. He believed that agriculture was an integral part of society as a whole, that the land-grant university was the people's university, and that it must provide not only specific scientific research but also knowledge to all citizens. In my mind, this is the foundation of the land-grant university system and a philosophy that needs to be continually renewed.

Besides his students and the producers he worked with, Dr. Kronstad found that his university administrators needed educating. He demonstrated to them the value of research and international involvement. He was a living example of the civic responsibility of a land-grant university to continuing the education of the general public. Now that I, too, am an administrator in a land-grant university, I have a deeper appreciation of his readiness to expand the horizons of his administrators.

If Dr. Kronstad had only been a research scientist, if he had never mentored a single student or changed the mindset of a single administrator, he would still be a champion in the field of wheat breeding. The economic impacts of the varieties he developed and released to the Pacific Northwest, the nation, and the world are well documented. It didn't matter how superior his latest variety was—to him it was just another to surpass with the next release.

Wheat varieties Yamhill and Stephens are forever connected to the Kronstad philosophy. Yamhill is unique in that it was developed for the acid-wet soils of the Williamette Valley, and greatly expanded wheat production in western Oregon. Stephens is a durable variety, has unsurpassed potential to break the yield barrier, and has wide-ranging adaptation. It is a variety that every plant breeder strives for in his or her career. It is known for returning profits to producers.

Dr. Kronstad viewed the genetic base from which he developed his varieties as though it were an artist's palette. Like an artist selecting and combining colors to create a painting, he could, with the same deftness, put together gene combinations with the potential to produce superior varieties or serve as parents for additional varieties. Nowadays we call this conventional breeding and we hanker after genetic engineering, forgetting that pioneers like Dr. Kronstad prepared the way for us.

The widespread adaptation of Dr. Kronstad's winter x spring crossing program illustrates how gene pools can be combined. Without a doubt, this program has stabilized and increased yield potentials in both winter and spring programs. I can personally attest to the increased productivity of spring wheats in the Northern Great Plains Region since we started applying this concept in our South Dakota plant breeding program in 1981.

Dr. Kronstad used every opportunity to select his superior genotypes from wide-ranging environments. The shuttle breeding program, for example, enabled selection for wide adaptation from the high yielding environments of western Oregon to the lower yielding, heat stressed environments of eastern Oregon. Once again, this strategy produced highly favorable results in Oregon and Pacific Northwest, and also worldwide.

Dr. Kronstad viewed germplasm as the lifeblood of a breeding program. He provided germplasm to anyone who could use it to serve the people. His only request was that the source of the germplasm be recognized. Such an attitude served plant breeding well in the past and it is one that should be maintained in the future.

Dr. Kronstad was a creative person. I find that the "Ten Contradictions of a Creative Individual" (Csikzentmihalyi 1996) sum up his creativity and reflect both the man and his ability to influence others:

1. Creative individuals have a great deal of physical energy, but they are often quiet and at rest.
2. Creative individuals tend to be smart, yet also naïve at the same time.
3. Creative individuals combine playfulness and discipline, or responsibility and irresponsibility.
4. Creative individuals alternate between imagination and fantasy at one end, and a rooted sense of reality at the other.
5. Creative people seem to harbor opposite tendencies on the continuum between extroversion and introversion.
6. Creative individuals are remarkably humble and proud at the same time.
7. Creative individuals tend to escape rigid gender role stereotyping.
8. Creative people are thought to be rebellious and independent.
9. Creative people are very passionate about their work, yet they can also be objective.
10. Finally, creative individuals may be subjected to disappointment, yet also great enjoyment.

Dr. Kronstad was all of these. He was an innovative teacher and plant breeder. He was a coach and mentor. He understood and fulfilled the civic responsibility of a university faculty member. He was fully engaged in his profession. He was an artist, a producer of varieties, an ambassador, and a thinker. He was creative and passionate about his work, his life, and the lives of others. He looked into the future.

Reference

Csikzentmihalyi, M. 1996. Ten contradictory dimensions of creativity. In: *Creativity: Flow and the Psychology of Discovery and Invention*, pp. 58-76. Harper Collins.

Wheat Research at Oregon State University: History and Transition

C.J. Peterson

The History

Dr. Warren E. Kronstad, Oregon State University wheat breeder and geneticist, died on 21 May 2000, leaving a tremendous legacy of contributions to wheat improvement. With a research career spanning nearly 40 years, there are few individuals who have had a greater impact on world agriculture. As we examine the contributions of the Oregon State University (OSU) wheat research program and the International Winter x Spring Wheat Program in this paper, we are essentially reviewing the professional career and contributions of Dr. Warren E. Kronstad.

From 1973 to 1999, Dr. Kronstad directed the International Winter x Spring Wheat Enhancement and Training Program (IWxSWP) in collaboration with OSU, the International Center for Maize and Wheat Improvement (CIMMYT), and the US Agency for International Development (USAID). This unique program focused on interdisciplinary research, germplasm enhancement, and graduate training, utilizing the expertise and complementary activities of OSU, CIMMYT and other international research centers, and over 200 national wheat research programs in developing countries. The program effectively extended the impact of the CIMMYT spring wheat improvement effort into the major winter wheat production areas of the developing world. Program goals included: enhancement of biodiversity and germplasm exchange through systematic hybridization of winter and spring wheat gene pools; graduate training and educational opportunities; technology transfer through exchange of germplasm and research information; and the establishment of long-term relationships among scientists, research centers, and organizations in developing countries. A novel and effective “shuttle breeding” strategy involving Oregon, Mexico, and Turkey was utilized to selectively identify valuable new gene combinations with unique adaptive traits and enhanced disease resistances. As a result of Dr. Kronstad’s efforts in germplasm development, increased genetic variability was achieved and deployed for many traits, including more durable disease resistance and more stable grain yields in stressed environments.

The OSU Wheat Program, through its leadership of the IWxSWP, has been the principal US program for promotion and support of international wheat germplasm exchange. In 27 years of the USAID-supported program, over 5,100 germplasm lines were developed and distributed in the form of screening nurseries. These nurseries have been distributed each year to more than 100 cooperators in over 44 countries. Since 1995, OSU has also provided support for distribution of the Facultative and Winter Wheat Observation Nursery (FAWWON) and helped to establish and distribute the Winter Wheat East European Regional Yield Trial (WWEERYT), both of which are coordinated by the CIMMYT program in Turkey. Through these trials, OSU has distributed an additional 1,300 germplasm lines to 44 breeding programs in North and South America.

IWxSWP germplasm has contributed to the development and release of many improved varieties that are now having impact worldwide. Today more than 20 million hectares are sown to wheat varieties developed through this program. In addition, 60% of CIMMYT spring wheat breeding material now includes contributions from winter parents, many of which were developed by OSU. Table 1 lists the major varieties derived directly from OSU or OSU-CIMMYT germplasm that were released by national agricultural research centers. These varieties are currently in production in Turkey, Afghanistan, Tajikistan, and Iran. In addition, there are now seven varieties in registration trials for upcoming release in the former Soviet states of Azerbaijan, Georgia, Turkmenistan, and Uzbekistan (Table 2), where they are expected to significantly contribute to the food supply and food security. There are also numerous released varieties and candidate varieties currently in registration trials that have parental contributions from germplasm developed by OSU and OSU-CIMMYT. OSU-CIMMYT germplasm can be found in the pedigrees of elite lines and early generation breeding stocks of wheat breeding programs throughout the world.

The graduate training provided through the OSU International Winter x Spring Program is, without question, the most important and enduring contribution made by the project to increasing world food supplies. During his career, Dr. Kronstad was Major Professor to a total of 106 graduate students from 24 countries. These students obtained 56 MSc degrees and 62 PhD degrees from OSU (Figure 1). A list of Dr. Kronstad's students (based on available historical records and reports) is shown in Table 3.

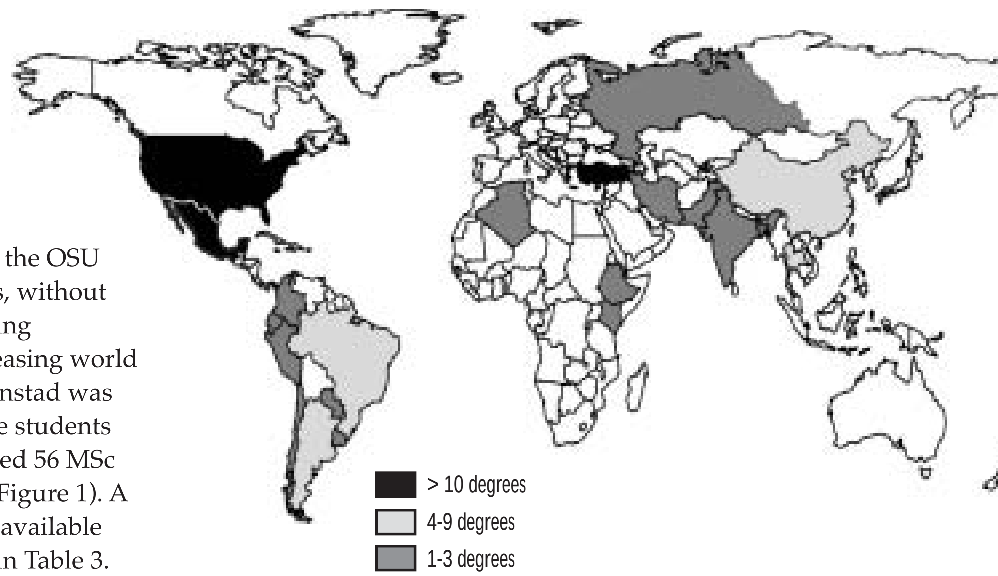


Figure 1. Graduate training at Oregon State University under the direction of Warren E. Kronstad.

Direct financial support for graduate training by USAID was increased ten-fold by funds received from other agencies and national programs. Students were given responsibility for important components of the

Table 1. Winter wheat cultivars released by national agricultural research systems derived from Turkey/CIMMYT/ICARDA IWWIP[1] lines or CIMMYT-Oregon crosses.

Acc. no.	Var. name	Year	Cross	Pedigree	Country
960396	KIRKPINAR79	1979	HYS/7C		Turkey
950154	ATAY85	1985	HYS/7C		Turkey
960396	NAVID	1991	HYS/7C		Iran
950513	GUN91	1991	F35.70/Mo	SWM7155-1A-1A-1A-0A	Turkey
990791	PAMIR94	1994	YMH/TOB//MCD/3/LIRA	SWM12289-7M-0M-8M-1M-3WM-0WM-0AFG	Afghanistan
950129	SULTAN95	1995	AGRI/NAC	SWM6599-2H-1H-3P-0P-5M-3WM-0WM	Turkey
990460	GUL96	1996	ID800994.W/VEE	SWM151342WM-0WM-0SE-1YC-0YC	Afghanistan
990837	RANA96	1996	CA8055/6/PATO(R)/CAL/3/7C//BB/CNO/ 5/CAL//CNO/SN64/4/CNO//NAD/CH	ICWH840431-2AP-2AP-1AP-1AP-0AP	Afghanistan
950920	Buck Oportuno	1996	PI/FUNO*2//VLD/3/CO723595	SWO802012-9H-4M-3WM-0WM	Argentina
463	ZARRIN	1996	NAI60/HEINE VII//BUC/3/F59.71/GHK	SWO791095	Iran
951327	KINACI97	1997	YMH/TOB//MCD/3/LIRA	SWM12289-7M-0M-8M-1M-3WM-0WM-4WM-2WM-0WM	Turkey
991540	YILDIZ 98	1998	55-1744/P101//MAYA/3/MUS/PRM//MAYA/ALD»S»	SWM8340587F-1P-0TE-23YA-0E	Turkey
991828	GOKSU99	1999	AGRI/NAC	SWM6599	Turkey
—	CETINEL 2000	2000	MLC/4/VPM/MOS95//HILL/3/SPN	OWC852672 -6H-0YC-0R-1YC-0YC-0E	Turkey

[1] International Winter Wheat Improvement Program.

Table 2. Winter wheat cultivars in registration trials during 2000.

Variety name	Cross	Pedigree	Country
GOBUSTAN	PEG//HD2206/HORK (2nd RBWON-SAA-2)		Azerbaijan
AZAMETLI 95	PRINIA (16 ESWYT-12)		Azerbaijan
MTSKHETSKAYA 1	TAST/SPRW//ZAR	ICWH840048 -3AP-1AP-2AP-0AP-1AP-0AP	Georgia
GUNCHA	HYS/7C//KRC(ES84-16)/3/SERI	SWM17323	Turkmenistan
BITARAP	SN64//SKE/2*ANE//3/SX/4/BEZ/5/SERI	SWM866442	Turkmenistan
GARAGUM	TRAKIA/KNR	TE3093	Turkmenistan
DUSTLIK	YMH/TOB//MCD/3/LIRA	SWM12289-7M-0M-8M-1M-3WM-0WM-0AFG	Uzbekistan
Cultivated without release:	Atay 85		Tajikistan
	Sultan 95		Tajikistan

research program and learned through hands-on participation. They gained fundamental knowledge and valuable work experience through a combination of course programs involving modern science and biotechnology, hands-on experience in field plant breeding, team research approaches, and technology development and application in thesis research. With assistance from his graduate students, Dr. Kronstad published in a wide range of research areas, including genetic tolerances to abiotic stresses, acid soils, and drought; genetics and enhancement of disease resistance; improved end-use quality; quantitative genetics and breeding methodology; tissue culture and doubled haploid technologies; utilization of novel

Table 3. Graduate students of Warren E. Kronstad, 1968-2001.

Country	Name	Degree goal	Year completed
India	Ganapathy, M.	PhD	1968
USA	Jones, D.	PhD	1968
India	Saini, S.K.	PhD	1968
Korea	Ihrke, C.	PhD	1970
USA	Peterson, C.	PhD	1970
Thailand	Charoenwatana, T.	PhD	1971
USA	Helm, J.	PhD	1972
Mexico	Alcala, M.	PhD	1973
Turkey	Bayraktar, A.	MSc	1973
Tunisia	Chemli, M.	MSc	1973
Turkey	Solen, P.	PhD	1973
Tunisia	Daaloul, A.	MSc & PhD	1974
Turkey	Dutlu, C.	MSc	1974
USA	Keim, D.	PhD	1974
Turkey	Indelen, E.	MSc	1975
Mexico	Maya de Leon, J.	PhD	1975
USA	Roberts, D.	PhD	1975
Turkey	Aktan, S.	MSc	1976
Turkey	Duratan, N.	MSc	1976
Turkey	Yakar, K.	MSc	1976
Iran	Vahabian, M.	PhD	1977
Colombia	Martinez-Racines, C.	PhD	1977
Mexico	Lopez, A.	PhD	1977
USA	Conway, M.	MSc	1977
Lebanon	Abi-Antoun, M.	PhD	1977
Turkey	Firat, E.	MSc	1978
Tunisia	Harrabi, M.	MSc	1978
Thailand	Petpisit, V.	PhD	1978
USA	Sears, R.	PhD	1979
Brazil	Lovato, C.	PhD	1979
Brazil	Camargo, C.	PhD	1979
USA	Alexander, L.	PhD	1980
USA	(Boulger) Verhoeven, M.	MSc	1980
USA	Oakley, S.	MSc	1980
USA	Schumaker, K.	MSc	1980
Mexico	Valencia-Villarreal, A.	PhD	1980
Turkey	Senel, H.	MSc	1981
Mexico	Ortiz, G.	PhD	1981
Korea	Min, H.	MSc	1981
USA	Mareck, J.	PhD	1981
Peru	Gomez-Pando, L.	MSc	1981
USA	Glenn, M.	PhD	1981
Turkey	Ekse, A.	MSc	1981
Dominican Rep.	Cuevas-Perez, F.	PhD	1981
Mexico	Brajcich, P.	MSc & PhD	1981
USA	Altman, D.	MSc	1981
Algeria	Benacef, N.	MSc	1982
Kenya	Boinnet, J.	MSc	1982
Ecuador	Corral, L.	PhD	1982
USA	Frederickson,J.	PhD	1982
USA	Hayes, P.	MSc	1982
Turkey	Hazar, N.	MSc	1982
Turkey	Kanbertay, M.	MSc	1982
Ecuador	Tola, J.	PhD	1983
USA	Marciniak, M.	MSc	1983
Korea	Choi, B.	MSc & PhD	1983
Colombia	Leal, D.	PhD	1984
Algeria	Maatoughi, E.	MSc	1984
USA	Stein, I.	MSc	1984
USA	Goldstein, C.	MSc	1985
Argentina	Lorenzo, A.	MSc & PhD	1985
USA	Rose, C.	MSc	1985
Mexico	Salmeron-Zamora, J.	PhD	1985
Tunisia	Yahyaoui, A.	MSc & PhD	1986
Pakistan	Khan, Noor-ul	PhD	1987
Argentina	Re, J.	PhD	1987
Mexico	Baltazar, B.	MSc	1987
Paraguay	Pedretti, R.	PhD	1987
China	Chen, C.	PhD	1987
Bangladesh	Rahman, M.	MSc	1988
Columbia	Medina, L.	MSc	1988
Uruguay	Verges, R.	MSc	1988
USA	Berge-Chandler, S.K.	PhD	1989
Mexico	Camacho-Casas, M.	MSc & PhD	1989
USA	Lewis, H.	MSc	1989
Pakistan	Masood, M	PhD	1989
Thailand	Tragoonrung, S.	MSc	1989
Turkey	Zencirci, N.	MSc	1989
Tunisia	Abdennadher, M.	MSc	1990
Argentina	Costa, J.	MSc & PhD	1990
Bangladesh	Das, M.	PhD	1990
Thailand	Vanavichit, A.	PhD	1990
China	Wang, S.	MSc & PhD	1990
Peru	Bruzzone, C.	PhD	1991
China	Chen, F.	PhD	1991
Mexico	Encinas, A.	MSc & PhD	1991
USA	Habernicht-Holmer, J.	MSc	1991
Kuwait	Albahouh, M.	MSc	1992
China	Mou, B.	MSc & PhD	1992
Tunisia	Rezgui, S.	PhD	1993
USA	(Goddik) Ruddenklau, H.	MSc	1994
USA	Larson, M.	MSc	1995
Ethiopia	Boru, G.	PhD	1996
Mexico	Briceno, G.	MSc & PhD	1996
Argentina	Cerono, J.	PhD	1996
Chile	Jobet, C.	PhD	1996
USA	Weight, C.	MSc	1996
Tunisia	Ammar, Karim	MSc & PhD	1997
Argentina	del Blanco, A.	PhD	1997
Brazil	Rosa, O.	PhD	1997
Peru	Mendoza, M.	PhD	1998
Georgia (USSR)	Bedoshvili, D.	PhD	1999
Brazil	Rosa, A.	MSc	1999
Uruguay	Castro, M.	MSc	2001
Argentina	Lopez, C.	PhD	2001

genetic resources; agronomy, management, and production stability; and physiology, yield components, and nitrogen use efficiency. Staff from CIMMYT, the International Rice Research Institute (IRRI), and the International Center for Tropical Agriculture (CIAT) were often involved in student advising, designing thesis research problems, or providing direct, on-site support for thesis research. Many of Dr. Kronstad's former students are now in highly respected leadership positions in their respective countries, within government service, international research centers, or major cereal research and extension programs.

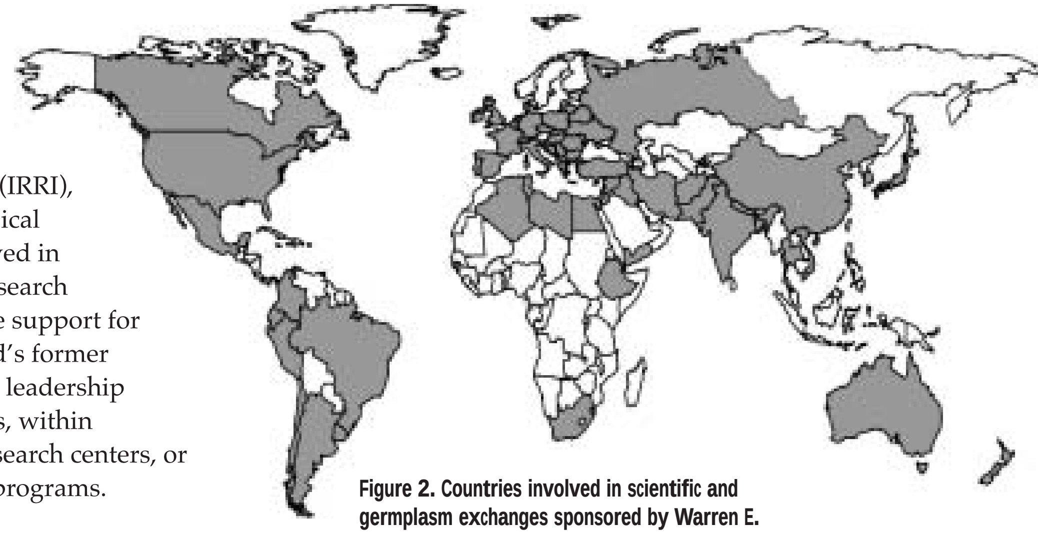


Figure 2. Countries involved in scientific and germplasm exchanges sponsored by Warren E. Kronstad, 1973-2000.

The IWxSWP provided educational and extension training opportunities for many mid-career and senior scientists from developing countries. Dr. Kronstad was involved in many levels of training activities which were highly effective means of disseminating technology, including non-degree training, regional and in-country symposiums, on-site exchanges of germplasm and information, and periodic review of national research programs. While his varietal development work had considerable direct economic impact, Dr. Kronstad's long term commitment and contributions to free germplasm exchange, scientific exchange, and technology transfer have had equal impact on the world wheat research community. Every major wheat growing area in the world has benefited from the germplasm and scientific exchanges coordinated and sponsored by Dr. Kronstad through the IWxSWP (Figure 2).

Dr. Kronstad's contributions to the US wheat industry are no less notable. Dr. Kronstad and his colleagues developed 13 high-yielding, disease resistant wheat varieties grown throughout the Pacific Northwest (PNW), increasing grain yields, production stability, disease resistance, and contributing to the economic viability of the wheat industry. Releases include the soft white wheat Stephens, which has dominated commercial production in Oregon for over 20 years, and major varieties such as Yamhill, Hyslop, McDermid, Hill, Malcolm, Gene, Temple, Weatherford, Winsome, and Foote. These varieties are largely responsible for a 50% increase in Oregon wheat yields that has occurred since 1970 (Figure 3).

The International Winter x Spring Wheat program and OSU-CIMMYT collaborations have had clear and recognizable payoffs to wheat producers in the US through the development and release of Oregon wheat varieties such as Gene, Hoff, Foote, Winsome, and Connie. Several major varieties grown in the US also have important parental contributions from varieties developed through OSU and OSU-CIMMYT collaborations. Madsen, the leading variety in Washington State from 1994 to 2000, has a major parental contribution from the OSU variety Hill 81. The Kansas State University hard winter wheat varieties Jagger and Betty have parental contributions from Stephens. Jagger has been the leading variety in Kansas and Oklahoma for several years now. Other examples include the soft wheat varieties Brundage and Lambert from the University of Idaho, which have parental contributions from Stephens, and the hard white variety Heyne from Kansas State, which has contributions from spring x winter germplasm. Although the IWxSWP program was closed down in 1999, the improved germplasm will continue to contribute to US and world food production for years to come.

Dr. Kronstad's achievements in variety development, germplasm development, genetics, international agriculture, teaching, and graduate training were recognized in prestigious awards from major scientific agencies, government agencies, foundations, and industry, both nationally and internationally. These include Fellow of ASA, CSSA, and AAAS; DeKalb Genetics, Crop Science Distinguished Career Award; Crop Science Award, Alexander von Humboldt Foundation Award; four Distinguished Professor Awards at Oregon State University; Presidential End World Hunger Award; Paul Harris Fellow Award of the International Rotary Foundation; USDA Distinguished

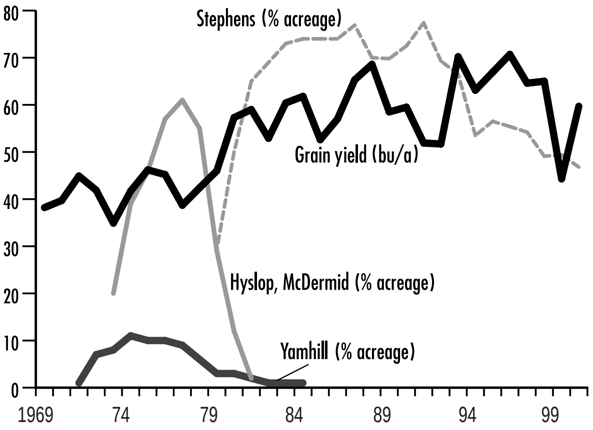


Figure 3. Wheat production in Oregon, 1969-2000. Average grain yield and variety distributions.

Service Award; Distinguished and Meritorious Service Awards of the American Farm Bureau; Washington State University Alumni Achievement Award; recognition from the governments of Turkey, Mexico, and many more. He held the Oregon State University Wheat Research Endowed Chair, which in 1998 was renamed the Kronstad Endowed Chair for Wheat Research.

Dr. Kronstad was a skilled teacher and will be greatly missed as a spokesman for state, regional, national, and international wheat communities. His commitment to education and training impacted people on all levels, from undergraduates and summer workers, to graduate students, wheat project staff, postgraduates, and visiting scientists. Just as notable were Dr. Kronstad's personal commitment, respect, and close friendships with the wheat growers of Oregon who have long been leaders in the US wheat industry. Through Kronstad's efforts and close relationships, the Oregon growers also developed a unique appreciation and understanding of basic, applied, and multidisciplinary research; the value of germplasm enhancement and exchange; the benefits of international scientific cooperation and open scientific exchanges; the value of US contributions to international development; and the worldwide contributions and impact of CIMMYT and the CGIAR network.

The Transition

Dr. Kronstad's retirement in 1999 initiated a period of transition in the OSU wheat research programs. The International Winter x Spring Wheat Enhancement Program was closed after 27 years of funding from USAID. And, after nearly 15 years in wheat research with the USDA-Agricultural Research Service in Lincoln, Nebraska, I joined OSU in the fall of 1998 to succeed Dr. Kronstad as Project Leader of the OSU Wheat Breeding and Genetics program. In joining the OSU Wheat Breeding program, the challenge was not how to replace or succeed Warren Kronstad, which is an inherently impossible task, rather, the challenge was how to build on the existing program strengths and traditions through the use of new technologies, new breeding strategies, novel genetic resources, and through building multidisciplinary and public-private research collaborations. The transition also provides a unique opportunity to reevaluate needs and opportunities in the wheat industry.

Even with the many contributions of Dr. Kronstad and OSU variety development efforts to date, tremendous challenges still confront our growers. Production costs and risks continue to escalate. Management practices are changing and evolving in attempts to improve environmental stewardship, production sustainability, and profitability. Drought and temperature stresses continue to limit grain yields, and we are experiencing increasingly erratic weather patterns. Disease and insect pressures are increasing and evolving in response to changing management and environmental conditions. The world grain market is increasingly sophisticated and competitive, placing increased demands on wheat end-use quality.

The primary goal of the OSU Wheat Breeding and Genetics Program—to provide our growers with new technologies and economic returns from breeding and genetics research in the form of wheat varieties with high-yield, broad adaptation, disease resistance, and superior end-use quality—has not changed. Our first steps toward accomplishing this goal are essentially "back to basics"; that is, to refocus efforts toward domestic breeding, renew long term collaborations, and then to build new partnerships and multidisciplinary research approaches for the future.

Faced with highly variable production conditions and constraints in the Pacific Northwest, Dr. Kronstad developed a broadly adapted, high-yielding germplasm base using a modified shuttle-breeding approach. The Hyslop Agronomy Farm in Corvallis was used for early generation selections under high yield, high rainfall conditions with significant foliar disease pressures. The Rugg-Barnett site outside of Pendleton provides a high yield, dryland, and intermediate rainfall site with minimal foliar disease pressures other than stripe rust. A third site at Sherman County Experiment Station in Moro provides for adaptation under very low rainfall conditions and significant soil disease pressures. These three sites provide very different biotic and abiotic stresses associated with wheat production. A shuttle of early generation materials between Hyslop and Pendleton, with complementary testing in Moro, has proven very effective in establishing broad adaptation in wheat varieties such as Stephens, released for production in the PNW.

The opportunity exists to increase grain yields and build on this broadly-adapted germplasm base by incorporating genes, traits, and selection strategies that exploit components of specific adaptation, that is, to develop genetic combinations that can exploit the unique production conditions or constraints within each of the major agroecological zones of the PNW. In 1999, an additional five test sites were established to more effectively sample these major agroecological zones, while also considering the changing crop management practices used in Oregon. An important priority was to establish breeding trials and facilitate selection under high residue management conditions. Growers are increasingly using high residue or direct seed practices to minimize soil erosion and moisture loss, but these same practices result in increased disease pressures and environmental stresses on the wheat crop.

Breeding for high residue management situations also requires renewed commitment and partnerships to improve genetic resistance to a wide array of diseases. New research efforts have been initiated to address cephalosporium stripe, fusarium dryland footrot, and strawbreaker footrot diseases in collaboration with OSU pathologists Dick Smiley and Chris Mundt. In addition to evaluating response of breeding lines and varieties, inoculated disease trials were initiated to evaluate promising introductions, new genetic stocks, synthetic wheats and their derivatives, and mapping populations for derivation of molecular markers. These trials have already provided exciting new leads for improving genetic resistances to cephalosporium stripe and dryland footrot diseases. The new CIMMYT synthetic wheats and their derivatives, which possess novel genes for disease resistance and stress tolerance, are also playing an important role in our breeding strategies for high residue and direct-seed conditions.

Improving end-use quality and capturing value from quality in the marketplace have long been important goals for the OSU breeding program. The PNW is known for producing and delivering high quality grain; however, that grain is marketed as a generic commodity using a US Grain Classification system that has little relationship to processing value and product functionality. World wheat buyers have changed dramatically in the past decade, with increased privatization and increased demands for improved grain quality. The challenge for the wheat industry now is to define, develop, diversify, and deliver quality, value, and functionality to our customers. This means more than just delivering kernel texture, protein content, and sound grain. Marketing wheat as a specific ingredient for high-value food products means optimizing protein quality, starch quality, and functionality to meet the needs of our most quality conscious customers.

Breeding and selection for product-specific quality will be critical components of any strategy to capture value from enhanced end-use quality. The US breeding programs have long strived to improve end-use quality of wheat, but the generic class marketing system has not rewarded those that produce and market improved quality. There is tremendous genetic diversity in proteins, starches, and mechanical processing attributes that can be exploited to improve product-specific qualities as desired by our premium customers. With product and marketing goals and input from our customers, US breeders can develop varieties with product-specific end-use qualities. The US wheat industry is changing and increasingly receptive to value-added marketing opportunities. Segregation, identity preservation, and partnerships for vertically integrated marketing are becoming priorities to enhance competitiveness and become more responsive to our customer needs.

We are currently exploring an array of strategies to segment and diversify the wheat market of the PNW. One such strategy is to develop “quality subclasses” within the more generic class structure of the US Grain Classification system. Ideally these subclasses would be based on end-use functionality and product applications. The hard white spring wheat Winsome, developed in collaboration between OSU and CIMMYT, is one small but important step in this effort. Winsome has end-use quality attributes appropriate for Asian noodle products and was released to Oregon growers in 2000. Hard white wheat development will continue as an important goal of the

OSU program as we address quality needs and opportunities in the Asian markets. Defining and delivering quality subclasses within the Soft White class will be more challenging. Segregation of soft white wheat on grain protein content is fairly common and the practice is increasing. However, opportunities are also are emerging for identity preserved marketing of very soft texture lines with superior cookie qualities, varieties with improved protein quality for use in flat breads, and varieties with partial waxy starches for noodle markets, not to mention the ongoing need to improve soft white wheat quality just to remain competitive in the international marketplace. Close communication with our customers, with producers, the grain trade, and milling companies will be critical if we are to make significant changes in how the US produces and markets wheat and captures value from enhanced end-use quality.

The Future

Public wheat breeding programs still dominate variety development efforts in the US. However, expectations and the role of public research programs are changing as private investments and advancements in biotechnology continue to grow. The measures of success are now economic impact and contributions to technology transfer. Land-grant universities are looking toward public-private partnerships to access new technologies, to provide funding for new research efforts, provide growers with novel genes and value-added traits, and to participate in commercialization of biotech products. These partnerships also will be important for establishing value-added and identity preserved marketing. Universities are struggling, however, with the associated intellectual property rights issues, technology licensing, and the exclusivity and confidentiality requirements of private industry.

At OSU, we are actively pursuing public-private partnerships as a means of bringing new technologies, such as herbicide resistance, to our growers. Public involvement and research contributions to risk assessment and technology stewardship also are important for gaining consumer acceptance of new biotechnologies. How we choose to accomplish this, however, is critical, as the legal and intellectual property rights issues will impact on cultivar development for decades. In evaluating opportunities and economic benefits of public-private partnerships, serving the interests of our growers remains our first priority. New approaches will be required to effectively manage public-developed intellectual properties and new measures of accountability will be required as we pursue public-private collaborations. However, our fundamental commitment to free germplasm exchange, as the foundation for all wheat improvement efforts, remains unchanged. OSU contributions to international germplasm development and exchange will continue (most evident through our ongoing collaborations with CIMMYT) through our supporting role in distribution of CIMMYT international nurseries and through direct exchanges with our many close friends and colleagues throughout the world.

The OSU Wheat Breeding Program was presented with a unique opportunity and major challenge in fall 2000, when Monsanto proposed the donation of the HybriTech PNW wheat germplasm stocks to OSU. From 1993 to 1999, HybriTech developed an aggressive hybrid wheat breeding program targeted for the Pacific Northwest. In September 1999, Monsanto closed all their US hybrid wheat breeding efforts, including the Boise-based program, but has since donated the HybriTech PNW germplasm to OSU in recognition of the public value of the wheat germplasm base and of OSU's contributions to its development through germplasm exchange. The opportunity presented to us was access to novel genetic stocks and advanced breeding lines for direct use in public variety development efforts for the PNW. The challenge was to manage breeding stocks that would essentially double the size of our current field program. In October 2000, we planted over 4,500 plots and 24,000 headrows from the seed stocks at our Pendleton research site. Included were 676 F_1 crosses, 920 hybrids, 1,331 segregating bulk populations, over 2,000 inbred lines, and nearly 600 populations of headrows. While OSU is the primary recipient and owner of the stocks, our intent is to manage the germplasm as a public resource, such that public research programs and growers throughout the PNW benefit from access and use of materials developed through HybriTech's breeding efforts. HybriTech had very talented breeders working in the PNW and had developed an excellent base of genetic material. Closure of the program was a reflection of the economics of the chemical hybridizing system used for seed production, not of breeding skills or progress. We are grateful to Dr. Sally Metz and the Monsanto Company for their commitment to wheat improvement and for the donation of these unique stocks to OSU.

Our goal, as we take on these many challenges and renew our commitment to the field, to our growers, and to the breeding community, is that the OSU breeding program remains, in itself, a lasting tribute to

Breaking Undesirable Correlations

R.M. DePauw

Traits of wheat may be negatively or positively correlated, and may be deemed desirable or undesirable, regardless of the sign of the correlation. For example, plant height and straw strength tend to be negatively correlated, yet this is a desirable correlation as shorter plants are preferred over excessively tall plants. Coleoptile length and plant height tend to be positively correlated, yet this is an undesirable correlation as, again, shorter plants are generally preferred. Grain yield is positively correlated with time to maturity. This is a desirable correlation in growing seasons with unlimited time or resources for plant growth but negative in high latitude environments where the growing season is often very limited.

Lukow and Preston (1998) reported on the relationship between protein concentration and wheat end-use suitability traits within the Canadian Western Red Spring (CRWS) wheat class. They examined the effects of protein segregates of 11.5-13.5% (on 13.5% moisture basis) on milling, dough rheological properties, and baking performance. The effect of protein segregation was statistically significant for test weight, flour ash, flour color, starch damage, farinograph absorption, farinograph dough development time, farinograph stability, extensiograph area, alveograph area, remix loaf volume, remix mixing time, sponge and dough loaf volume, sponge and dough mixing time, and Canadian short process loaf volume. Segregation for protein concentration was not significantly related to the end-use suitability traits of thousand-kernel weight, flour yield, extensigraph height, and Canadian short process mixing time.

The high protein concentration and protein quality of CRWS wheat are primary reasons for its worldwide demand. The price of wheat, in constant dollars, traded internationally, has been decreasing for the past 30 years (Prabhu and Rajaram 1999). To maintain economic viability, wheat producers have sought to reduce their unit costs by increasing grain yield per unit area; however, grain yield and protein concentration are negatively related, with correlations ranging from -0.2 to -0.8 (Guthrie et al. 1984; Halloran 1981; Loffer and Busch 1982; O'Brien and Ronalds 1984). While processors want high protein and high end-use suitability, and farmers want high yielding cultivars to improve their profitability, it is the wheat breeders who are challenged to resolve this conflict.

DePauw et al. (1985) discussed the association between grain yield, protein concentration, and time to maturity. They hypothesized that these three traits are interrelated and can be thought of as three axes having a common origin. The dimensions along the three axes determine the shape of a tetrahedron. Assuming that no genes for grain yield, days to maturity, or protein concentration are incorporated into a breeding gene pool, fixing one character at a certain level, and then trying to increase the level of the second character, results in a reduction in the level of the third.

Genotypic differences for both nitrogen uptake and remobilization have been reported (Austin et al. 1977; Beninati and Busch 1992; Loffler and Bush 1982; Loffler et al. 1985; McKendry et al. 1995). Selecting genotypes that have improvements in these component traits may lead to increases in grain protein concentration but, because these nitrogen traits are influenced by the environment, they may be difficult to modify (May et al. 1991). Clarke et al. (1990) concluded that nitrogen uptake, harvest indices, translocation, and utilization were all strongly associated with dry matter production and partitioning. They questioned the strategy of selecting for higher grain yield while maintaining protein concentration by selecting for component traits. Rather, they suggested selecting directly for grain yield and grain protein concentration.

Quantitative genetic principles can be used to address the possibility of indirect selection. If one assumes equal selection intensities, an equation provided by Falconer (1952) shows the ratio of correlated (indirect) response to direct response as:

$$Cr_y/R_y = r_g[h_x]/h_y$$

where:

Cr_y = the correlated response for the primary trait (protein concentration);
R_y = the response for the primary trait when selecting directly for it;
r_g = the genetic correlation between the primary trait and the secondary trait (nitrogen-partitioning components);
h_y = the square root of the heritability of the primary trait;
h_x = the square root of the heritability of the secondary trait.

Indirect selection would be expected to be more efficient than direct selection whenever the ratio of correlated response to direct response is greater than one. Indirect selection is more effective than direct selection when there is a large genetic correlation between the two traits and the heritability of the secondary trait is larger than that of the primary trait. The relative cost of measurement of the two traits must also be considered. Given that protein concentration can be easily measured with near infrared (NIR) spectroscopy and is moderately to highly heritable, it seems likely that direct selection for grain protein concentration is the preferred option.

In this paper I will report some of the results from our breeding program that disrupt these undesirable correlations of grain yield, protein concentration, and time to maturity using principles of direct selection rather than indirect selection.

Mechanization for planting, culturing, and harvesting small plots has enabled breeders to evaluate vastly larger populations with the same resources compared to 30 years ago. NIR spectroscopy has been developed to measure wheat protein concentration in a very rapid, low cost, and environmentally friendly manner. Computer hardware and software have enabled breeders to measure and analyze a multitude of variables on very large populations grown at numerous sites. These changes have allowed us to simultaneously select for grain yield, protein concentration, time to maturity, and all of the other productivity and marketability traits required in a successful new cultivar.

To be eligible for the CWRS wheat class, a new cultivar must exhibit improvements in productivity traits, disease resistance, or end-use suitability. It cannot exhibit a reduction in any trait, especially functionality. A reduction of 0.3% in protein concentration would be unacceptable.

We challenged ourselves to disrupt the undesirable correlations by increasing grain yield or protein concentration without a decline in any other attribute of a candidate cultivar. Novel sources of grain protein or yield and protein were crossed with elite, locally adapted CWRS parents (Table 1).

Table 1. Parentage of crosses of high protein parents with locally adapted, elite wheat lines.

Year	Cross	Parents[1]
1989	89-1	ND643/BW621//BW591
	89-2	93349/BW621//BW591
	89-3	ND643/BW123//BW131
	89-4	93349/BW123//BW131
1990	90-1	SD2980/BW621//BW591
	90-2	ND640/BW621//BW591
	90-3	BW591*2/BW621
	90-4	SD2980/ND643//L8509-N5A
	90-5	ND640/ND643//L8509-N5A
	90-6	SD2980/93349//L8509-N5A
	90-7	ND640/93349//L8509-N5A

[1] ND643 = Columbus/*T. dicoccoides*//Len;
93349 = Atlas 66/Nap Hal/2/Skorospelka 35/NE701137/5/Nap Hal/CI13449/4/Sel 14-53/3/Lancer/2/Altas 66/Commanche;
ND640 = Columbus/Butte;
SD2980 = Butte*2/MN7125;
L8509 = BW90*2/BW553.

The F_2 seed was inoculated with common bunt [caused by *Tilletia laevis* Kuhn in Rabenh. and *T. caries* (DC.) Tul. & C. Tul.] and grown as individual plants in a leaf rust (caused by *Puccinia recondita* Roberge ex Desmaz.) and stem rust (caused by *P. graminis* Pers.:Pers. f.sp. *tritici* Eriks. & E. Henn.) epiphytotic nursery. The F_3, F_5, and F_7 generations were grown as head rows in a winter nursery near Brawley, California, to multiply seed for early generation grain yield tests. In the F_4, F_6, and F_8 generations, we screened for quantitative and qualitative traits in multi-row plots grown in replicated trials at two locations. Reaction to leaf and stem rust was assessed and resistant materials were selected. We practiced simultaneous selection for grain yield and grain protein concentration. Grain protein concentration was assessed on a composite of the two replicates from each location using NIR spectral analysis. To determine the effectiveness of simultaneously selecting for grain yield and protein concentration, inbred F_9 lines were grown in trials with four replications at four locations, and designated Western Bread Wheat 'A'- test.

We evaluated the success of these crosses by comparing the inbred lines to Katepwa, the best hard red spring wheat cultivar at the time. Progeny in all crosses varied for both grain yield and protein concentration. The regression of protein concentration on yield was not significant in 15 of the 26 crosses and generations (not shown).

Protein was regressed on grain yield for the selected F_9 lines and the checks. Two lines were constructed with the same slope as the protein-yield regression slope through points one standard deviation (for protein) above or below the mean protein concentration of

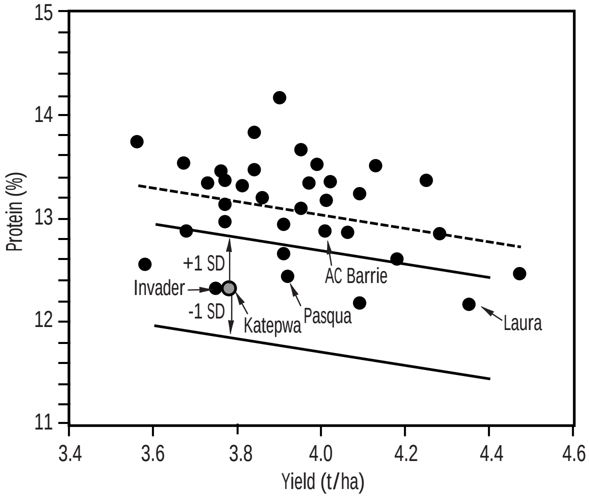


Figure 1. Regression of protein concentration on grain yield of F_9 lines and checks grown in replicated trials at four locations in 1995. The dashed line is the protein-yield regression line, and the solid lines represent 1 standard deviation above and below the mean protein of the check Katepwa, forming a "Katepwa yield-protein band".
Source: DePauw et al. (1998).

Katepwa, forming a "Katepwa yield-protein band" (Figure 1). The criterion used to assess the progress of the improvement of the yield-protein relationship was the number of lines above the hypothetical Katepwa yield-protein band compared to the number below. In two of the Western Bread Wheat 'A'- tests, the Katepwa yield-protein band was below the experiment-wide regression line and, in one case, it included the regression line.

The 1990 crosses produced the greatest number of agronomically desirable lines (Table 2), the majority of which had grain protein concentrations more than one standard deviation greater than Katepwa. Of the 63 F_9 lines developed from all crosses, 44 were above the Katepwa yield-protein band and only one was below.

Table 2. Performance of progeny from 1989 and 1990 crosses with high protein parents (see Table 1) evaluated in the Western Bread Wheat 'A'- tests in 1994 and 1995 following selection for agronomic performance, grain quality, and response to diseases from F_4 to F_8.

Test year	No. lines tested	Lines differing by more than 1 SD[1] from the Katepwa yield-protein band: Less	Greater
1994	15[2]	1	2
1995	14[3]	0	11
	34[4]	0	31

[1] Standard deviation.
[2] Progeny from crosses 89-1, 89-2, 89-3, and 89-4.
[3] Progeny from crosses 90-1, 90-2, 90-3.
[4] Progeny from crosses 90-4 to 90-7.

These results demonstrate that breeders can exploit genetic opportunities to improve both grain yield and protein concentration.

The new wheat cultivars AC Barrie (McCaig et al. 1996), AC Cadillac (DePauw et al. 1998), and AC Elsa (Clarke et al. 1997) all have higher grain yields and higher protein concentrations (Table 3; Figure 2). These cultivars are derived from various combinations of Neepawa, Columbus, Laura, and BW90 (DePauw et al. 1986). Laura has the high protein cultivar Atlas 66 in its parentage, and BW90 has the high protein cultivar World Seeds 1809 in its parentage, as well as Sonora 64, Tezanos Pinto Precoz, and Tobari 66.

Economic considerations may be used to determine the incremental value of grain yield and protein. The incremental value of the grain and protein concentration have been calculated using the average values for CWRS wheat in-store at Vancouver from 1991/92 to 1999/2000. No. 1 CWRS wheat with no protein premium averaged CDN$ 183.93/t. During this period, the protein premium averaged CDN$ 18.00/t for the range of No. 1 CWRS, i.e., from no protein premium to 13.4% protein. The protein premium for each 0.10% increment of protein above 13.4% averaged CDN$ 1.64/t.

Table 3. Incremental value (CDN$/ha) for grain and protein of some wheat cultivars differing in grain yield and protein concentration.

Cultivar	Yield (t/ha)	Incremental value ($/ha)	Protein (%)	Incremental protein value ($/ha)	Total incremental value ($/ha)	Total incremental value adjusted for handling and freight deductions[1]
Katepwa	3.12	0	13.4	0	0	0
AC Barrie	3.33	38	13.9	26	65	54
AC Cadillac	3.38	48	13.9	27	75	62
AC Elsa	3.45	61	13.8	23	84	68
McKenzie	3.43	57	13.4	6	63	48
AC Splendor	3.07	(-9)	14.3	40	31	34

[1] Handling, elevating, and freight charges for wheat delivered from Saskatchewan averaged CDN$ 49.24/t.

Lower yielding cultivars that have outstanding protein concentration, such as AC Splendor, can be more profitable than higher yielding, lower protein cultivars, such as Katepwa. However, it is most advantageous to use cultivars that have both higher grain yield and higher protein concentration; for example, five years after being released, AC Barrie was grown on over 3 million hectares in Canada (Fedak 1999).

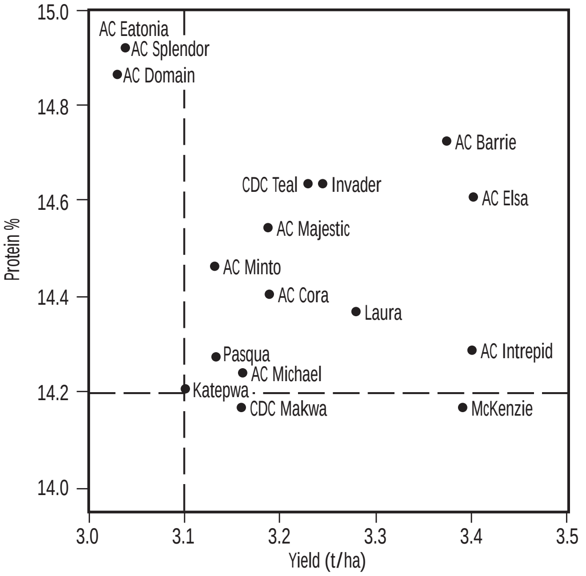


Figure 2. The relationship between protein and grain yield in Canada Western Red Spring cultivars grown at 22-27 dryland sites per year in the Saskatchewan Advisory Council Trials, 1986-99. Protein concentration was measured from 1994 to 1999.
Adapted from DePauw et al. (1998).

Wang et al. (1999; 2000) have investigated grain yield, yield components, dry matter accumulation and partitioning, phasic development, water use characteristics, nitrogen uptake, and remobilization patterns of new high-yielding, high-protein cultivars relative to some older cultivars. They grew these cultivars in replicated trials for three years. Significant differences among cultivars were reported for biomass, harvest index, and yield components (kernel number, spikes per plant, kernels per spike, kernel weight, and yield per spike). The new cultivars had heavier spikes but did not achieve this by expressing the components in a similar manner. Some of the new cultivars had significantly improved water use efficiency, nitrogen uptake, and nitrogen remobilization. In general, the new cultivars had lower levels of nitrogen in the leaves and stems compared to the older cultivars.

Direct selection for increased grain yield and protein concentration resulted in the identification of genotypes with one or both of these traits, albeit rarely. Time to maturity was changed in some types but not in others. Grain yield, protein concentration, and time to maturity were manipulated individually and in combination. These traits were sufficiently independent of other productivity traits, end-use suitability factors, and disease resistance to be recombined to make ‘field ready’ cultivars.

References

Austin, R.B., M.A. Ford, J.A. Edrich, and R.D. Blackwell. 1977. The nitrogen economy of winter wheat. *Journal of Agricultural Science Cambridge* 88:159-167.

Beninati, N.F., and R.H. Busch. 1992. Grain protein inheritance and nitrogen uptake and redistribution in a spring wheat cross. *Crop Science* 32:1471-1475.

Clarke, J.M., C.A. Campbell, H.W. Cutforth, R.M. DePauw, and G.E. Winkleman. 1990. Nitrogen and phosphorus uptake, translocation, and utilization efficiency of wheat in relation to environment and cultivar yield and protein levels. *Canadian Journal of Plant Science* 70(4):965-977.

Clarke, J.M., R.M. DePauw, T.N. McCaig, M.R. Fernandez, R.E. Knox, and J.G. McLeod. 1997. AC Elsa hard red spring wheat. *Canadian Journal of Plant Science* 77:661-663.

DePauw, R.M., J.B. Thomas, R.E. Knox, J.M. Clarke, M.R. Fernandez, T.N. McCaig, and J.G. McLeod. 1998. AC Cadillac hard red spring wheat. *Canadian Journal of Plant Science* 78:459-462.

DePauw, R.M., J.B. Thomas, and T.F. Townley-Smith. 1986. Spring wheat production in the Brown and Dark Brown soil zones of Western Canada. In: A.E. Slinkard and D.B. Fowler (eds.), *Wheat Production in Canada*, pp. 27-45. Saskatoon, SK: Saskatchewan University Extension Press.

Fedak, B.A. 1999. Canadian Wheat Board Variety Survey 1999-2000. www.cwb.ca/other/varsurv/results99.htm.

Guthrie, D.A., E.L. Smith, and R.W. McNew. 1984. Selection for high and low grain protein in six winter wheat crosses. *Crop Science* 24:1097-1100.

Halloran, G.M. 1981. Grain yield and protein relationships in a wheat cross. *Crop Science* 21:699-701.

Loffler, C.M., and R.H. Busch. 1982. Selection for grain protein, grain yield, and nitrogen partitioning efficiency in hard red spring wheat. *Crop Science* 22:591-595.

Loffler, C.M., T.L. Rauch, and R.H. Busch. 1985. Grain and plant protein relationships in hard red spring wheat. *Crop Science* 25:521-524.

Lukow, O.M., and K.R. Preston. 1998. Effects of protein content on wheat quality. In: D.B. Fowler, W.E. Geddes, A.M. Johnston, and K.R. Preston (eds.), *Wheat Protein Production and Marketing,* pp. 48-52. Saskatoon, SK: Saskatchewan University Extension Press.

May, L., D.A. Van Sanford, C.T. MacKown, and P.L. Cornelius. 1991. Genetic variation for nitrogen use in soft red x hard red winter wheat populations. *Crop Science* 31:626-630.

McCaig, T.N., R.M. DePauw, J.G. McLeod, R.E. Knox, J.M. Clarke, and M.R. Fernandez. 1996. AC Barrie hard red spring wheat. *Canadian Journal of Plant Science* 76:337-339.

McKendry, A.L., P.B.E. McVetty, and L.E Evans. 1995. Selection criteria for combining high grain yield and high grain protein concentration in bread wheat. *Crop Science* 35:1597-1602.

O’Brien, L., and J.A. Ronalds. 1984. Yield and quality interrelationships amongst random F_3 lines and their implications for wheat breeding. *Australian Journal of Agricultural Research* 35:443-451.

Pingali, P.L., and S. Rajaram. 1999. Global wheat research in a changing world. In: P.L. Pingali (ed.), *CIMMYT 1998-99 World Wheat Facts and Trends. Global Wheat Research in a Changing World: Challenges and Achievements,* pp. 1-18. Mexico, D.F.: CIMMYT.

Wang, H., T.N. McCaig, R.M. DePauw, and J.M. Clarke. 1999. High-yield, high-protein wheat cultivar study: growth characteristics and yield. In: Proceedings of the Soils and Crops 1999 Workshop, pp. 395-397.

Wang, H., T.N. McCaig, R.M. De Pauw, and J.M. Clarke, 2000. Do high-yield and high-protein wheat cultivars use more water? In: Proceedings of the Soils and Crops 2000 Workshop, pp. 534-538.

Drivers for Change in Australian Wheat Breeding

P.S. Brennan

Introduction

Wheat breeding in Australia is relatively young. Until 1886, the Australian wheat industry relied largely on British cultivars. In 1886 at Lambridge, just outside where Canberra is now located, William Farrer commenced breeding wheat in a private capacity using crossing to combine attributes. Farrer developed effective if stormy partnerships with leading scientists in associated disciplines and augmented his breeding through original research.

Cooperation between private sector breeders and scientists in associated disciplines has since been the model for much of the Australian wheat breeding industry, except that there has been very rapid movement away from private to public funding. Currently the vast majority of Australian wheat breeding is sponsored by either a university or the State Department. Since the advent of grower investment in agricultural research, there has been an increasing reliance on the Grains Research and Development Corporation (GRDC) (and its predecessors) for financial support. It is estimated that Australia spends AU$ 23 million per year on wheat breeding, with AU$ 10.5 million contributed by the GRDC. Approximately 60% of GRDC funding comes from grower statutory contributions according to the Primary Industry and Energy Research and Development Act of 1989.

Current Structure of the Australian Wheat Breeding Industry

Conventional breeding of high quality spring wheat varieties is undertaken at nine centers located across Australia (Table 1). Well-resourced grain quality laboratories support all centers, with the exception of Narrabri, which is equipped to assess early-generation quality but outsources quality evaluation of subsequent generations. Plant pathology support varies from very good in Adelaide and Toowoomba to almost non-existent in other centers.

Table 1. Structure of the Australian wheat breeding industry.

Location	Agency[1]	Region[2]	Geographic responsibility[3]	Area (000 ha)	No. of breeders
Spring wheat					
Perth	AgWest	Western	WA	6,840	2.25
Adelaide	Univ of Adelaide	Southern	SA, Vic, S. NSW	6,753	3.00
Horsham	DNRE	Southern	SA, Vic, S. NSW	6,753	1.00
Wagga	NSW Ag	Southern	SA, Vic, S. NSW	6,753	2.00
Narrabri	SU	Northern	N. NSW, Qld	3,670	2.00
Toowoomba	DPI	Northern	N. NSW, Qld	3,670	2.00
Winter wheat					
Canberra	CSIRO	N/A	Australia		1.00
Hybrid wheat					
Narrabri	SU/Private	Northern	NSW, Qld	5,612	1.00
Durum wheat					
Tamworth	NSW Ag	Northern	Australia	?	1.00

[1] AgWest = Department of Agriculture, Western Australia; DNRE = Department of Natural Resources and Environment, Victoria; NSW Ag = Department of Agriculture, NSW; SU = University of Sydney; DPI = Department of Primary Industries, Queensland; CSIRO = Commonwealth Scientific and Industrial Research Organisation.

[2] Western = Western Australia; Southern = South Australia, Victoria, and NSW south of Dubbo; Northern = NSW north of Dubbo and Queensland.

[3] WA = Western Australia; Vic = Victoria; NSW = New South Wales; Qld = Queensland.

Hybrid wheat breeding has been conducted in Australia since the early 1960s but has not had great impact. Indeed, two of the successful products from the hybrid program, Vulcan and H46, are inbreds.

Production of long-season feed wheats has been proposed as a viable alternative to wool in higher rainfall areas of the Southern Region (South Australia, Victoria, and NSW south of Dubbo). Long-season wheat varieties are also seen as an option for grazing sheep at the crop's vegetative stage, followed by grain production. Breeding of long-season feed wheat has been undertaken by the CSIRO (Commonwealth Scientific and Industrial Research Organisation) in Canberra.

Durum wheat breeding commenced as a component of the bread wheat breeding program located at Tamworth. In 1995, the Tamworth group (NSW Agriculture) relinquished bread wheat breeding to devote its full resources to durum breeding. This has been very successful as Australian durum is currently competing strongly on the international market.

Achievements of the Australian Wheat Breeding Industry

Australia has invested heavily in wheat breeding research. Throughout its long history, this internationally recognized research effort has focused on pest and disease resistance (particularly the rusts and, more recently, nematodes), product quality (with emphasis on the role of glutenin proteins and noodle quality), and genotype x environment interactions (and how they affect progress on genetic yield gains).

This paper will attempt to assess the value of this research and the returns on Australia's investment in wheat breeding by evaluating the economic impact of the varieties produced as a result of this investment.

To date, there has been no overall economic assessment of the impact of wheat breeding in Australia. Consequently, this paper will rely on hard information and draw inferences that would be better served if considered by a professional economist. The benefits derived from Australian wheat breeding since the commencement of grower-levy-funded research in the mid 1960s are:

- Yield improvement: Direct or indirect comparisons of major varieties grown in the mid 1960s with current varieties.
- Risk reduction: Quantitative assessment of the economic benefits of breeding for resistance to biotic and abiotic stresses.
- Market access: Economic assessment of major advances in the quality of Australian wheat varieties that have enhanced their competitive advantage in some markets or facilitated substantial penetration of new markets.

Yield improvement

For the Northern Region (NSW north of Dubbo, and Queensland), no direct comparisons are available between Mendos, the main variety grown in 1965, and Baxter, released in 1998 and currently exhibiting considerable potential. However, indirect comparisons give Baxter a 33% yield advantage, which roughly correlates to a genetic yield gain of 1% per annum. This is equivalent to a current annual increase of income in excess of AU$ 150 million for growers in the Northern Region.

There are two reliable studies on the impact of breeding on yields in the Southern Region. Helyar (1999) estimated that the yield increase in southern NSW between 1977 and 1997 was 0.6% per year. If this improvement had been realized over the entire period of the grower-levy investment in grains research (some 35 years), it would be equivalent to an increase of over AU$ 100 million per year in income for wheat growers in southern NSW.

Black (1998) estimated a 1% increase in yield per year over the 30 years to 1996 from breeding research conducted at the University of Adelaide. This is equivalent to an annual increase in income in excess of AU$ 110 million per year for South Australian wheat growers.

Indirect yield comparisons of wheat varieties grown in Victoria suggest an improvement of 0.75% per year. The long-term improvement in Western Australia from 1860 to 1984 is also of this magnitude (Perry and D'Antuono 1989).

The genetic yield gains in Australia have been measured against the gains achieved, reported, and recorded in Cambridge, United Kingdom (Table 2; Godden and Brennan 1988) and were found to compare favorably. It should be noted that genotype x environment interactions are so small for wheat yield in the UK that breeders pay little attention to them. In fact, most yield assessment is confined to one site each year (Angus, personal communication). Also, yield improvement in the UK has been greater in feed wheat, where no quality characteristics are required.

Table 2. Yield increases due to new varieties in Cambridge, United Kingdom.

	Yield increase (%)	
Period	**Feed wheat**	**Bread wheat**
1947-82	1.33	0.56
1962-82	1.95	0.92
1972-82	1.60	0.82

Biotic and abiotic stress resistance/ tolerance (lower risk)

Most crops do not reach their genetic yield potential due to the effects of pests, diseases, poor soils, and unfavorable environmental conditions. Wheat is no exception to this, as recently illustrated by the AU$ 190 million production losses due to yellow spot disease in the Northern Region in 1998.

An economic assessment of production losses due to pests and diseases has been made for Australia (Brennan and Murray 1998). The potential and actual losses caused by major diseases where a genetic solution is possible have been extracted from this report and are shown in Table 3. Brennan and Murray (1998) estimated potential production losses of nearly AU$ 1.3 billion due to pests and diseases in any one year. Actual losses are AU$ 298 million, suggesting that breeding for pest and disease resistance has an annual value to Australian wheat farmers of just under AU$ 1 billion; that is, a quarter to one-third of the annual gross value of wheat production in Australia. Losses due to one disease would, in most situations, preclude losses due to other diseases. Consequently, the above information should be treated as a guide to the magnitude of progress in stress tolerance / resistance breeding only.

Of particular note is the reduction in actual production losses as a result of breeding for the "older" diseases (the rusts and flag smut). There is also considerable potential for improvement in breeding for resistance to pests and diseases such as yellow spot and crown rot (important more recently due to farmers' adoption of stubble retention), or to the recently recognized root lesion nematodes.

Breeding for tolerance to soil disorders such as toxic levels of boron and low soil pH has been a major focus of the South Australian and southern New South Wales breeding efforts in recent years. There has been substantial success in both states, though no economic assessment of the impact of the research has been done, to the author's knowledge. The adoption of tolerant varieties by growers in affected areas has been very high (anecdotal evidence), which indicates the considerable economic value of the varieties.

Estimated total losses due to disease and pests are equivalent to the genetic gains achieved through breeding over the last 35 years.

Improvement in processing quality

The Australian Wheat Board (AWB) allocates a grade to a variety at the time of its release which specifies the maximum return paid to growers for the particular variety and reflects only its inherent quality-related properties. A specific classification is conditional on a variety meeting the minimum standards for a number of quality attributes identified by the AWB as being significant in the manufacture of a range of products.

The minimum level for quality attributes and the actual attributes required for a particular classification have changed over time. This is due to changes in market destination, competition, and an increased awareness of the quality required for manufacturing products classified as excellent, which has often been

Table 3. Estimated cost (AU$ million / year / GRDC[1] region) of actual and potential damage caused by the major pests and diseases of wheat in Australia.

	Northern[2]		Southern[3]		Western[4]		Australia	
Stress	Actual	Potential	Actual	Potential	Actual	Potential	Actual	Potential
Stem rust	0.2	48.8	0.02	28.4	1.2	23.5	1.5	100.7
Leaf rust	0.9	39.6	2.6	35.7	6.0	23.9	9.5	99.2
Stripe rust	0.6	31.3	10.5	149.5	0.0	0.0	11.1	180.8
Flag smut	0.0	6.9	0.1	28.4	0.1	10.4	0.3	45.6
Yellow spot	2.7	10.7	3.2	20.6	43.2	107.3	49.1	138.6
Septoria tritici	0.0	1.1	13.2	98.7	15.1	52.3	28.3	152.1
S. nodorum	0.1	0.4	0.5	4.4	56.9	142.1	57.5	146.9
Crown rot	21.3	71.7	34.7	85.6	34.7	3.0	56.3	160.4
Cereal cyst nematode	0.0	0.1	36.0	86.0	0.7	15.6	36.7	101.6
Root lesion nematode	33.3	69.5	2.4	11.1	0.0	0.0	35.7	80.5
Root lesion nematode	1.4	5.5	6.8	35.1	3.7	3.7	11.9	44.3
Blackpoint	4.5	6.0	1.5	8.5	3.1	15.9	0.1	30.4
Total	65.0	292.0	112.0	592.0	165.0	398.0	298.0	1,281.0

[1] Grains Research and Development Corporation.

[2] NSW north of Dubbo and Queensland.

[3] South Australia, Victoria, and NSW south of Dubbo.

[4] Western Australia.

Source: Brennan and Murray (1998).

the result of GRDC funded research.

Changes in quality requirements necessitate substantial and constant communication between marketers and the breeding program. This interaction has been responsible for considerable and well-targeted improvement in the processing quality of Australian wheat. The economic impact of this improvement has been estimated at 0.5% per annum (CIE 1999).

Thanks to research/marketer/breeder interactions, Australian wheat is the wheat of choice in three large international markets, two of which are high paying: the udon noodle market in Japan and the yellow alkaline noodle market in Japan and Southeast Asia. In both markets Australian wheat is much preferred to US and Canadian wheat, and accounts for a large quantity of wheat produced in the Western and Northern GRDC regions. Wheat segregated for the udon noodle market in Japan realizes a premium of AU$ 20-35/t. The third market is the Middle East flat bread market, where Australian wheat has a quality advantage over that from other countries.

Future Directions

The operating environment for all plant improvement changed dramatically in the last decade of the twentieth century. Many factors, both national and international, have driven these changes.

Private sector investment in gene technology

The unprecedented investment in gene technology by the private sector is the overriding driver of change in plant breeding. This is still true, though less so, if you accept that the world is best served through the exclusion of transgenically-derived crops from our food chain. Molecular marker assisted selection, though still in its infancy, has the potential to deliver considerable efficiencies to plant breeding. However, much of the enabling technology is currently covered by patent—a trend that will increase greatly through private sector investment in genomics and bioinformatics.

If you accept that transgenically-derived crop varieties will contribute positively to society through improved productivity, disease resistance, processing quality, and human nutrition, while decreasing the enormous environmental impact that is the current hallmark of modern agriculture, then the current private sector investment in gene technology is even more significant. The Australian wheat breeding industry will be compelled to operate efficiently and effectively in a commercial environment to gain access to the biotechnology tools required to underpin the international competitiveness of the Australian wheat industry. However, I do not believe that the public sector has the skill or the commitment to do so.

Reduction of public agency investment in private good research

The lack of commitment to private good investment by the public sector is another current driver of change, both nationally and internationally. Public sector investment in the Australian wheat breeding industry is estimated at AU$ 23 million. My strong belief is that many public agencies would prefer to invest much less than they currently do; indeed, this has occurred in a number of agencies in the last decade. This reduced commitment is eroding the efficiency of Australian wheat breeding and, consequently, the Australian wheat industry.

Economic instruments are being developed in Australia to generate replacement investment through the advent of a robust plant breeders rights system and the qualified acceptance of an endpoint royalty system by key grower organizations.

Career drivers

The attitudinal change in Western society from altruism to materialism is also a powerful driver of change in plant improvement. Students entering tertiary training are aware of the relatively limited remuneration prospects from a scientific career in the public sector. Many Australian universities have reported a decrease in average tertiary admission scores required for science, and some have lowered admission levels in agricultural science. Public sector awards do not appear to offer any prospect of competitive remuneration to attract elite professionals into public sector plant improvement.

Improved varietal outcomes

There is a compelling perception within the Australian wheat industry that the current level of investment is sufficient to generate more and better varieties as required. This perception is supported by the recent large reduction in wheat growers’ income due to biotic and abiotic (sprouting and frost) stresses for which there are current genetic solutions. These include yellow spot in northeastern Australia, which cost AU$

300 million in 1998, leaf rust in Western Australia in 1999, and frost and sprouting in southern and Western Australia in 1998. In Australia, there are no "low risk" varieties, that is, those that have resistance and/or tolerance to all of the major stresses that could be anticipated in their target regions. There is no doubt in my mind that there is sufficient investment in the Australian wheat breeding industry to provide every grower with a high yielding, low risk variety whose quality is internationally competitive for all realistic planting opportunities. For this to be realized, however, a substantial and painful reorganization of the current investment is needed.

Conclusions

My contention is that the current arrangements within the Australian wheat breeding industry make it incapable of dealing with the ownership of genetic tools, the downsizing of investment, attracting elite professionals, or delivering varieties that would utilize all relevant, currently available genetic tools to maximize grower returns. I cannot envisage any accommodation of these drivers of change in the Australian wheat breeding industry without private sector involvement. The challenge for Australia will be to capture the value in the current system for exploitation in the new operating environment.

References

Black, I.D. 1998. A review of the impact of public sector applied research and development for the South Australian wheat industry. SARDI Research Report Series No. 21.

Brennan, J.P., and G.M. Murray. 1998. *Economic Importance of Wheat Diseases in Australia*. Wagga Wagga, NSW: NSW Agriculture.

CIE (Centre for International Economics). 1999. Evaluation of Wheat Quality Programs. Confidential Report to the Grains Research and Development Corporation.

Godden, D., and J.P. Brennan. 1988. Contribution of new varieties to yield increases. In: K.S. McWhirter, R.W. Downes, and B.J. Read (eds.), Proceedings of the Ninth Australian Plant Breeding Conference, pp. 43-44.

Godden, D., and J.P. Brennan. 1994. Technological change embodied in southern NSW and British wheat varieties. *Review of Marketing and Agricultural Economics* 62(2):247-260.

Helyar, K.R. 1999. Developing agricultural systems that are sustainable: Experience in New South Wales with non-irrigated crop-pasture rotation systems. In: International Workshop on Land Use and Sustainable Development in the Loess Plateau, Northwest China.

Perry, M.W., and M.F. D'Antuono. 1989. Yield improvements and some associated characteristics of some Australian spring wheat cultivars introduced between 1860 and 1982. *Australian Journal of Agricultural Research* 40:457-72.

Germplasm Derived from Spring x Winter Crosses: Adaptation and Performance in Central/West Asia and North Africa

H.-J. Braun, M. Mergoum, A. Bagci, H. Ekiz, M. Keser, K. Yalvac, and H. Ketata

History of Spring x Winter Crosses

The International Maize and Wheat Improvement Center (CIMMYT) has been involved in winter wheat breeding since the 1960s, when the spring x winter crossing program was initiated in Chile by Dr. Joseph Rupert and later continued at Davis, California, USA. This program was subsequently transferred to Oregon State University (OSU) under the overall leadership of Professor Warren E. Kronstad.

CIMMYT has had a dynamic spring x winter crossing program and has shared its genetic material with OSU since 1972. While CIMMYT has focused mainly on spring wheat selections, OSU has top-crossed F_1 lines with winter wheats.

In 1971, CIMMYT became directly involved with Turkey's winter wheat improvement program through its association with the Rockefeller Foundation/Government of Turkey wheat research program. From the beginning, the Turkey/CIMMYT/ICARDA[1] International Winter Wheat Improvement Program (IWWIP) was based heavily on spring x winter crosses and, today, more than 50% of lines distributed in the International Nurseries derive from these crosses.

Wheat Production in Central/West Asia and North Africa

The 10 countries with the highest per capita wheat consumption in the world are all located in the Central/West Asia and North Africa (CWANA)[2] Region. Wheat is the staple food in these countries; more than 90% of wheat grown is directly consumed, providing more than 50% of the daily calorie uptake for many families. Due to its dietary importance, most countries in CWANA strive to produce as much wheat as possible, making it the dominant crop in their production systems. No other region in the world devotes such a high proportion (up to 75% in Morocco) of its arable land to cereal production.

The total wheat area in CWANA is 34.6 million hectares.[3] Of this, 16.7 million ha are sown to spring wheat, 17.9 million ha are sown to winter and facultative wheat (WFW), 22.4 million ha are rainfed, and 12.2 million ha are irrigated (Table 1). More than 80% of the spring wheat area is planted to CIMMYT-derived germplasm, but the percentage of the WFW area sown to CIMMYT materials is much lower. This is partly because WFW areas in CWANA are often poorly developed and, as a result, the adoption of new varieties is slow. Also, WFW breeding started much later than spring wheat breeding, and progress is slower because only one cycle is grown per year compared to two cycles of spring wheat using the shuttle breeding method practiced at CIMMYT-Mexico.

The exchange of WFW germplasm with the Central Asian Republics (CAR) only started to a significant degree in 1994, and its impact is limited after such a short period. Most commercially grown varieties in CAR originated from Russia or were developed locally. However, lines from the IWWIP are competitive (due, in particular, to the combination of high yield potential and yellow rust resistance) and are included in registration trials.

---

[1] International Centre for Agricultural Research in the Dry Areas.

[2] CWANA includes countries in North Africa, Ethiopia, Sudan, the Middle East, West Asia, NWFP of Pakistan, and the eight Central Asian Republics.

[3] This figure excludes 11.5 million ha of spring wheat in Northern Kazakstan (ME6).

Adaptation Requirements for Central/West Asia and North Africa Region

In WANA, 79% of the WFW area is rainfed compared to 36% in CAR (Table 2). If the rainfed winter wheat area of Kazakstan is excluded, nearly all (85%) of the remaining wheat area in CAR is irrigated. The agroclimatic variation within CWANA is extreme. Wheat is produced in 8 of 12 mega-environments (MEs) defined by CIMMYT (Table 1). The amount and distribution of rainfall, the temperature regime, daylength, and the presence of biotic and abiotic stresses all influence the adaptation of wheat to a given region.

Wheat is grown across highly diverse environments within CWANA, and the range of climatic extremes found within a few hundred kilometers is greater than in any other wheat-based system. This environmental diversity is illustrated by the temperature extremes experienced in Turkey's wheat growing areas. Within

Table 1. Wheat area (000 ha) in the Central Asian Republics (CAR) and West Asia and North Africa (WANA) according to mega-environment (ME).

Country	ME1	ME2	ME4A	ME6[1]	Total SW	ME7	ME8	ME9	Total FW	ME10	ME12	Total WW	Total FWW	Total wheat
CAR														
Armenia	30		30		60	120			120			0	120	180
Azerbaidjan	180		120		300	150		75	225		75	75	300	600
Georgia	10		20		30		130	40	170			0	170	200
Kazakhstan				11500			300		300	200	1,000	1,200	1,500	1,500
Kyrgyzstan	30		20		50	130	120		250		50	50	300	350
Tadjikistan	60		40		100	150		50	200			0	200	300
Turkmenistan	10				10	590			590			0	590	600
Uzbekistan					0	1,000		310	1,310			0	1,310	1,310
Total CAR	320		230	11500	550	2,140	550	475	3,165	200	1,125	1,325	4,490	5,040
WANA														
Algeria			1,350		1,350			245	245				245	1,595
Egypt	1,039				1,039									1,039
Libya	30				30									30
Morocco	230	50	2,100		2,380			200	200				200	2,580
Tunisia		227	600		827									827
Afghanistan	400		1,025		1,425			300	300		300	300	600	2,025
Pakistan (NWFP)						100		600	700	100	200	300	1,000	1,000
Iran	1,000	500	500		2,000	500		1,900	2,400	700	1,300	2,000	4,400	6,400
Iraq	100		1,380		1,480									1,480
S. Arabia	326				326									326
Syria	575	100	900		1,575			100	100				100	1675
Turkey	200	1,200	1,100		2,500	100	800	1,500	2,400	500	4,000	4,500	6,900	9,400
Yemen	30		70		100									100
Jordan			50		50									50
Lebanon	5		25		30									30
Ethopia	50	50	850		950									950
Total WANA	3,985	2,127	9,950		16,062	700	800	4,845	6,345	1,300	5,800	7,100	1,3445	2,9507
Total CWANA	4,305	2,127	10,180	11,500	16,612	2,840	1,350	5,320	9,510	1,500	6,925	8,425	1,7935	3,4547

[1] Not included in totals.

Table 2. Facultative and winter wheat area (000 ha) in West Asia and North Africa (WANA) and the Central Asian Republics (CAR) according to growth type and water regime.[1]

	FWW			FW			WW		
	Total	Irrigated	Rainfed	Total	Irrigated	Rainfed	Total	Irrigated	Rainfed
WANA	13,445	2,800	10,645	6,345	1,500	4,845	7,100	1,300	5,800
CAR	4,490	2,890	1,600	3,165	2,690	475	1,325	200	1,125
Total	17,935	5,690	12,245	9,510	4,190	5,320	8,425	1,500	6,925

[1] Excluding 11.5 million ha spring wheat in N. Kazakstan.

a distance of only 350 km, temperatures range from -42°C in Kars in the northeast to +46°C in Diyarbakir in the southeast. Similarly, annual rainfall in northeastern Turkey decreases from 1400 to 280 mm over a distance of 250 km.

Winterhardiness

The actual level of winterhardiness required in most winter wheat growing areas around the world does not exceed that of Bezostaya 1. Based on a 1996 survey, winterkill damages wheat crops in farmers' fields in more than one year in every ten mainly in North America, Ukraine, and Russia, whereas in large areas of CWANA and most of Europe, winterkill does not often cause damage (Braun et al. 1998). Within WANA, when the proper sowing date is adhered to, winterkill damage is confined mainly to rainfed areas in eastern Turkey and northwestern Iran. Winterkill is not a major problem in most wheat producing areas in CAR. The coldest winters occur in southern Kazakstan, and this is reflected in the high level of winterhardiness in lines developed there. Among 60 entries in the First Winter Wheat East European Yield Trial (WWEERYT, see also below), cultivar Zhetisu from Almaty had the best scores for winter survival using data from eight locations.

The average coldhardiness of selections derived from spring x winter crosses is generally lower than that of selections derived from winter x winter crosses. However, coldhardiness of the best spring x winter derived cultivars is equal to that of cultivars derived from winter x winter crosses (Braun 1997). Growth habit clearly separates winter-hardy and winter-tender types. The correlation (r=0.71**) between growth habit and winterkill (using data from the 5th-7th Facultative and Winter Wheat Observation Nursery (FAWWON) suggests that growth habit can be used as an alternative trait in selecting for cold tolerance in years with mild winters.

Adaptation of Spring x Winter Crosses to Central/West Asia and North Africa

In 1990, the review report of the IWWIP stated "…that the WANA region requires primarily facultative germplasm…" and "…that Spring x Winter crosses have to be the approach to find such lines." The systematic exploitation of spring x winter crosses has been a major objective of the activities carried out by CIMMYT-Mexico, OSU, the Turkey/CIMMYT/ICARDA IWWIP, and by more than 150 national programs. Within the IWWIP, a three-way approach has been used to select the best derivatives from spring x winter crosses:

1. Topcrosses of spring x winter F_1 from Mexico to winter wheat and selection conducted in Turkey.
2. Selection in Turkey of segregating populations derived from the CIMMYT-OSU spring x winter crossing program. Segregating populations (mainly F_1 and F_2) obtained from CIMMYT-Mexico or from OSU (F_3 and F_4).
3. Reselection of advanced lines from CIMMYT-Mexico and OSU germplasm.

This approach combines several advantages. Advanced facultative lines selected in Mexico are often too tender to survive severe winters, and advanced lines selected at Oregon (at 45° latitude) are sensitive to photoperiod and, though very high yielding, often have an overly long grainfilling period. Braun et al. (1995) showed that Turkish winter wheat cultivars reach anthesis later than cultivars from China and the Great Plains, USA, but have a shorter grainfilling period. Furthermore, Turkish and Mexican winter wheats have the highest grainfilling rates per day. Crossing these diverse gene pools and shuttling the material from Mexico to Turkey via Oregon has proved very successful. The highest yielding entries in IWWIP nurseries and most of the high yielding lines released from IWWIP, or those included in registration trials, are derived from spring x winter crosses (Table 3).

In summary, cold tolerant germplasm could be grown in most winter wheat areas in the WANA Region. This is strongly supported by the fact that indigenous Turkish and Iranian germplasm is characterized by a combination of relatively good winterhardiness in a facultative wheat background with a low vernalization requirement. Gerek 79, for example, which is typical of this type of germplasm, headed and matured when sown in Thailand (C. Mann, personal communication).

Adaptation of Lines Derived from Spring x Winter Crosses to Central and Eastern Europe and the Commonwealth of Independent States

The wide adaptation of winter wheat derived from spring x winter crosses is also evident in the results of the first WWEERYT conducted in 1999. This nursery comprised 60 entries and 4 checks from IWWIP and wheat programs in Central and Eastern Europe (CEE), CWANA, and the Great Plains of the USA, and was grown at 22 locations where these programs operate. Agri//Bjy/Vee had the second highest mean yield across locations and was equal to or better than the checks at 10 locations (Figure 1). However, like most other cultivars in the nursery, Agri//Bjy/Vee lacked adaptation to northern Ukraine, which has severe winters and requires a higher level of winterhardiness than most other winter wheat growing areas. Interestingly, the most widely-adapted entry was ERYT26221 from Mironovsk in Ukraine, which yielded equal to or better than the checks at 13 locations. This entry was derived from a mutation program; the parents, TXGH2895 and Trakia, were lines from Texas and Bulgaria. This cross clearly demonstrates the continuous benefits of germplasm exchange.

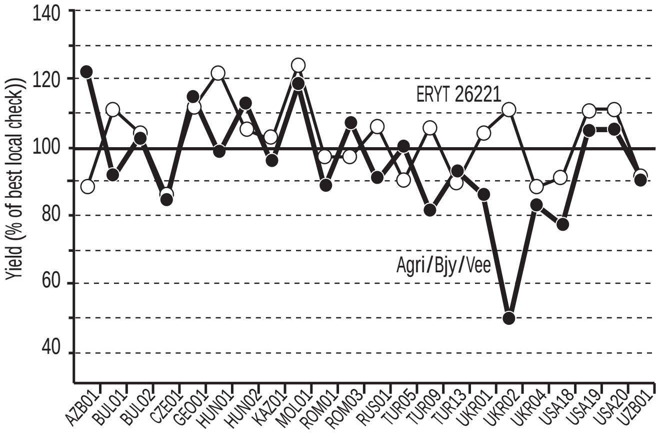


Figure 1. Grain yield (% of best 4 local checks) of the 2 highest yielding entries across 22 locations in the First Winter Wheat East European Yield Trial 1998/99. Yield of best local check = 100%.

A major difference in adaptation requirements

Table 3. Winter wheat cultivars released by national agricultural research systems derived from Turkey/CIMMYT/ICARDA[1] IWWIP[2] lines or CIMMYT-Oregon crosses.

Cultivar name	Year	Cross[3]	Cross #	Pedigree	Country released
Registered varieties					
KIRKPINAR79	1979	HYS/7C			TR - Edirne
ATAY85	1985	HYS/7C			TR - Eskisehir
NAVID	1991	HYS/7C			Iran
GUN91	1991	F35.70/Mo	SWM7155	-1A-1A-1A-0A	TR - Ankara
PAMIR94	1994	YMH/TOB//MCD/3/LIRA	SWM12289	-7M-0M-8M-1M-3WM-0WM-0AFG	Afghanistan
SULTAN95	1995	AGRI/NAC	SWM6599	-2H-1H-3P-0P-5M-3WM-0WM	TR - Eskisehir
GUL96	1996	ID800994.W/VEE	SWM15134	-2WM-0WM-0SE-1YC-0YC	Afghanistan
RANA96	1996	CA8055/6/PATO(R)/CAL/3/7C//BB/CNO/5/CAL//CNO/ SN64/4/CNO//NAD/CH	ICWH840431	-2AP-2AP-1AP-1AP-0AP	Afghanistan
Buck Oportuno	1996	PI/FUNO*2//VLD/3/CO723595	SWO802012	-9H-4M-3WM-0WM	Argentina
ZARRIN	1996	HATUSHA = NAI60/HEINE VII//BUC/3/F59.71/GHK	SWO791095		Iran - Myandoab
KINACI97	1997	YMH/TOB//MCD/3/LIRA	SWM12289	-7M-0M-8M-1M-3WM-0WM-4WM-2WM-0WM	TR - Konya
YILDIZ 98	1998	55-1744/P101//MAYA/3/MUS/PRM//MAYA/ALD"S"	SWM8340587F	-1P-0TE-23YA-0E	TR - Eskisehir
GOKSU99	1999	AGRI/NAC	SWM6599	-2H-1H-3P-0P-5M-3WM-0WM	TR - Konya
CETINEL 2000	2000	MLC/4/VPM/MOS95//HILL/3/SPN	OWC852672	-6H-0YC-0R-1YC-0YC-0E	TR - Eskisehir
C73-5	2000	SPN/MCD//CAMA/3/NZT	SWM777627	-17H-4H-1H-0H	Iran Mashad
ALPASLAN	2001	TX69A509-2//BBY2/FOX	TX78V2154	-2YC-0YC-2YC-0YC	TR - Erzurum
IZGI	2001	CA8055/KUTLUK	ICWH900312	-0AP-0YC-0YC-1YC-0YC	TR - Eskisehir
ALPU01	2001	ID800994.W/VEE	SWM15134	-1WM-0WM-0SE-0YC-HRC*-6YC-0YC	TR - Eskisehir
SÖNMEZ	2001	BEZ//BEZ/TVR/3/KREMENA/LOV29/4/KATIA1	TE4732A	-0T-0YC-0YC-5YC-0YC	TR - Eskisehir
NENEHATUN	2001	ND/P101//Blueboy	SWM584	-0P-1P-2P-0H	TR - Erzurum
Included in registration trials					
MTSKHETSKAYA 1		TAST/SPRW//ZAR	ICWH840048	-3AP-1AP-2AP-0AP-1AP-0AP	Georgia
TACICA		TAST/SPRW//ZAR	ICWH840048	-3AP-1AP-2AP-0AP-1AP-0AP	Tajikistan
GUNCHA		HAMSI = HYS/7C//KRC(ES84-16)/3/SERI	SWM17323	-0SE-0YC-1YC-0YC	Turkmenistan
BITARAP		BITARAP=AKULA-1=SN64//SKE/2*ANE/3/SX/4/BEZ/5/SERI	SWM866442	-1H-0YC-3YC-0YC	Turkmenistan
BDME98-3S		AKULA-2	SWM866442	-1H-0YC-5YC-0YC	TR - Konya
GARAGUM		TRAKIA/KNR	TE3093	-0T-18R-5R-0R-25R-0R	Turkmenistan
DOSTLIK		YMH/TOB//MCD/3/LIRA	SWM12289	-7M-0M-8M-1M-3WM-0WM-4WM-2WM-0WM	Uzbekistan
BDME98-3K		HN7/OROFEN//BJN8/3/SERI82/4/74CB462/TRAPPER//VONA	EWT8913	-SE-0YC-2YC-0YC	TR - Konya

[1] International Centre for Agricultural Research in the Dry Areas.

[2] International Winter Wheat Improvement Program.

[3] Underlined = spring parent.

between wheat growing areas in CWANA and neighboring CEE is due to the winters in CEE, which are often more severe. Rainfall is generally higher in CEE and most wheat areas are classified as ME11. Consequently, diseases other than yellow rust (the most significant disease in CWANA), in particular leaf rust, powdery mildew, and *Septoria* spp., cause highest losses.

Cultivar Release in Central/West Asia and North Africa

Winter and facultative wheats derived from spring x winter crosses have had a major impact on wheat production in CWANA, particularly in irrigated areas. Table 3 lists the cultivars recently released or presently in registration trials in CWANA, developed within the Turkey/CIMMYT/ICARDA/OSU IWWIP. All except two are derived from spring x winter crosses, a program closely associated with Professor Kronstad. Often a line is selected or released by a number of different national agricultural research systems (NARS), indicating that it has wide adaptation. The most important spring wheat donor was Seri 82, which appears in the pedigree of many widely-adapted spring x winter crosses.

Future Challenges

Early maturing cultivars for irrigated areas

Water regime strongly influences the maturity range required in irrigated areas in CWANA. Supplementary irrigation, common in Turkey and part of Iran, requires cultivars with high yields and relatively early maturing dates. One example is Kinaci 97, which was released in Turkey, and also in Afghanistan as Pamir 94 and in Uzbekistan as Dostlik. In areas where water is abundant and provided free or at low cost, farmers tend to grow late maturing, often photosensitive varieties, which require 5-10 irrigations. In northeastern Iran, farmers' yields can reach up to 12 t/ha using late maturing French and Hungarian cultivars, and by applying 4 irrigations in fall and 6 irrigations in spring. In Uzbekistan, the locally developed cultivar Ulubek 600 is among the highest yielding registered varieties for irrigated areas, though it is also one of the latest. In Turkey, Atay 85 (a HYS/7C derivative) and Sultan 95 (a Agric/Nac cross) are both photoperiod sensitive but are high yielding under full irrigation.

Breeding for early maturing cultivars with improved water use efficiency has not been a priority for most WFW breeding programs in CWANA; in fact, due to selection for maximum yield, late maturing varieties have been favored. With growing public concern over water shortages, and the increase in intensive crop rotations that require earlier maturing varieties, breeding for early cultivars that are adapted to supplementary irrigation regimes will become a high priority for most countries in CWANA. Turkmenistan, Uzbekistan, and Azerbaijan annually redraw 27, 3, and 2 times more freshwater, respectively, than the natural inflow (WRI 1998).

The subsequent increased demand for earlier cultivars will most likely be sourced from spring x winter crosses. The adaptation and potential of such cultivars is evident from registration trials in Uzbekistan (Table 4). Dostlik (Kinaci 97) out-yielded the local check Sanzar 8 by 8% across 10 locations, covering a wide range of yields and agronomic practices. Only in fully irrigated trials did the late maturing variety Polovchanka yield slightly higher. Considering the current issues of timely water and fertilizer availability faced by farmers in CAR, access to widely adapted cultivars with flexible responses to varying agronomic practices will considerably reduce farmers' risks. Results from the 2nd-4th Elite Yield Trials show that elite IWWIP germplasm with higher yield potential, improved quality, and yellow rust resistance is available for utilization by NARS.

Cultivars for rainfed areas

Wheat has to compete for water with more valuable

Table 4. Grain yield of wheat cultivars Sanzar 8 (local check), Polovchanka, and Dostlik in on-farm trials in four regions of Uzbekistan, 1999/2000.

Region	No. irrigations	Sanzar 8 (kg/ha)	Polovchanka (kg/ha)	(% LC)	Dostlik (kg/ha)	(% LC)
Galla-Aral	Rainfed	1,360	1,300	96	1,580	116
Kashkadarya						
Loc 1	2	4,330	3,270	76	4,350	100
Loc 2	2	3,970	3,470	87	4,230	107
Loc 3	3	5,830	5,400	93	6,400	110
Jizzak						
Loc 1	3	5,920	5,650	95	5,990	101
Loc 2	4	5,780	6,300	109	6,500	112
Loc 3	4	7,470	7,940	106	8,030	107
Khorezem						
Loc 1	3	6,100	6,160	101	6,300	103
Loc 2	4	5,650	6,250	111	7,420	131
Loc 3	4	6,000	6,900	115	6,040	101
Mean		5,672	5,704	101	6,140	108

Note: Data provided by PFU-CGIAR, Tashkent.

crops in CWANA, so it is expected that rainfed wheat will remain dominant. In contrast, rainfed wheat supplemented by irrigation in dry years will gain importance in CAR. To date, all released cultivars developed by IWWIP are targeted for irrigated areas. This is partly because prior to the initiation of IWWIP in 1988, few spring x winter crosses made by the CIMMYT-OSU program were specifically targeted for rainfed areas. Accordingly, IWWIP has emphasized crosses between well-adapted rainfed varieties in CWANA (nearly all of which are highly susceptible to rusts) and Mexican spring wheats. BDME98-K = HN7/OROFEN//BJN8/3/SERI82/4/74CB462/ TRAPPER//VONA is derived from such a cross and is the highest yielding entry in the Turkish registration trials for rainfed winter wheat areas in 1998-2000.

Northwestern Iran is one of the most severely-stressed wheat producing areas in the world due to a combination of late fall rains, rapidly falling temperatures, and a lack of rain after flowering. In this area, mainly landraces are cultivated, since introduced wheat cultivars, including those from the Central Plateau, lack general adaptation. A shuttle breeding program was initiated between Turkey and Iran to combine their gene pools. Turkish cultivars possess good levels of drought tolerance and winterhardiness, and have high yield potential in years of high rainfall—a trait that often cannot be exploited in Iran due to late fall rains. Iranian cultivars have good drought tolerance and rapid grainfill and spring growth, but have not been exploited in Turkey due to their mostly poor agronomic type when grown under Turkish rainfed conditions. Both gene pools possess traits of great potential for wheat breeding in rainfed areas, which the new shuttle breeding program aims to combine.

Achievements of Professor Warren E. Kronstad in Agriculture in Turkey

Professor Warren Kronstad first visited Turkey in 1966 as part of a USAID (United States Agency for International Development) mission. He returned to Turkey in 1967 and again in 1968. The latter visit was made at the request of the Government of Turkey to study the Mexican and Anatolian wheat programs, which had resulted from surveys made in 1966 and 1967. He attended the 3rd Rockefeller Foundation Wheat Seminar in Ankara in 1970, attended a travelling seminar in 1992, and was the keynote speaker at the 5th International Wheat Genetics Symposium in Ankara in June 1996.

The objective of Kronstad's early visits was to evaluate Mexican wheats and to assist in the establishment of the National Wheat Improvement Program (a joint venture between Turkey and OSU). Oregon was chosen because its coastal and plateau wheat growing conditions are similar to those found in Turkey. Though the practices developed in Oregon had tremendous potential for Turkey, disseminating the information was a major problem. For this reason, Prof. Kronstad and others recommended that 12 farmers and county agents from spring wheat growing areas in Oregon and Washington State work directly with the Turkish Extension Department. Nine farmers worked in Turkey for three months and three farmers worked for one year. These farmers were important contributors to the success of the Turkish Green Revolution. It should be noted that the Green Revolution on the Central Anatolian Plateau was the first to occur in rainfed areas. In India and Pakistan, the Green Revolution first took place in irrigated areas.

Prof. Kronstad played a key role in the import of Mexican wheat into Turkey. When the Turkish delegation visited Mexico to buy 22,000 tons of wheat, Kronstad advised them not to buy Sonora 64 due to its susceptibility to yellow rust. This was crucial advice that stopped Mexican wheat varieties from potentially gaining a bad reputation. Nonetheless, the introduction of Mexican semidwarf varieties in Turkey met with disapproval and resistance from some agriculturists, and any argument was used to hinder their successful introduction. When two Mexican children died from eating seed that had been treated with mercury-based chemicals, semidwarf varieties received a lot of negative attention in the Turkish press, who implied that the wheat itself was poisonous.

In spite of this, the yield advantage of the Mexican varieties in coastal areas was so significant that by 1972, high yielding Mexican varieties covered 97% of the wheat area in the Mediterranean region, 35% in the Aegean, and 40% in South Marmara—a total of around 1 million ha. Since 1979, four varieties (Kirkpinar, Atay, Sultan, and Yildiz 98) originating from the OSU/CIMMYT Spring x Winter Program have been released in Turkey, and many of the Oregon-derived cultivars have been used as parents in developing Turkish varieties.

Kronstad had a major impact on Turkish wheat research through his involvement in training Turkish wheat researchers. Since 1970, 9 Turkish scientists have received an MSc in plant breeding from OSU, and 19 Turkish scientists from the Ministry of Agriculture and Rural Affairs (MARA) have received an MSc in breeding, agronomy, or economy. On their return to Turkey, many of these researchers went on to gain prominent positions, from Institute Director to Deputy Undersecretary.

Professor Warren E. Kronstad was the "godfather" of the so-called Oregon Mafia in Turkey—an example of a truly good mafia. Many times he told the story of how he would take homesick Turkish students to Pendleton, Oregon—an area that looks so much like the Central Anatolian Plateau. Due to his warm feelings for Turkey and Turkish students, Prof. Kronstad looked after all Turkish scholars, whether they were his students or those studying under other professors. No other foreign agricultural researcher was as respected in Turkey as Prof. Warren E. Kronstad, and he will certainly occupy an prominent place in the modern history of Turkish agriculture.

References

Braun, H.-J. 1997. Winter hardiness of bread wheats derived from spring x winter crosses. *Acta Agronomica Hungary* 45(3):317-328.

Braun, H.-J., M. Aydin, and M. Kalayci. 1995. Variation of grain filling of 54 facultative and winter wheats grown on the Central Anatolian Plateau of Turkey. Proceedings of the 20th Hard Red Winter Wheat Conference.

Braun, H.-J., A.I. Morgounov, H. Ekiz, M. Keser, N. Zencirci, V. Eser, H. Ketata, and G. Marcucci. 1998. Breeding priorities of winter wheat programs. In: *Wheat: Prospects for Global Improvement*. Proceedings of the 5th International Wheat Conference. Developments in Plant Breeding, Vol. 6, pp. 553-560. Dordecht, The Netherlands: Kluwer Academic Publishers.

World Resources Institute (WRI). 1998. *A Guide to the Global Environment*, pp. 304-

Opportunities for Wheat Improvement: The Role of Crop Physiology Revisited

H.J. Spiertz and A.H.C.M. Schapendonk

Introduction

Wheat is a cereal crop that is able to grow under a wide range of conditions. For many decades, breeders and crop physiologists have studied the processes and traits that determine yield and crop performance under contrasting conditions. Most studies on global food security are based on trends in yield improvement of cereal crops, with wheat being the model crop (Evans and Fischer 1999). In this paper we will highlight some of the scientific achievements that have contributed to a better understanding of the growth, productivity, and stability of the wheat crop.

Achievements in Process-Based Crop Research

Wheat yield performance has been studied intensively. The following studies have been particularly important in understanding yield potential and limitations:

- Phenology of the wheat plant, conducted by Feekes prior to 1940, Wageningen, NL.
- Quantification of leaf photosynthesis in relation to light, temperature, and ambient CO_2, conducted by Gaastra prior to 1960, Wageningen, NL.
- Concept of leaf area index and duration, conducted by Watson prior to 1965, Rothamsted, UK.
- Concept of modeling crop growth and potential yield, conducted by de Wit prior to 1970, Wageningen, NL.
- Concept of “ideotypes” conducted by Donald in 1970, Australia; and Evans prior to 2000, Canberra, Australia.
- Concept of interception of solar radiation and crop photosynthesis, conducted by Monteith prior to 1975, Nottingham, UK.
- Spike development, conducted by Kirby prior to 1980, Cambridge, UK.
- Concept of sink-source interaction, conducted by Wardlaw prior to 1980, Canberra, Australia.
- Role of biomass yield and harvest index, conducted by Austin prior to 1985, Cambridge, UK.
- Role of nitrogen in yield formation, conducted by Spiertz prior to 1980, Wageningen, NL.
- Role of drought and heat stress, conducted by Evans and Fischer prior to 1980, Canberra, Australia; and Reynolds et al. prior to 2000, Mexico.
- Role of climate change and acclimation, conducted by Schapendonk et al. prior to 2000, Wageningen, NL.

Wheat research attained the leading position in crop science through a combination of sound physiological concepts, experimentation under controlled and field conditions, and integration of disciplinary knowledge of plant x environment interaction by mechanistic modeling. Such research has contributed to the development of research-based crop management with time- and dose-specific crop protection and nitrogen fertilization. This in turn has resulted in good yield performance and yield stability. Dynamic plant x environment interactions should be considered explicitly because the scope for germplasm improvement for productivity only is relatively small; major improvement will only be achieved in combination with intensive and adapted management. This opens new perspectives for combining the most recent crop varieties with the most appropriate management technologies.

Plant breeding has benefited least from advances in physiology because of the wide gap in understanding between the functioning of the whole plant and the empirical selection of traits during the breeding process. Further research into gene x plant x crop x environment interactions will contribute to a better and earlier assessment of the yield potential and yield stability of new genotypes (Gutierrez-Rodriguez et al. 2000; Morgan 2000). Molecular-based plant breeding has become so powerful for modifying the genetic base of a genotype that traditional plant breeding can no longer rely on only testing the new material in field plots. Advanced evaluation methods under standardized conditions applied in combination with crop models are required.

Yield Trends and Yield Potential

Yield is generally expressed as the fraction of aboveground biomass harvested as grain at a standardized moisture content (e.g., 14%). Yield potential is the maximum yield that can be achieved under experimental conditions by a given cultivar in a given environment for a growing season of defined duration (Sheehy 2001). Maximum yield is the yield predicted by a simulation model for a given cultivar under defined climatic conditions without biotic and abiotic stresses or yield reduction. Attainable yield is the maximum achievable yield for an adapted cultivar under current management practices in a given environment.

De Wit (1965) made the earliest assessments of maximum wheat yield for a defined environment on the basis of leaf photosynthesis measurements and theoretical assumptions about light interception, respiration, and assimilate distribution. However, when simulation studies calculated maximum grain yields of 10 t/ha under temperate growing conditions in northwestern Europe, it became clear that there was a considerable gap between actual and potential yields. From 1970 to 1990, this gap was almost bridged by annual increases in actual yields of about 3%. This progress was not caused by a change in the photosynthetic rates of individual leaves, but by an increase in total biomass through enhanced photosynthetic longevity of the canopy. This was a result of genetic improvement in lodging resistance and an increase in inputs such as nitrogen fertilizer and chemical crop protection (Spiertz et al. 1992).

The high yield potential of modern wheat cultivars was mainly associated with an increase in harvest index and not with increased biomass (Austin et al. 1980). The link between genetic improvement of wheat cultivars and advanced crop management resulted in increases in both biomass and the harvest index, which, in turn, boosted actual wheat yields under favorable conditions. However, the harvest index for wheat cannot be increased beyond 62% (Austin et al. 1980), and since wheat is already close to this theoretical threshold, there isn’t much scope for future increases in potential yield by manipulating this characteristic. Therefore, increasing biomass production must ultimately be regarded as the main method for further improving potential yields (Dreccer 2000).

Opportunities for Genetic Improvement

It is a matter of common sense that yield has limits. Yield is constrained by numerous factors including the availability of carbon dioxide and soil nitrogen, which become fixed and concentrated in dry matter, and the rate at which they can be supplied, either by mass transport or diffusion. Within the crop, the rate of processes that produce dry matter is limited. Because our understanding of these processes is based on existing cultivars, the prospects for increasing yield potential requires the use of mechanistic models based on biophysical and biological laws (Sheehy 2001). Despite the skepticism concerning modeling of actual yields, it is generally accepted that models are powerful research tools for assessing the yield potential of genotypes with well-defined traits under optimum growing conditions. A major drawback of current simulation models is the relatively small amount of attention paid to the development and functioning of sinks in relation to crop functioning. We have a much lower understanding of processes like the initiation of organ development and related changes in carbon and nitrogen fluxes compared to those related to light interception and crop photosynthesis. Yet it is clear that knowledge of sink-related processes is essential to the progress of genetic yield improvement.

Recent advances in genomics and gene function studies have allowed us to understand the detailed genetic basis of many complex traits such as flowering time, culm length, and the stay green characteristic. There are numerous examples of where the results of a genetic modification have fallen short of expectations because of the stable nature of physiological characteristics. This stability is due to the strong mutual feedback between the physiological characteristics and other physiological or morphological properties. In addition, many interactions are still poorly understood, partly due to the complex way they are affected by different phenological stages of the crop. However, there are now several striking examples showing that most of the variation underlying these seemingly complex characters has been mapped to a very small number of quantitative trait loci.

Within the next few years, it is likely that other important agronomic traits will be explained in terms of a relatively small number of key genes. This will only impact on breeding perspectives in cases where it is possible to not only quantify the effect of gene activity on physiology and morphology, but also to integrate these effects over the life cycle of the crop. This quantitative life cycle analysis will require the upscaling in time and space of processes occurring at the organ level to responses of the crop canopy over time. The upscaling of processes is based on models that use physiological and morphological data as inputs, and generate parameters of canopy processes in space and time. One component of the overall model should be dedicated to spatial upscaling, that is, predicting instantaneous canopy processes from discrete physiological and morphological data. The other model component should be dedicated to integrating the effect of gene activity over time. An example of such an approach is given in Figure 1.

Grain yield under favorable growing conditions is mainly sink limited, especially for wheat (Spiertz 1978; Reynolds et al. 2000). For this reason, much emphasis has been placed on understanding the mechanisms that determine spikelet formation, fertility, and grain set (Slafer et al. 1994).

The juvenile spike development period, particularly the rapid spike growth phase (which has a duration of approximately 20 d), is critical in determining wheat yield potential when final grain number is fixed (Fischer 1985). This is not only because it determines the partitioning of photoassimilates to yield, but also because it influences the photosynthetic assimilation rate during grainfilling. The relative duration of the juvenile spike growth period shows genetic variability, which is determined by the different alleles present for photoperiod and vernalization sensitivity. Slafer et al. (1996) hypothesized that final grain number and yield potential might be improved by manipulating these genes to increase the relative duration of the juvenile spike growth. Thus, sink formation could be stimulated—an advantage that would be most profitable when the grainfilling rate or the duration of the grainfilling period is extended.

Carbon and Nitrogen Economy of Wheat

Between 50% and 80% of total leaf nitrogen is allocated to photosynthetic machinery, which is why the short-term regulation and long-term acclimation of photosynthesis, with respect to nitrogen costs, are major subjects of ecophysiological studies. Nitrogen is a basic component of the physiological machinery and is often limiting. Consequently, its allocation to and its subsequent distribution within the photosynthetic machinery play a major role in the optimization of photosynthesis. When irradiance is low, an investment of nitrogen into Rubisco and other enzymes and cofactors of the electron transport and metabolic pathways will not be beneficial to growth. More beneficial will be the allocation of nitrogen to light-absorbing complexes, or the acceleration of leaf expansion to increase light interception. Conversely, under high irradiance levels, a greater investment in the metabolic and electron transport pathways (to increase their capacity) will be more beneficial than increasing light interception. Therefore, an optimum nitrogen profile in a canopy should reflect the requirements of the most responsive processes under the given environmental conditions. In studies conducted by Dreccer (2000), the light-associated leaf nitrogen distribution changed dynamically during crop growth and was regulated by nitrogen availability, not by atmospheric CO_2 concentration.

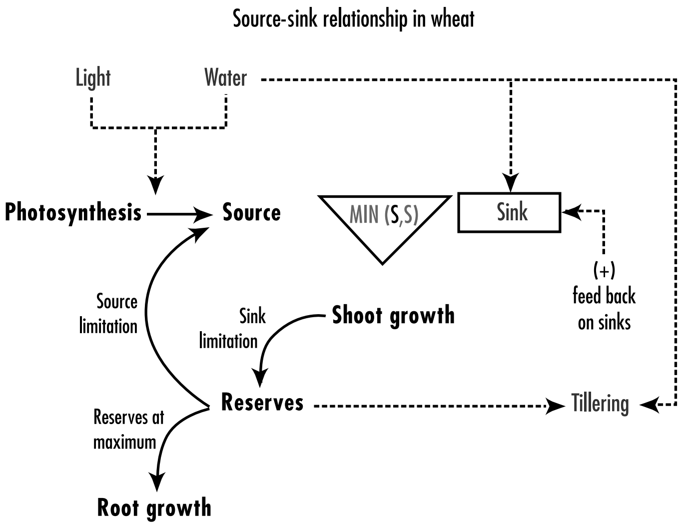


Figure 1. Flow diagram LINGRA-CC. The sink limitation is characterized by temperature-dependent leaf area increase. Leaf area increase is derived from leaf elongation, leaf formation rate, and tillering rate. The amount of carbon necessary to meet the demands of the resulting Dai should be counterbalanced by a carbon source, i.e., rate of photosynthesis. This includes the allocation of carbon to other parts of the plant, such as the roots and stubble. Carbon partitioning in LINGRA is dependent on water availability and the magnitude of the storage pool. The source is calculated by the Farquhar photosynthesis subroutine. Leaf photosynthesis is described by two rate-limiting processes, i.e., the production of reducing equivalents in the electron-transport chain and the rate of carbon fixation in the Calvin cycle. At low irradiance levels, the electron-transport rate, equivalent to energy delivery, is limiting.

The carbon and nitrogen economy of the wheat plant affect the rate and duration of grain growth. The primary source of these elements during grainfilling is leaf photosynthesis, however, sources and sinks change over the course of grainfilling. Peduncle and lower internodes often increase in dry weight and soluble sugar content up to about two weeks after anthesis, particularly under conditions of high assimilation and retarded grain development (Spiertz 1977). Rate of grain growth is determined by temperature—under raised temperatures, nitrogen allocation to the grains increases faster than carbohydrate allocation. Hence, during grainfilling under elevated temperatures, the reallocation of nitrogen from vegetative parts to the grains is increased. High temperatures also cause the earlier senescence of the green organs of the wheat plant; however, this can partly be offset by late nitrogen applications if water is not limiting.

Duration of grain growth is inversely related to temperature and is genetically determined. Under warm conditions, the demand for assimilates (200-350 kg/ha/d) by the rapidly growing grains cannot be met by daily photosynthesis; hence, reallocation from reserves in the vegetative parts is essential for maintaining grain growth. Under temperate conditions, the demand for assimilates by the growing grains is lower, and grainfilling lasts longer due to retarded senescence of the vegetative parts. Moderate temperatures and high radiation levels are optimal for obtaining high yields because grainfilling can occur over a longer period and source activity remains high due to high irradiance and the longevity of photosynthesis.

Nitrogenous compounds required for grain growth are mainly supplied by the vegetative parts of the plant and, to a smaller extent, from post-anthesis uptake. At final harvest, about 75-80% of the total aboveground nitrogen yield is located in the grains, thus, the harvest index for nitrogen is considerable higher than for carbon (Spiertz et al. 1978). The ratio between the allocation of starch and proteins in the grains influences baking quality.

Response of the Wheat Crop to Water Stress

Water stress during the vegetative and reproductive development stages reduces tillering, leaf area development, and grain set, and consequently lowers the photosynthetic capacity and the potential sink capacity to the same degree. During grainfilling, water stress mainly affects current assimilation by reducing photosynthetic area and photosynthetic activity (Fisher and Turner 1978). Higher temperatures are often associated with high evaporative demands. Under such conditions, water stress not only increases the proportion of current assimilates translocated to the grains, but may also increase the contribution from assimilates stored prior to the beginning of rapid grain growth. Bidinger et al. (1977) found that water stress did not affect the absolute contribution to grain yield of assimilate stored prior to anthesis. However, relative to grain yield, the contribution rose from 12% when there was no water deficit to 22% when there was a deficit during grainfilling.

The process of CO_2 assimilation inevitably leads to water loss from the crop to the atmosphere. Since CO_2 assimilation follows a saturation curve, and transpiration is more or less a linear function of irradiance, a curvilinear relationship between the rates of the two processes is expected. Water stress can indirectly reduce the photosynthetic rate by stomatal closure or directly by a reducing the photosynthetic capacity of the enzymatic processes. There is, however, no consensus on the primary site of reduction in photosynthesis. There is also no agreement on whether photoreactions in the thylakoid membranes or biochemical reactions of the Calvin cycle are most affected. Furthermore, most experiments do not distinguish between water stress and heat stress.

The relative importance of the effects of water stress depends very much on timing. Photosynthesis under water stress is initially less inhibited than transpiration. This is because the CO_2 concentration gradient is increased by stomatal closure, while the water concentration gradient remains the same; therefore, water use efficiency is enhanced. After a few days, however, water stress directly reduces the photosynthetic capacity, either by down-regulation of electron transport or by affecting the carboxylation enzymes that lower the mesophyll conductance, thereby lowering the water use efficiency (Schapendonk and Spitters 1989). Stomatal closure and lower mesophyll resistance show a correlated response to water stress that leads to a constant ci/ca ratio. Thus, photosynthesis and transpiration are equally reduced, and water-use efficiency tends to decrease to a value approximately equal to the nonstressed condition. In general, it appears that the immediate effect of drought on physiological parameters is much greater than the integrated seasonal effect because of the close relationship between whole crop transpiration and leaf area (i.e., growth). In other words, impaired leaf area development will conserve water for later use and, therefore, smooth the temporary effects.

In general, dry matter yield is proportional to the total transpiration loss of the crop. The ratio between transpiration and assimilation is strongly influenced by stomatal behavior and amounts to 100 kg H_2O per kg CH_2O for C_3 species under average radiation and humidity conditions. In terms of dry matter, this value ranges between 125 and 150 kg H_2O per kg dry matter. Conversely, when stomatal regulation is absent (i.e., when stomata are fully open in the light and completely closed in the dark), the transpiration coefficient under identical conditions varies between 175 and 200 kg H_2O per kg dry matter.

Response of the Wheat Crop to Nutrients at Elevated CO_2 Levels

A higher concentration of soluble sugar and/or starch and a reduction in nitrogen concentration per unit dry weight are often found in plants under elevated CO_2 levels (van Oijen et al. 1998). Nitrogen availability stimulates biomass production by directly affecting both the source of carbohydrates (i.e., leaf photosynthesis) and the sink (i.e., leaf area expansion and tiller formation). Therefore, interactive effects between nitrogen availability and the level of atmospheric CO_2 can be expected. High nitrogen supply prevents photosynthetic acclimation to high CO_2 in wheat by stimulating tiller growth and partially preventing a drop in tissue nitrogen concentration that is often observed at high CO_2. These findings have led to the conclusion that acclimation to high CO_2 is primarily a response to nitrogen availability. The response of canopy photosynthesis to nitrogen availability can change under high atmospheric CO_2 if acclimation occurs, that is, photosynthesis and the production of photosynthetic enzymes decrease, and nitrogen is reallocated within the photosynthetic machinery and within the plant (Dijkstra et al. 1999).

The effects of increased atmospheric CO_2 on crop growth and dry matter allocation may change if the nutrient supply becomes insufficient for maximum growth. It may also cause changes in minimum nutrient concentration of plant tissue and, hence, in the nutrient use efficiency or yield nutrient uptake ratios of the crop. Wolf et al. (1996) carried out pot experiments with spring wheat in the glasshouse at ambient and doubled CO_2 concentrations, and at different levels of N, P, and K. They found that doubling the ambient CO_2 resulted in a large increase in total biomass and grain yield when the nutrient supply was optimum. When N and K were strongly limited, the CO_2 effect was approximately halved; when P was strongly limited, the effect was almost nil. Doubling the CO_2 level resulted in a 10% reduction in minimum N concentration in plant tissue, but did not affect the minimum P concentration.

The results of experimental research and simulation modeling on the effects of cultivar improvement of elevated CO_2 and temperature on wheat growth and yields show obvious trends, although emphasis is mainly given to the response of conventional cultivars selected for the current climatic conditions.

The qualitative effects of elevated CO_2 and temperature on physiological processes, growth, and yield of wheat can be described as follows:

Higher CO_2

- Increased rate of photosynthesis, especially during the middle of the day, resulting in a higher biomass yield.
- A higher water-use efficiency due to stomatal regulation in C_3 plants.

Higher temperature

- Enhanced crop development rate, and shorter development phases and growth duration.
- Accelerated grain growth and shorter grainfilling duration.

Fangmeier et al. (1999) assessed nutrient concentrations and grain quality in spring wheat grown under elevated CO_2 concentrations at different nitrogen rates at several sites in Europe. They found that nitrogen acquisition by the crop did not match carbon acquisition under enriched CO_2 conditions. Correspondingly, grain nitrogen concentrations decreased by 15%, on average, when CO_2 concentrations were almost doubled. As a consequence, grain quality (i.e., Zeleny and Hagberg values) was reduced. It was concluded that, despite the beneficial effect of CO_2 enrichment on growth and yield of C_3 cereal crops, a decline in flour quality due to reduced nitrogen content is likely in a world rich in CO_2.

Concluding Remarks

Growth and yield of a wheat crop is the result of interactive responses of the plants to weather and soil factors. Assuming optimal crop protection, crop growth is governed by environmental conditions and water and nutrient availability, whereas grain yield also depends heavily on the storage capacity of the ear and, consequently, on the allocation of assimilates during grainfilling. Crop development strongly influences ear initiation and formation, which in turn affect the potential number of grains and hence the sink capacity during grainfilling.

In the future, more emphasis should be given to defining new ideotypes that are adapted to milder conditions during winter and spring, and temperature extremes during flowering and grainfilling. Extending the early development phases, especially from ear initiation to flowering, may contribute to increased grain numbers (sink capacity). This is a prerequisite for making optimal use of the higher supply of photosynthates under elevated CO_2 levels. From experiments conducted under controlled conditions, it may be concluded that an increase of 25-30% in potential grain yield is possible. A potential grain yield of about 15 t/ha requires a stand of at least 600 heads/m^2 with a minimum of 50 grains/head. The nitrogen demand of such a high yielding crop can only partially be supplied by nitrogen reallocation from the vegetative parts. Substantial nitrogen uptake would therefore need to take place during the post-flowering period.

References

Austin, R.B., J. Bingham, R.D. Blackwell, L.T. Evans, M.A. Ford, C.L. Morgan, and M. Taylor. 1980. Genetic improvement in winter wheat yields since 1900 and associated physiological changes. *Journal of Agricultural Science* 94:675-689.

Bidinger, F., R.B. Musgrave, and R.A. Fischer. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. *Nature* (London) 270:431-433.

Dreccer, F.M. 2000. Radiation and nitrogen use in wheat and oilseed rape crops. PhD dissertation. Wageningen University, The Netherlands. 133 pp.

Dijkstra, P., A.H.C.M. Schapendonk, K. Groenwold, M. Jansen, and S.C. van de Geijn. 1999. Seasonal change in the response of winter wheat to elevated atmospheric CO_2 concentration grown in Open-Top Chambers and field tracking enclosures. *Global Change Biology* 5:563-576.

Evans, L.T., and R.A. Fischer. 1999. Yield potential: its definition, measurement and significance. *Crop Science* 39:1544-1551.

Fangmeier, A., L. De Temperman, L. Mortensen, K. Kemp, J. Burke, R. Mitchell, M. van Oijen, and H.-J. Weigel. 1999. Effects on nutrients and on grain quality in spring wheat crops grown under elevated CO_2 concentrations and stress conditions in the European, multi-site experiment 'ESPACE-Wheat'. *European Journal of Agronomy* 10:215-229.

Fischer, R.A. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science* 108: 447-461.

Fischer, R.A., and N.C. Turner. 1978. Plant productivity in the arid and semi-arid zones. *Annual Review of Plant Physiology* 29:277-317.

Gutiérrez-Rodriguez, M., M.P. Reynolds, and A.Larqué-Saaveda. 2000. Photosynthesis of wheat in a warm, irrigated environment. II. Traits associated with genetic gains in yield. *Field Crops Research* 66:51-62.

Morgan, J.M. 2000. Increases in grain yield of wheat by breeding for an osmoregulation gene: relationship to water supply and evaporative demand. *Australian Journal of Agricultural Research* 51:971-978.

Oijen, van, M., A.H.C.M. Schapendonk, M.J.H. Jansen, C.S. Pot, J. van Kleef, and J. Goudriaan. 1998. Effects of elevated CO_2 on development and morphology of spring wheat grown in cooled and non-cooled open-top chambers. *Australian Journal of Plant Physiology* 25:617-626.

Reynolds, M.P., M.I. Delgado, B. M.Gutiérrez-Rodriguez, and A. Larqué-Saavedra. 2000. Photosynthesis of wheat in a warm, irrigated environment. I. Genetic diversity and crop productivity. *Field Crops Research* 66:37-50.

Schapendonk, A.H.C.M., C.J.T. Spitters, and P.J. Groot. 1989. Effects of water stress on photosynthesis and chlorophyll fluorescence of five potato cultivars. *Potato Research* 32:17-32.

Sheehy, J.E. 2001. Will yield barriers limit future rice production? In: J. Nösberger, H.H. Geiger, and P.C. Struik (eds.), *Crop Science: Progress and Prospects*. CAB International. 416 pp.

Slafer, G.A., D.F. Calderini, and D.J. Miralles. 1996. Yield components and compensation in wheat: Opportunities for further increasing yield potential. In: M.P. Reynolds, S. Rajaram, and A. McNab (eds.), *Increasing Yield Potential in Wheat: Breaking the Barriers*, pp. 101-134. Mexico, D.F.: CIMMYT.

Slafer, G.A., E.H. Sattore, and F.H. Andrade. 1994. Increase in grain yield in bread wheat from breeding and asso ciated physiological changes. In: G.A. Slafer (ed.), *Genetic Improvement of Field Crops*, pp. 1-67. New York, NY: Marcel Dekker.

Spiertz, J.H.J. 1977. The influence of temperature and light intensity on grain growth in relation to the carbohydrate economy of the wheat plant. *Netherlands Journal of Agricultural Science* 25:182-197.

Spiertz, J.H.J. 1978. Grain production and assimilate utilization of wheat in relation to cultivar characteristics, climatic factors and nitrogen supply. *Wageningen Agricultural Research Report* 881:1-32.

Spiertz, J.H.J., H.D.J. van Heemst, and H. van Keulen. 1992. Field-crop systems in North-Western Europe. In: C.J.Pearson (ed.), *Ecosystems of the World: Field Crop Ecosystems*, pp. 357-371. Amsterdam, The Netherlands: Elsevier.

Spiertz, J.H.J., and N.M. de Vos. 1983. Agronomical and physiological aspects of the role of nitrogen in yield formation of cereals. *Plant and Soil* 75:379-391.

Wit, de, C.T. 1965. Photosynthesis on leaf canopies. *Wageningen Agricultural Research Report* 663:1-57.

Wolf, J., L.G. Evans, M.A. Semenov, H. Eckersten, and A. Iglesias. 1996. Comparison of wheat simulation models under climate change. I. Model calibration and sensitivity analyses. *Climate Research* 7:253-270.

In Celebration of a Life Well-Lived

R. Karow

The Department of Crop and Soil Science and the College of Agricultural Sciences at Oregon State University (OSU) are proud to be sponsors of the Warren. E. Kronstad Commemorative Symposium. The OSU and the International Maize and Wheat Improvement Center (CIMMYT) have had a long and mutually beneficial relationship. Each organization has been involved in the growth and development of the other and we know that this relationship will continue. Dr. S. Rajaram and other CIMMYT scientists are active participants in the OSU wheat breeding project and Department of Crop and Soil Science educational programs. Furthermore, new OSU scientists attending this symposium are making connections that will carry us into the future.

It is very fitting that we gather at CIMMYT for this symposium. It is also appropriate that the event is not a memorial service but a forum for remembering and analyzing the successes and failures of the past, as well as for projecting the future. Warren would be pleased with this format and even more so with the audience. His friends and colleagues are gathered together to celebrate his life and career, and, more importantly, a number of the next generation of wheat breeders are here to listen and learn. They have the opportunity to hear about the past in order to avoid an earlier generation's mistakes and can learn about the challenges and opportunities of the future, as seen through the eyes of respected scientists from around the world. Opportunities for such learning and interaction are rare.

We sincerely thank Dr. Rajaram for his leadership in developing this symposium, and Professor T. Reeves and CIMMYT for being ever gracious hosts. We look forward to continued success as partners in world wheat development and improvement.

A brief history of Warren's life and accomplishments is an appropriate beginning to this symposium.

Warren E. Kronstad was born on 3 March 1932 in Bellingham, Washington. Following active military service from 1952 to 1954, he attended Washington State University (WSU) where he received a BSc in agronomy in 1957 and an MSc in plant breeding and genetics in 1959. He then joined the ARS-USDA[1] wheat breeding program at WSU as a research assistant with the late Dr. O.A. Vogel. From 1959 to 1963, Dr. Kronstad served as an instructor in the Farm Crops Department at Oregon State University and received his PhD in 1963. He remained at OSU and, in 1963, was appointed project leader of Cereal Breeding and Genetics. He continued to serve in this role, and many others, until his retirement on 31 December 1998.

Dr. Kronstad was an early innovator in the field of biometric modeling to gain insight into parental selection and genetic variation within segregating populations. This contribution was recognized as one of the major accomplishments in plant breeding during the 20th century at the First International Plant Breeding Symposium held at Iowa State University in 1965. The information gained through this basic research was a significant contribution in itself, but Dr. Kronstad was able to apply this knowledge through the development of genetically superior cultivars including soft white winter wheats Yamhill, Hyslop, McDermid, Stephens, Hill, Malcolm, Gene, Temple, Weatherford, and Foote; hard white wheats Winsome and Ivory; the hard red winter wheat Hoff; the winter durum wheat Connie; winter barleys Casbon, Adair, and Scio; and winter oats Lane and Amity. By utilizing suitable environmental stresses to better understand the interaction between genotype and environment, Dr. Kronstad and his research team were successful in developing winter wheat varieties that not only have superior yield potential but also yield stability when grown across environmentally diverse locations and over years.

The Wheat Breeding Project generated grant funds in excess of US$ 15 million under Dr. Kronstad's leadership. Funding came from a diverse set of agencies including the Oregon Wheat Commission, the United

---

[1] Agricultural Research Service, United States Department of Agriculture.

States Department of Agriculture (USDA), the United States Agency for International Development (USAID), the National Institute of Health (NIH), the National Aeronautics and Space Agency (NASA), and the Rockefeller Foundation.

Dr. Kronstad's contributions extend far beyond the domestic arena. He was actively involved in international wheat improvement activities from the 1960s. He began his work in Turkey and was part of a team that led the country from deficit to surplus wheat production. For the last 20 years, Dr. Kronstad directed a large international program that focused on the systematic crossing of winter and spring wheat germplasm to produce high yielding, widely adapted germplasm for the lesser developed countries of the world. In collaboration with CIMMYT, and with funding from the Rockefeller Foundation and USAID, germplasm from this hybridized pool has resulted in varietal releases by national programs in at least 20 developing countries.

When asked about his research contributions, Dr. Kronstad was always quick to point out that his success was due to the achievements of his team. He said that his accomplishments were those of many dedicated people including project staff, graduate students, and the hundreds of young people who worked with his project over countless summers.

Dr. Kronstad was not content in the field of research alone. For more than thirty years, he was an educator both in and out of the classroom. He taught undergraduate classes in cytogenetics, plant breeding, genetics, and cereal production. He was a recipient of the Outstanding Teacher Award in the Department of Crop and Soil Science. He also served as major professor for more than 100 graduate students from more than 27 countries. Many of these are now leaders in their native countries, making a lasting impact on agriculture.

Dr. Kronstad's achievements have been recognized by many awards. The wheat producers of Oregon and the American Farm Bureau Federation recognized Dr. Kronstad's contribution to agriculture on many occasions and with numerous awards including the Distinguished Service Award, the Outstanding Achievement Award, the Service to Agriculture Award, and Agriculturist of the Year. But perhaps the highest tribute to his success was the establishment of the Wheat Research Endowed Chair: a US$ 1,000,000 endowment, funded by the Oregon wheat producers and matched by Oregon State legislature. He also received the Oregon State University Distinguished Professor Award, the Alexander von Humboldt Foundation Prize, the CSSA Crop Science Research Award, the Oregon State University Alumni Association Distinguished Professor Award, the Distinguished Service and Graduate Training Award, awards from the Governments of Mexico and Turkey, the USDA Distinguished Service Award for Education and Information, and the 1991 Presidential End Hunger Award. He was also a Fellow of the ASA, CSSA, and AAAS.

Last but not least, Warren was a friend to students, colleagues, and growers, both near and far, and was a proud husband, father, and grandfather. His contributions will be remembered for generations to come.

Participatory Crop Improvement in Wheat in High Potential Production Systems

J.R. Witcombe and D.S. Virk

Introduction

We describe the results of farmer participation in varietal improvement in wheat in more favorable agricultural environments—high potential production systems (HPPSs)—where abiotic factors (soil fertility and water availability) generally do not limit production. This research was initially developed as an alternative to the top-down, transfer-of-technology approach to agricultural research and extension, since such methods had failed in many marginal environments where there was little or no adoption of modern varieties (e.g., see Witcombe et al. 1998a for research conducted in India).

Over the last ten years, participatory research has produced substantial evidence to show that participatory varietal selection effectively identifies varieties preferred by farmers, and that these varieties are usually not officially recommended. Examples of participatory research funded by the Department of International Development (DFID) in India include Joshi and Witcombe (1996; 1998) in rice, maize, chickpea, and black gram; Halaswamy et al. (2001) in finger millet; and Rana et al. (2001) in sorghum.

Participatory plant breeding has also been successful in marginal areas, for example, rice at high altitudes in Nepal (Sthapit et al. 1996), rice in eastern India (Kumar et al. 2001a), and maize in western India (Goyal et al. 2001) and eastern India (Kumar et al. 2001b). Genetic gains achieved by these breeding programs have been in the order of 3-5% per annum from the first cross to the first impact in farmers' fields (Witcombe et al., unpublished).

Participatory research has been claimed to be most important in marginal areas because these areas are complex, diverse, and risk prone; however, favorable areas are also complex and diverse, and no agricultural enterprise is without risk. Hence, Witcombe (1999) argued for the use of participatory techniques in favorable areas where the adoption of modern varieties is slow and, at times, incomplete.

In this paper, we first examine the need for participatory research in wheat in favorable areas, and then describe the results of this research conducted in Lunawada, Gujarat, India.

Varietal Testing, Release, and Extension are Inefficient in High Potential Production Systems

The efficiency of varietal release and popularization has been commonly measured as the proportion of varieties grown by farmers that are the products of modern plant breeding, known as modern varieties (MVs) or high yielding varieties (HYVs). This, however, is a crude measure that can hide inefficiencies in the system, so we assess efficiency in wheat using three criteria:

- How broad is varietal diversity? (If varietal diversity is broad then socioeconomic and physical diversity are catered for and genetic vulnerability is reduced.)
- How quickly are cultivars replaced? (If replacement is fast then the breeding programs are producing a continuous flow of new, acceptable cultivars that are efficiently popularized.)
- Are all, or at least most, released varieties adopted by farmers? (If most released varieties are adopted then the trials system is efficiently selecting varieties preferred by farmers.)

Efficiency criteria

Varietal diversity in wheat is low in high potential production systems. We collected data for varietal diversity in wheat in three HPPSs in India: Punjab; Lunawada, Gujarat; and Bareilly District, Uttar Pradesh. In all systems varietal diversity was low, with the most common variety always occupying more than 50% of the wheat area and often about 90%. The predominant varieties were PBW 343 (Arttila) in the Punjab, Lok 1 in Gujarat, and UP 2338 in Uttar Pradesh. In the Punjab—the only area for which we have data over time—varietal diversity declined dramatically from 1981/82 when the most popular variety WL711 covered 52%, to 1999/2000 when PBW 343 occupied 87% of the area (Figure 1). This low varietal diversity is of great concern since wheat is vulnerable to epidemics of yellow (stripe) rust (caused by *Puccinia striiformis* West. f. sp. *Tritici*), which can cause significant losses (Mamluk et al. 1989; Danial and Danial 1995).

Cultivar replacement in wheat is slow in high potential production systems. In Lunawada, Gujarat, the predominant variety in 1997 was Lok 1, released in 1981. Although we have no quantitative data, interviews with scientists and farmers indicated that this variety has been predominant for over 15 years. In the Punjab, the predominance of variety HD 2329 was long lived (Figure 2). It covered over 30% of the wheat area for 10 years and over 60% for 6 years.

Many released varieties are not accepted by farmers. Variety HD 2329 occupied about 16% of the wheat area in the Punjab before it was released in 1985, and it became the predominant variety from 1985 to 1996. During this time, 17 new wheat varieties were released, though none occupied more than 8% of the wheat area (Figure 3) and only PBW 343, released in 1995, was widely accepted by farmers. While the varietal testing system identifies varieties as superior, farmers find many not to be so.

Conclusions on efficiency criteria

None of the three criteria developed to achieve an efficient varietal identification and release system were met in the case studies. However, it must be emphasized that a further measure of success was fully met: Does the system make genetic yield gains over longer periods of time? Hence, participatory research is not introduced to fix a failing system, but to make a successful system more efficient. Having diagnosed that the system does have inefficiencies, we now examine the reasons for these.

Why is the System Inefficient?

Witcombe et al. (1998b) and Packwood et al. (1998) analyzed the multilocational trials system for marginal areas in India and found that:

- The trial sites poorly represented the cropping areas.
- The trials were inappropriately managed and so did not represent the environments found in farmers'

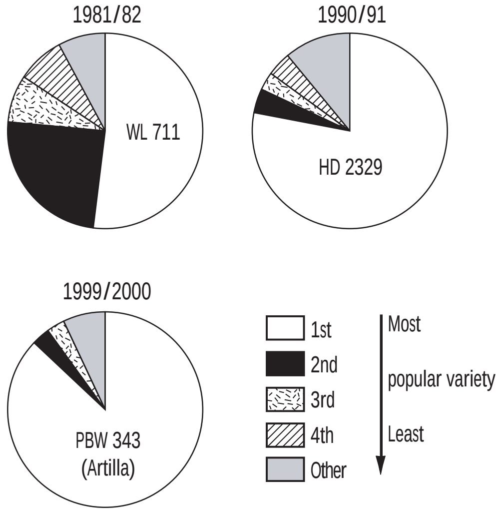


Figure 1. Increasing varietal uniformity in wheat in the high potential production system of the Indian Punjab.

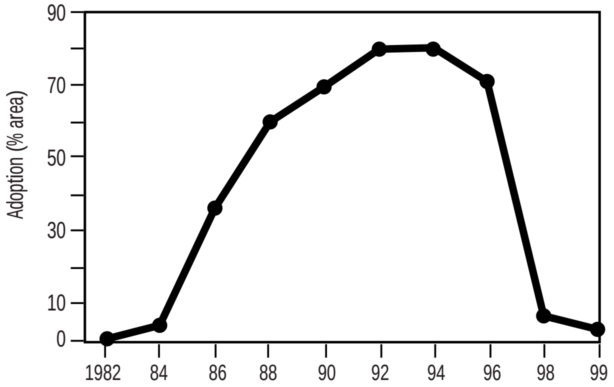


Figure 2. Low temporal diversity of wheat in the Punjab—long-lived dominance by a single variety, HD 2329.

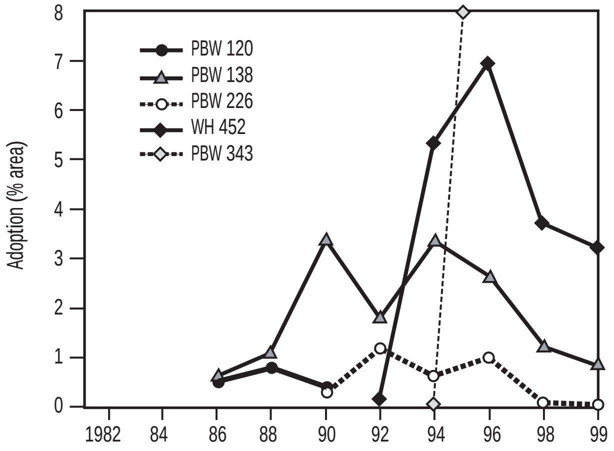


Figure 3. Adoption of five released wheat varieties by farmers in the Punjab, India.

Source: Dr Joginder Singh, Punjab Agricultural University, Ludhiana, India.

fields.
- Varieties in the multilocational trials were selected against those that were most likely to be specifically adapted, i.e., varieties that were much earlier or later than other entries in the trials.
- The selection strategies placed undue emphasis on yield so that any trade-off between multiple traits was too limited.

It may be surprising to note that most of these results for marginal environments also apply to more favorable environments.

Trial sites poorly represent cropping areas

The number of trial sites that can be accommodated in a multilocational trials system is severely limited by cost. There are only two trial sites of wheat in the Indian Punjab to represent about three million hectares. Although the trials are divided by zone, these zones are very large to better target environments, hence they encompass a diverse range of growing conditions. Furthermore, the number of trials within a zone is, of necessity, low.

Trial environments are not representative of farmers' fields

Trials designed for marginal environments are grown under far superior management to that occurring in farmers' fields (Packwood et al. 1998), hence, varieties specifically adapted to the harsher conditions of farmers' fields will not be selected. This disadvantage is not found to anywhere near the same extent in HPPSs; however, a new source of error related to the timing of sowing is introduced in these areas. Rainfed crops are all planted at the same time after the first significant rains, whereas irrigated crops can be planted at different times. Most farmers in Lunawada, Gujarat, sow their wheat in early December, which is neither particularly timely for achieving maximum yields, nor particularly late. The multilocational trials, however, are divided into timely-sown and late-sown trials, with neither closely representing farmers' practices (Figure 4). In the Punjab, farmers plant their wheat increasingly early (in 1999, over 80% was planted before 15 November; Figure 5); however, only 30% of the timely-sown trials are planted before this date (Figure 6).

It is of concern that the timely- and late-sown trials poorly represent farmers' practices because there is significant genotype x planting-date interaction. This problem can be solved by extending the range of planting dates over which the trials are conducted, but this is resource demanding and only farmer participatory trials will accurately sample the actual distribution of sowing dates. When another factor is considered—the increasingly limited availability of irrigation water—the number of planting date x water regime options becomes too large to accommodate in a conventional multilocational trials system.

Multilocational trials do not allow for specific adaptation

Earliness is a desirable trait in some HPPSs because it can provide additional cropping options for farmers—for example, early maturing wheat can allow a late harvest of rice or an additional subsequent legume crop—and although wheat yields may decline, the overall system productivity or profitability can increase. In the All India Coordinated Wheat Improvement Project trials there is a strong trend towards selecting late maturing entries in both timely- and late-sown trials. In the 1999/2000 trials (NIVT 1B), Raj 4022, which yielded 8% (430 kg/ha) less than PBW 343 but matured 14 days earlier, was rejected (Figure 7). This shows that farmers may prefer to trade off a yield loss of 430 kg/ha against the potential gains of an earlier harvest of around two weeks.

The selection strategy in multilocational trials does not allow a trade-off between traits

Trials for marginal and favorable environments share the same selection criteria, as well as undue emphasis on yield and a lack of emphasis on other traits considered important by farmers. High selection pressure for yield prevents the promotion or release of entries that excel in other highly desirable traits. Data on other traits are collected but are seldom used in promotion and release decisions (Witcombe et al. 1998b).

There are many traits that are difficult to measure in scientist-managed multilocational trials, and it is certainly not possible to record all of the important economic traits. Trait evaluation is limited mainly to those that are easy to measure in the field. Many traits, such as cooking quality, taste, higher market acceptability, and storability are usually not assessed until the variety is released. They are used to describe a variety rather than as target traits in the breeding process.

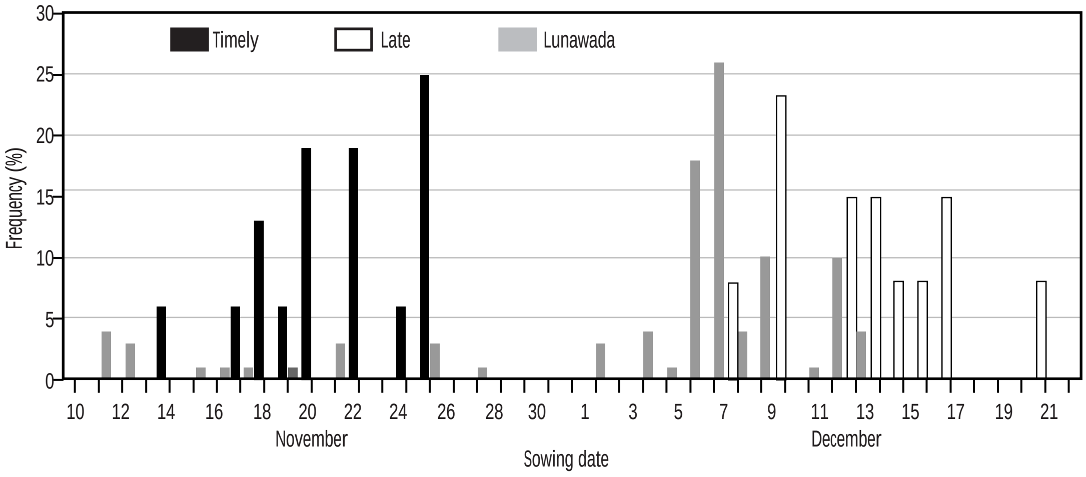


Figure 4. Sowing date of wheat: timely- and late-sown All India Coordinated Wheat Improvement Project trials in the Central Plain Zone, 1999/2000 vs. farmers' practices in six villages in Lunawada, Gujarat, India, 1996 and 1997.

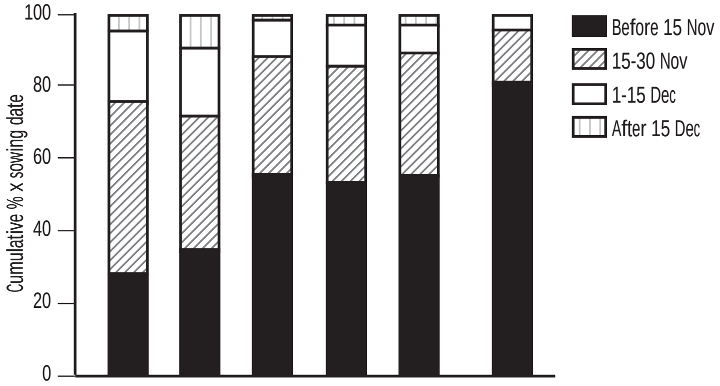


Figure 5. A trend in earlier sowing of wheat in the Punjab, India.

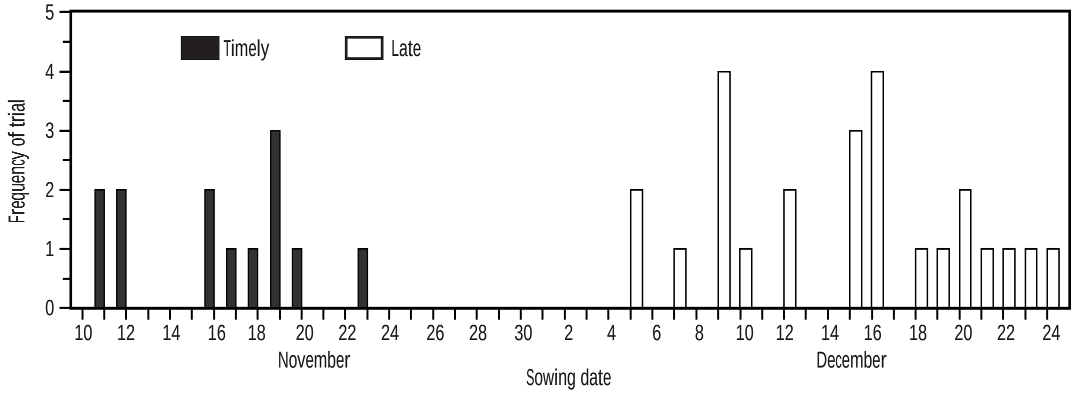


Figure 6. Sowing date of wheat in timely- and late-sown trials in the Punjab, 1999/2000. By 15 November, 80% of farmers had sown their wheat while only 30% of the timely trials had been sown.

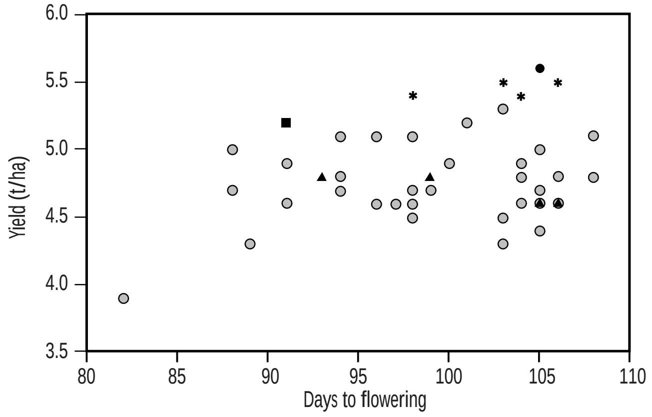


Figure 7. Selection for late-maturing entries in All India Coordinated Wheat Improvement Project trials (NIVT 1B), 1999/2000. Yield of unselected entries ●, selected entries *, check varieties ▲, and Raj 4022 ■ (not selected).

If due consideration is to be given to the farmer-relevant traits in scientist-managed multilocational trials, selection must be made using multiple-trait selection indices including traits such as earliness, fodder yield and quality, grain quality, and market price. Although it is possible to select complex selection indices based on farmer surveys, these will change over time and vary between regions and socioeconomic classes. Measuring all of these traits will add considerably to the costs of multilocational trials. Participatory research is by far the simplest way of taking into account any trade-off between traits. Farmer participation in varietal evaluation would allow many farmer-relevant parameters to be assessed, including taste, cooking quality, threshability, and storability (Witcombe and Joshi 1995; 1996).

Participatory Research–Participatory Varietal Selection

Methods

So far we have only tested participatory varietal selection (PVS) for wheat where farmers select among varieties that are already released and publicly available, and are being grown on their own farms under their own management (Witcombe and Joshi 1996). This is a PVS model that can be readily adopted by a nongovernmental organization (NGO), for example, since it does not require access to a breeding program or breeding materials. In the first year of the PVS trials we tested a range of readily available HYVs; in the second year we added varieties that had been released for late-sown conditions; and in the third year we added early varieties.

Using the basic PVS method, each farmer was given 2-5 kg of seed, depending on seed availability. The farmer grew the test variety under his or her management in a paired plot design, i.e., the test variety was grown alongside the farmer's preferred variety (Figure 8), which initially was Lok 1, although farmers used other varieties in later years. We also conducted single-replicate trials of all test varieties, which were grown in several fields in each village where the PVS trials were undertaken. This design resembles CIMMYT's mother-baby trial design developed by agronomists in southern Africa (Snapp 1999) and further developed and tested by Julien de Meyer and Marianne Bänziger (personal communication) at CIMMYT-Zimbabwe for large-scale participatory trials.

Figure 8. A farmer-managed participatory research trial of wheat in Lunawada, Gujarat, India.

We also compared two other PVS methods: farmer managed participatory research (FAMPAR) and informal research and development (IRD). FAMPAR is a classical empowerment model that involves intensive interaction with farmers (Chambers 1989). Typically, trials are jointly evaluated during farm walks, followed by focus group discussions and formal surveys. The second system, IRD, is a functional extension model developed by Lumle Agricultural Centre, Nepal (Joshi and Sthapit 1990) in which interaction with farmers is minimized. Farmers are given the seed of new varieties as well as an explanation of possible testing methods. Evaluation is based on informal, post-harvest interviews (termed anecdotal methods), demand for seed, and adoption levels. The IRD method requires only one tenth of the researcher time required by FAMPAR for the same number of farmers and villages.

Results

Participatory trials

We quickly found that it was much easier to conduct PVS trials in favorable rather than marginal environments. In favorable environments, farmers had higher literacy levels and were more educated, so there was a more rapid understanding of the purpose of the trials. Also, the fields available for the trials were large and level, and the trials plots occupied only a small proportion of farmers' land, even if the plots were large.

Many of the test varieties produced significantly higher yields than Lok 1 (Figure 9), however, many yielded similarly to the newly released varieties GW 496 and GW 503. At the very least, PVS offered a possible solution to low varietal diversity. It also promoted the spread of recommended variety GW 496 and identified weaknesses in recommended variety GW 503, namely, that it was lower yielding than GW 496 in farmers' fields, it matured slightly later, and it had slightly inferior grain quality to Lok 1 and GW 496.

The varieties offered in the PVS trials provided farmers with many choices. Over a period of five years (1996/97-2000/01), 28 varieties were tested by farmers in nearly 1,000 trials conducted in the project villages. In the third and fourth years of the trials, two varieties, Raj 3756 and Raj 3077, were identified with a superior combination of traits to GW 496, and were higher yielding and earlier than Lok 1. These varieties were tested in the first year (1996/97) but could not be included in trials in the second year because of a lack of seed. Neither of these varieties is recommended for cultivation in Gujarat.

Farmers respond to agronomic adjustments once they are convinced that they will benefit from them. For example, when long duration and high yielding varieties PBW 343 and K 9107 were made available in 1996/97 and 1997/98, farmers perceived that sowing these varieties early would improve their performance. In the first year, farmers planted 82% of trials by 24 December, according to their usual practice, however this became progressively earlier. Eighty percent of trials were planted by 17 December in 1997/98, by 6 December in 1998/99, and by 24 November in 2000/01. (There was no data for 1999/2000.)

Farmers' adoption of varieties

The adoption of a variety by a farmer reflects a decision-making process that takes all of the varietal traits into consideration. Unlike formal trials, there is no limit on the number of traits involved, and no limit on how those traits are traded off. In 1998/99, participating farmers in Panchmaudia Village (Lunawada, Gujarat) adopted PVS varieties such as PBW 226, PBW 343, and Raj 3077 offered in 1996/97, and varieties K 9107, HD 2501 and Kundan offered in 1997/98 (Figure 10). This is third-season adoption, a much better indicator of acceptance than second-season adoption, which tends to be combined with experimentation.

Most importantly, among the participants of the PVS trials, resource-poor farmers were no more averse to taking risks in testing and adopting new varieties than wealthier farmers (Figure 11). This was due to the initial supply of free seed which eliminated differences in access to the new varieties.

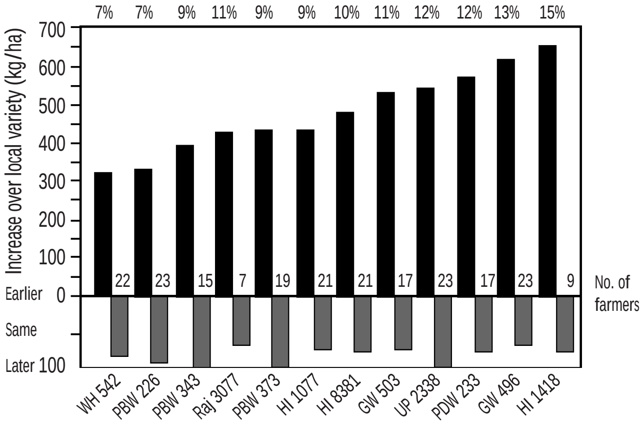


Figure 9. Twelve wheat varieties yielded more than predominant variety Lok 1 in participatory trials in Lunawada, Gujarat, 1996/97. Of these test varieties, only GW 496 and GW 503 are recommended in Gujarat. Flowering characteristics are calculated as an average of the scores given by farmers where 0 = earlier than Lok 1, 50 = equal to Lok 1, and 100 = later than Lok 1.

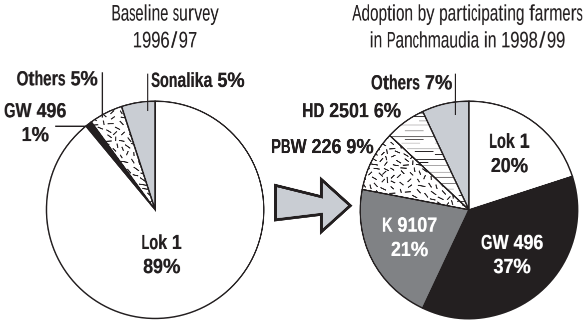


Figure 10. Adoption of wheat varieties following participatory varietal selection in Panchmaudia Village, Lunawada, Gujarat, India.

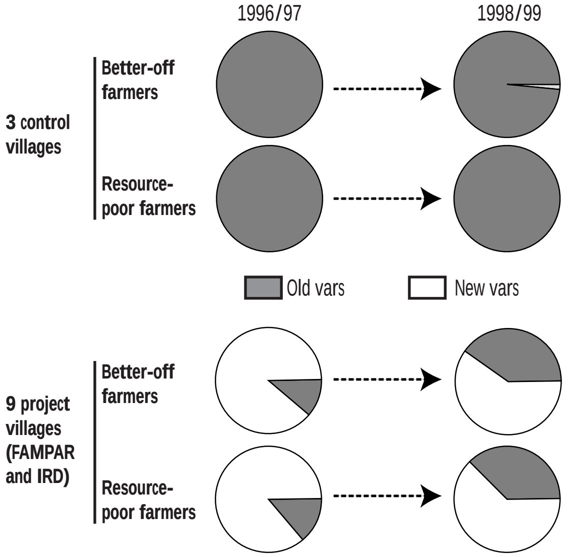


Figure 11. Extent of third-season adoption of new wheat varieties offered in a participatory varietal selection program by participating

The preferred varieties were transferred from farmer to farmer, until drought in 1999/2000 reversed this trend. Despite the duration and severity of the drought, farmers with unlimited irrigation facilities continued to grow K 9107 and PBW 343 in 2000/01 for their high yields.

Comparison of FAMPAR and IRD

The adoption of new varieties was estimated in six FAMPAR villages and three IRD villages in 1997/98. The agreement between the two methods was very good, whether estimations were based on the percentage of farmers or percentage area (Figure 12). Given this agreement, it can be concluded that IRD is a much more cost-effective method, though this does not mean that only IRD should be used. A balance of intensive FAMPAR and extensive IRD will give the optimal balance between detailed research data and extension research.

Discussion and Conclusions

Plant breeding programs aimed at favorable agricultural environments have to target a vast number of different environmental conditions present in farmers' fields, including a wide range of possible planting dates in irrigated systems, varying availability of irrigation water, and different socioeconomic requirements for the balance between harvesting straw and grain. An analysis of multilocational trials for wheat in India showed that they failed to adequately represent the environmental diversity occurring there. However, all multilocational-testing systems are constrained by costs and cannot represent the total diversity present in farmers' fields without becoming extremely expensive. A cost-effective alternative to increasing the number of formal trial sites is to encourage farmers to become more actively involved in varietal testing.

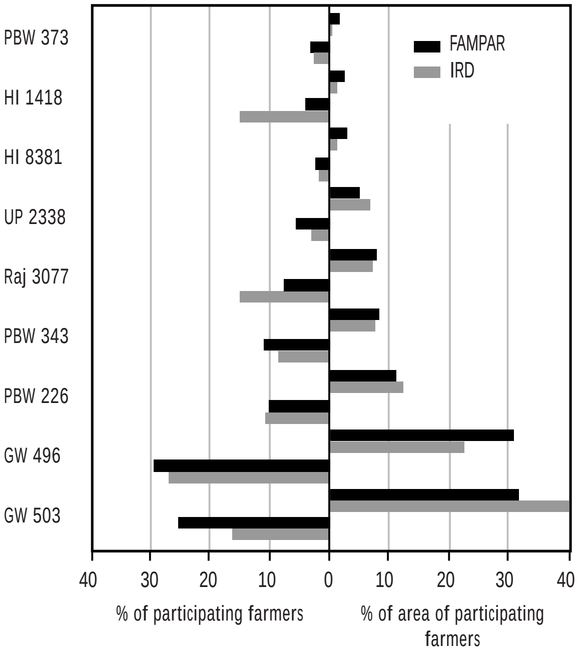


Figure 12. Adoption of new wheat varieties following participatory varietal selection by farmer managed participatory research (FAMPAR) (six villages) and informal research and development (IRD) (three villages), 1997/98. Varieties were grown from farm-saved seed from the 1996/97 harvest.

Although formal multilocational trials systems poorly represent their target environments, many varieties from these trials have been selected, officially released, and enthusiastically adopted by farmers. This success, based on the criterion that farmers grow modern varieties, is due to the broad adaptation of most advanced cultivars, which prevents significant genotype x environment interaction across many of the target environments. Most centralized breeding programs select for wide adaptation during the breeding process, and all programs select for wide adaptation by multilocational testing.

However, based on other criteria—that farmers grow old cultivars and only a small proportion of new cultivars is adopted—this system is less successful because it has limited varietal diversity. Therefore there is scope for improvement—one example being an increase in the number of testing sites to better cover the diversity of target environments. Recognizing these problems, many private-sector breeding companies in the US and Europe carry out numerous "strip trials" with farmers (so called because farmers grow the varieties in strips across the length of their fields). Unfortunately, the bulk of this work has been poorly documented by the private sector, which has priorities higher than publishing research methods. This lack of published data makes it more difficult to argue for an extensive system of farmer trials with practitioners of more formal trial systems from the public sector.

In our research on wheat in an HPPS in Gujarat, the PVS system was highly effective in rapidly identifying superior varieties and was easier to conduct in this environment than in marginal environments. The research benefits were more rapid because the spread of seed from farmer to farmer was facilitated by the much higher seed multiplication rates and increased yield stability found in more favorable environments. The PVS program identified varieties that farmers liked but were not officially recommended, increased the speed of adoption of a more recently released recommended variety (GW 496), and identified a less popular, recently released variety (GW 503). There was very good agreement between the results of intensive participatory methods and cheaper, extensive methods.

Seed availability was a major constraint, however, and sometimes it could not be obtained. When seed was found and farmers liked the variety, it was often difficult to procure more from sources outside the research project, as was the case for varieties Raj 3077 and Raj 3756.

The success of PVS is less consistent in favorable environments than in marginal areas. In HPPSs, success is reduced where recently released varieties have been extensively adopted; in marginal areas, official releases are rarely successful, so PVS test varieties usually compete with landraces or extremely old varieties. Our research in Gujarat coincided with the eventual adoption of GW 496, following its release in 1990. The PVS results from this region were a complete success against Lok 1, but only a qualified success against GW 496. Similarly, in the Punjab, PVS varieties competed with PBW 343 rather than HD 2329, which had been the predominant variety for many years. Hence, in the Punjab, in particular, where PBW 343 is still the highest yielding entry in multilocational trials, a PVS system that only tests released varieties is unlikely to be highly successful.

Participatory varietal selection can be used to select among advanced lines as well as released varieties. For example, currently there are several early-maturing trial entries with yields almost as high as PBW 343 that may be preferred by farmers for their earliness. This suggests that employing PVS earlier in the trials system could improve its efficiency. Indeed, PVS needs to form an integral part of public-sector trials in the same way that strip trials are an essential part of private-sector breeding efforts. This could be achieved by doing a participatory testing of entries simultaneously with the first (initial varietal trial) or second year (advanced varietal trial) of multilocational testing. The main constraint to routinely incorporating participatory approaches in varietal trials for favorable environments is not a lack of resources; it is the need to change people’s views on how a firmly established system of varietal testing should work.

Both PVS and strip trials increase the number of trial sites and their relevance to farmers early in the testing system. PVS is just one of several possible means of involving farmers to achieve this end but is more effective than on-farm trials, commonly used in formal trial systems in South Asia, which give farmers limited (often only one or two varieties) or no varietal choice. Furthermore, these varieties have been selected by scientists after three years of multilocational testing. The farmer’s involvement is too little (with too few varieties) and too late (after three years of formal trials).

Our research was conducted only on varieties that had been released in India, so the genetic variation available to the PVS program was limited. Since all of these released varieties have passed through the sieve of multilocational trials, there was a poor choice of the early-maturing varieties that farmers may have preferred. This constraint of limited genetic variation can be removed by employing participatory plant breeding (PPB). The success of PPB has been clearly demonstrated in DFID-supported research in marginal environments in rice (two released varieties: one in Nepal and one in eastern India) and maize (two released varieties: one in western India and one in eastern India). So far there are no well-documented examples of the success of participatory plant breeding for HPPSs, but there are promising results from rice research in its early stages in Nepal. These results are supported by the theory that genetic gains are higher when selection is conducted in the target environment; however, the scope of empirical evidence is limited (Simmonds 1984; Ceccarelli 1987; Ceccarelli and Granado 1989), and more research on the efficacy of selection conducted in the target environment is required and, preferably, quantification of increases over more centralized selection.

Although increased production in marginal environments is desirable, it will not provide the surplus grain required to feed expanding urban populations. If the increasing demand for food is to be met, most of the production increases will have to take place in more favorable agricultural environments where most of the world’s food is grown. A wider adoption of participatory varietal selection in favorable environments could give both immediate and long-term production increases that would improve food security and benefit the poor, who spend most of their income on food.

Acknowledgements

Thanks are due to Mr. B.S. Raghuwanshi and Mr. P.S. Sodhi (Project Manager) of Gramin Vikas Trust for the DFID-funded 'Western India Rainfed Farming Project' for their help in the conduct of this research. This document is an output from research projects (R6748, R7542 and R7323 Plant Sciences Research Programme) funded by DFID for the benefit of developing countries. The views expressed are not necessarily those of DFID.

References

Ceccarelli, S. 1987. Yield potential and drought tolerance of segregating barley populations in contrasting environments. *Euphytica* 36:265-274.

Ceccarelli, S., and S. Granado. 1989. Efficiency of empirical selection under stress conditions in barley. *Journal of Genetics and Breeding* 43:25-31.

Chambers, R. 1989. Reversal, institutions and change. In: R. Chambers, A. Pacey, and L.N. Thrupp (eds.), *Farmer First: Farmer Innovation and Agricultural Research*, pp. 181-195. London, UK: Intermediate Technology Publishing.

Danial, D.L., and D.L. Danial. 1995. Durable resistance in wheat to yellow rust in Kenya. In: *Breeding for Disease Resistance with Emphasis on Durability*, pp. 1-24. Proceedings of a Regional Workshop for Eastern, Central and Southern Africa. Wageningen, the Netherlands: Wageningen Agricultural University.

Goyal, S.N., A. Joshi, and J.R. Witcombe. 2001. Participatory crop improvement in maize in Gujarat, India. In: Proceedings of an International Symposium on Participatory Plant Breeding and Participatory Plant Genetic Resource Enhancement: An Exchange of Experience from South and South East Asia. CGIAR System Wide Programme on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation.

Halaswamy, B.H., B.T.S. Gowda, A. Seetharam, D.S. Virk, and J.R. Witcombe. 2001. Participatory varietal selection in finger millet. In: Proceedings of an International Symposium on Participatory Plant Breeding and Participatory Plant Genetic Resource Enhancement: An Exchange of Experience from South and South East Asia. CGIAR System Wide Programme on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation.

Joshi, K.D., and B.R. Sthapit. 1990. Informal research and development (IRD): A new approach to research and extension. LARC Discussion Paper 1990/4. Lumle Agricultural Research Centre, Pokhara, Nepal.

Joshi, A., and J.R. Witcombe. 1996. Farmer participatory crop improvement. II. Participatory varietal selection, a case study in India. *Experimental Agriculture* 32:461-477.

Joshi, A., and J.R. Witcombe. 1998. Farmer participatory approaches for varietal improvement. In: J.R. Witcombe, D.S. Virk, and J. Farrington (eds.), *Seeds of Choice. Making the most of new varieties for small farmer,* pp. 172-190. Oxford IBH, New Delhi, and Intermediate Technology Publications, London.

Kumar, A., D.K. Ganguli, S.C. Prasad, J.S. Gangwar, D.S. Virk, and J.R. Witcombe. 2001a. Participatory plant breeding in maize for the Chhotanagpur plateau of eastern India. In: Proceedings of an International Symposium on Participatory Plant Breeding and Participatory Plant Genetic Resource Enhancement: An Exchange of Experience from South and South East Asia. CGIAR System Wide Programme on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation.

Kumar, R., D.N. Singh, S.C. Prasad, J.S. Gangwar, D.S. Virk, and J.R. Witcombe. 2001b. Participatory plant breeding in rice in eastern India. In: Proceedings of an International Symposium on Participatory Plant Breeding and Participatory Plant Genetic Resource Enhancement: An Exchange of Experience from South and South East Asia. CGIAR System Wide Programme on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation.

Mamluk, O.F., M.P. Haware, K.M. Makkouk, and S.B. Hanoumik. 1989. Occurrence, losses and control of important cereal and food legume diseases in West Asia and North Africa. In: *Tropical Agricultural Research Series, 1989*. No. 22, pp. 131-140.

Packwood, A.J., D.S. Virk, and J.R. Witcombe. 1998. Trial testing sites in All India Co-ordinated Projects—How well do they represent agro-ecological zones and farmers' fields? In: J.R. Witcombe, D.S. Virk, and J. Farrington (eds.), *Seeds of choice: Making the most of new varieties for small farmers*, pp. 7-26. Oxford IBH, New Delhi, and Intermediate Technology Publications, London.

Rana, B.S., S.L. Kaul, C. Appaji, Parbhakar, N.S. Kalyanshetty, B.V.S. Reddy, J.R. Witcombe, and D.S. Virk. 2001. Participatory varietal selection in *Rabi* sorghum in India. In: Proceedings of an International Symposium on Participatory Plant Breeding and Participatory Plant Genetic Resource Enhancement: An Exchange of Experience from South and South East Asia. CGIAR System Wide Programme on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation.

Simmonds, N.W. 1984. Decentralised selection. *Sugarcane* 6:8-10.

Snapp, S. 1999. Mother and baby trials: a novel trial design being tried out in Malawi. In: TARGET. The Newsletter of the Soil Fertility Research Network for Maize-Based Cropping Systems in Malawi and Zimbabwe. January 1999. Zimbabwe: CIMMYT.

Sthapit, B.R., K.D. Joshi, and J.R. Witcombe. 1996. Farmer participatory crop improvement. III. Participatory plant breeding, a case study of rice in Nepal. *Experimental Agriculture* 32:479-496.

Witcombe, J.R. 1999. Do farmer-participatory methods apply more to high potential areas than to marginal ones? *Outlook on Agriculture* 28(1):43-49.

Witcombe, J.R., and A. Joshi. 1995. The impact of farmer participatory research on bio-diversity of crops. In: L. Sperling and M.L. Loevinsohn (eds.), *Using diversity-enhancing and maintaining genetic resources on-farm*, pp. 87-101. International Development Centre.

Witcombe, J.R., and A. Joshi. 1996. Farmer participatory approaches for varietal breeding and selection and linkages to the formal sector. In: P. Eyzaguirre and M. Iwanaga (eds.), *Participatory Plant Breeding,* pp. 57-65. Rome, Italy: International Plant Genetic Resources Institute (IPGRI).

Witcombe, J.R., A.J. Packwood, A.G.B. Raj, and D.S. Virk. 1998a. The extent and rate of adoption of modern cultivars in India. In: J.R. Witcombe, D.S. Virk, and J. Farrington (eds.), *Seeds of Choice: Making the Most of New Varieties for Small Farmers*, pp. 53-58. Oxford IBH, New Delhi, and Intermediate Technology Publications, London.

Witcombe, J.R., D.S. Virk, and A.G.B. Raj. 1998b. Resource allocation and efficiency of the varietal testing system. In: J.R. Witcombe, D.S. Virk, and J. Farrington (eds.), *Seeds of Choice: Making the Most of New Varieties for Small Farmers*, pp. 135-142. Oxford IBH, New Delhi, and Intermediate Technology Publications, London.

International Agricultural Research as a Global Public Good: A Review of Literature, Issues, and the CGIAR Experience

D.G. Dalrymple

Economic growth itself has been largely determined by the capacity to use new technologies, whether developed at home or abroad.
Nathan Rosenberg (1982)

The common or collective benefits provided by government are usually called "public goods" by economists, and the concept of public goods is one of the oldest and most important ideas in the study of public finance.
Mancur Olson (1971)

Introduction

The proper use of public funds has been a subject of public debate since Adam Smith (2000:779) wrote *The Wealth of Nations* in 1776.[1] It continues with, if anything, increased fervor. Recently, for example, *The Economist* noted the experiences of Tony Blair, Prime Minister of the United Kingdom, in this realm: while his emphasis has turned in favor of public spending and bringing about improvements in public service, the magazine cautions that in any second term, "the longer-term war will be about public spending."[2] Although Smith laid the basis for the concept of public goods, he did not use the term directly and it has taken a long time for the phrase to become an important focal point for public discussion.

Recently, this situation has started to change in the international arena, where increasing attention is being given to global public goods (GPGs) in both the United Nations Development Program (UNDP) and the World Bank. UNDP has sponsored a collection of papers on the subject (Kaul et al. 1999) and the World Bank will soon do the same (Gerard et al., forthcoming). The World Bank, moreover, has initiated a large study of the activities that it has sponsored that are of a GPG nature. Interest has also been stimulated by the writings of Jeffrey Sachs, who mentioned the role of agricultural research (Sachs 1999; 2000). Accordingly, the topic was the subject of some presentations (including one by Sachs) and discussions at the October 2000 meeting of the Consultative Group on International Agricultural Research (CGIAR) (CGIAR 2000a).[3]

These organizations and individuals have recognized that many of the important economic and social problems of the developing countries transcend national political boundaries and require a broader approach than is possible in individual country projects or loans. This point has, of course, been recognized for some time by those involved in the establishment and operation of the CGIAR, but now is taken much more seriously by a broader section of the development community.

---

[1] Smith stated famously, "The third and last duty of the sovereign or commonwealth is that of erecting and maintaining those public institutions and those public works, which, though they may be in the highest degree advantageous to a great society, are, however, of such a nature, that the profit could never repay the expense to any individual or small number of individuals, and for which it therefore cannot be expected that any individual or small number of individuals should erect or maintain."

[2] "Very flash, Gordon." *The Economist*, March 10, 2001, pp. 18.

[3] A transcript of the Sachs talk, "Globalization and the Poor", may be found in the "Transcript of Proceedings" in the CGIAR Secretariat library (October 23, pp. 194-216); no manuscript was submitted.

Within the CGIAR, the wheat breeding program operated by the International Maize and Wheat Improvement Center (CIMMYT) has been one of the longest running, most important, and most successful GPG activities to date. It, and counterpart activities in other international centers, may not have been placed in a GPG context by some of its participants or many others; hence, I thought that I might try to do so. I will start by outlining some of the major characteristics of GPGs, and show that they relate to or interact with international agricultural research.[4]

Evolution of Definitions

The term global public good appears to be fairly simple and intuitively appealing in contrast to some other terms that have their roots in economics, but it is not entirely self explanatory. And its definition has evolved and broadened over time. Systematic formulation of the theory began with Paul Samuelson in the mid 1950s and application to global challenges began in the 1960s (Kaul et al. 1999:xxiii; Samuelson 1954; 1955).

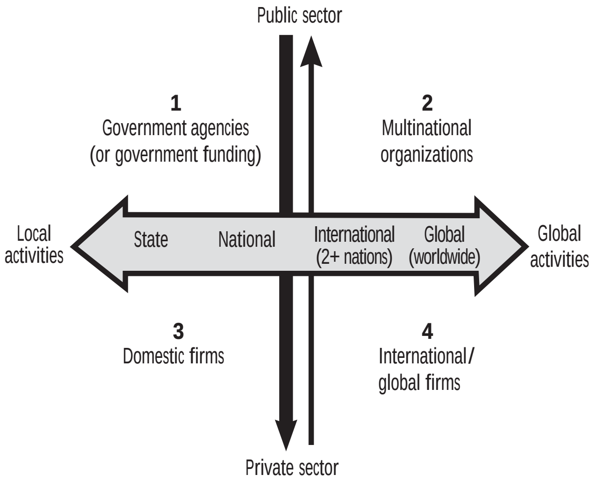


Figure 1. Relationship of public and private sectors of varying geographic scope in provision of science-based goods.

Note: It is assumed that each quadrant interacts with each other, although it is recognized that traditionally the private sector has drawn more from the public sector than vice versa. The degree to which this is true, however, is changing as the priate sector becomes more important in some areas of scientific research and has an increasing hold on intellectual property rights.

The basic concept of public goods was originally conceived of in terms of necessary goods and services that could not be expected to be provided by the private sector. They were *freely available to all* and, as in the case of knowledge, *would not be diminished by use.* As they were intended for use within a given set of political boundaries, it was natural that they should be paid for by the government of that political unit, or in combination with the next larger and lower unit (e.g., some package of national, state, and local government). Public funding was, however, often inadequate, leading to an undersupply problem.

Over time, it was increasingly recognized that many important social problems extended beyond the purview of one nation and that a broader approach was needed—in some cases involving neighboring nations, subregions, regions, and finally the global or worldwide community.[5] In some cases, global public organizations were established, such as the Food and Agriculture Organization of the United Nations (FAO), but they generally had little involvement in research and development. Current interest is more strongly driven by health and environmental problems that have more of a science and technology base and often require further research and development. This has led to more involvement with the private sector. These multiple relationships are illustrated in Figure 1.

In formal terms, any goods which are not purely public or private are considered impure public goods (Cornes and Sandler 1996). But as David has written, "The term 'public good' does not imply that such commodities cannot be privately supplied, nor does it mean that the government must produce it." Indeed, he continues, "A well-functioning science and technology system requires getting the correct balance and maintaining active communications between these two quite different types of organizations because the special capabilities of each are required to sustain the pace of economic innovation and economic growth over the longer term." Moreover, he sees both types as

---

[4] CIMMYT economists have made significant contributions to this subject. See Winkelmann (1994). The work of the Economics Program under the leadership of Derek Byerlee will be cited extensively later in this paper.

[5] This expansion involved a steadily greater degree of internationalization and leads to the need to draw a seemingly small but important semantic distinction. In formal definitional terms, "international" may include as few as two nations while "global" is defined as being worldwide (*Webster's*). Thus there can be a significant difference in geographic inclusiveness. The two words, however, are often used interchangeably. Within the CGIAR system, international clearly prevails over global as a title, though its core-funded activities are a combination of international public goods (IPGs) involving many nations and GPGs (restricted or targeted projects generally involve fewer nations but still usually fall in the the IPG category).

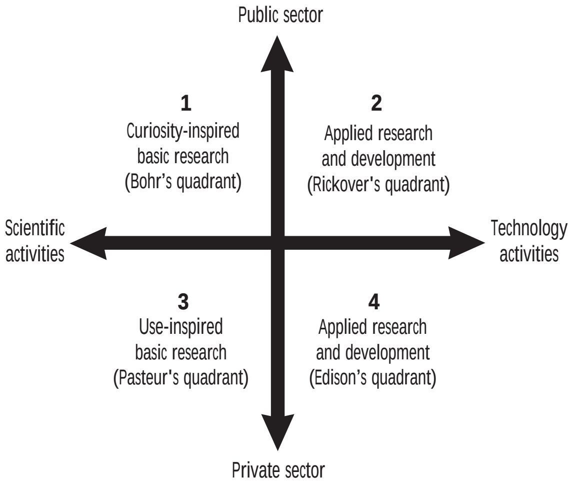


Figure 2. Quadrant model of organization of public and private scientific research and technology development.

Source: Adapted from Ruttan (2001:537) (in turn adapted by Ruttan from two other sources).

Note: The principal changes from the Ruttan variant of the model involved: 1) repositioning the quadrants, 2) modification of some titles and labels, and 3) elimination of arrows showing the interaction between quadrants (to simplify the graphics).

being necessary to permit society to respond to a variety of problems—“challenges whose solution will call for the creation of more effective modes of international scientific and engineering collaboration” (David 2001). The generalized relationships between these groups are depicted in Figure 2.

Thus it is easy to see how public international agricultural (and associated natural resource) research (Dalrymple 2000:15-37) fits readily into an international or global public goods framework. According to the GPG classification system developed by Sandler, it would fall in the “best shot” category. This group involves a *concerted approach* depending on *focused technical expertise*, which benefits from *economies of scale*, and which is organized for production and delivery in a “*mission-oriented manner*” (World Bank 2001).[6] This is a remarkably apt characterization of the CGIAR System.

Organizational and Funding Issues

Global public goods (or international public goods relevant to many nations) of the type produced by the CGIAR System are, as depicted in Figure 1, at one end of the public goods spectrum and fit into quadrant 2. They also fit into quadrant 2 (applied research and development) of Figure 2. GPGs should, by definition, be of value to a very large number of people around the developing world. But they are also beyond the reach of many international organizations that have been set up for other purposes and generally have a fairly limited science / technology and research / development component. They may also be beyond the reach of many individual bilateral assistance agencies. Thus, the provision of GPGs of this nature represents a significant organizational and funding challenge.

The CGIAR was particularly fortunate in this respect because it built on the early success of two research centers, IRRI (the International Rice Research Institute) and CIMMYT, which were established by the Rockefeller and Ford Foundations. The foundations had a long history of experience in science and agricultural research (Rockefeller) and international agricultural development (Ford). Moreover, the time was ripe: it was a period of concern about world food shortage and a time when many bilateral donors had a strong interest in agriculture and funding to back up this interest. The establishment of the CGIAR benefited from excellent leadership, in part provided by the World Bank, the two foundations, the co-sponsors (FAO and UNDP), and some of the donor nations. As a result, the process took only about two years (from 1969 to 1971). An independent Technical Advisory Committee (TAC) was included from the start (see Baum 1986).[7] In addition, bilateral donors were providing strong support for the development of national research institutions that complemented the global effort of the centers. It was a most fortunate alignment of circumstances, organizations, and structure which would be very difficult—impossible, I would say—to repeat.

While the term GPG was not mentioned in the early years of the CGIAR, the concept did play a role in the thinking of TAC[8] and recently has moved into the lexicon and funding programs of the donor community.

---

[6] For further discussion of this category see Kanbur et al. (1999) and Kaul et al. (1999:487-488).

[7] By comparison, it reportedly took about 80 years to create the World Health Organization and get it running, despite the clear benefits to all countries from controlling the spread of disease (Kindelberger 1986).

[8] A report by TAC (1992) stated that, “In planning and determining priorities in international research, consideration will be given to the maximization of spillover effects that will result from research activities. Over the longer term, supranational rationalization of a good deal of research is a logical goal, with significant savings for participating, partner nations.”

The editors of a recent study sponsored by UNDP estimated that "…one aid dollar in four supports global public goods rather than just the purely national concerns of poor countries" (Kaul et al. 1999:xxxiii). And some more detailed data on funding of this broad class of activities has recently been compiled by the World Bank (World Bank 2001:116-119).

The World Bank report distinguishes between *core* activities designed to produce international public goods (IPGs) and *complementary* activities (concessional loans) which help countries to consume them, in the process creating valuable national public goods (NPGs). Core activities include both 1) global-regional programs with a transnational or multi-country interest in mind, and 2) country-based activities that generate transnational benefits. International agricultural research is considered an example of the first core group. IPGs are divided into five categories: health, environment, knowledge, peace and security, and financial stability. Knowledge is basically composed of research activities and institutions; research is also a component of the health and environment sectors.

The study then examines trends in funding from the 1970s to the late 1990s for country-based official assistance (ODA) (grants and concessional loans). Overall, it appeared that a growing proportion of development assistance was allocated to IPGs. In the late 1990s, core represented about 3.5% of the total and concessional about 15%. In the case of core programs, which represented about US$ 2 billion in the late 1990s, funding for health, the environment, and peace keeping[9] grew significantly while funding for knowledge generation and dissemination stagnated. In the case of concessional programs, funding totaled about US$ 8 billion: health was the most important and increased substantially; knowledge was second but declined during the 1990s. The report found that spending on knowledge has been "sluggish, with complementary spending on educational facilities and training severely curtailed." And, more specifically, "core spending on agricultural and livestock research has been stagnant."[10]

While the overall increase in funding for IPG / GPG is heartening, the data clearly indicate that the growth has not taken place in agriculture—which appears to face substantial competition in a number of categories, but particularly from health.

Characteristics of Research

Research is clearly an omnipresent component of the World Bank classification of IPG / GPG. Yet it is not clear how research is defined. Research may take many forms, ranging from fairly basic on one hand to quite applied on the other, with the line between research and development rather fuzzy. Science and technology are basic components and range from the physical to the biological to the social sciences.

It might be argued that science, by its basic nature as a form of knowledge, is more likely to be inherently a global public good than is technology, which is often the adaptation of scientific knowledge to particular circumstances and needs. Thus scientific discovery may have a greater degree of "spillover" than technology. Also, science may be more amenable to centralization than technology.[11] In the case of technology, and especially in the case of agriculture, it is necessary to have adequate adaptive research and development capacity in recipient nations.[12]

This leads us into two key questions: 1) the economics of size in research and 2) the factors influencing spillovers and spillins. The first area appears to have received relatively little study, and early work was

---

[9] It should be noted that Adam Smith's original list of public activities that should be funded by the state included 1) defense, 2) justice, and 3) public works and institutions (Smith 2000:747-878). Some current activities presently included in the public goods concept, such as cultural heritage, might seem to go well beyond this grouping, but not necessarily beyond a broad reading of his original concept (fn. 1).

[10] Two further pieces of information would be useful, if available: 1) a summary comparison of research data in all categories; and 2) specific data for global-regional programs. In the case of the latter, it is noted elsewhere in the report that they "attracted only limited attention."

[11] In addition, "modern science has made inventions more universal…by providing insight into the mechanism behind the invention" (Mokyr 1990).

[12] Rosenberg (1982:246-249; 258) has commented on this issue in a general historical context and it has been proven many times over in agriculture. More recently, Evenson has noted that every important crop genetic improvement program in developing countries required 20 years of work before success was achieved (e-mail, March 12, 2001. See fn. 30 for further detail on the Evenson study).

largely based simply on size of the research enterprise and the firm.[13] The second has been the subject of somewhat greater attention. Both are interrelated. Some particularly useful work on both has been sponsored by, or done by, CIMMYT economists (Maredia and Byerlee 1999; Fuglie and Schimmelpfenning 2000).

Byerlee and Traxler (2000) suggest that economies of size in research are more likely to be found in areas such as chemistry, molecular biology, and genomics, which require a substantial fixed investment in laboratory infrastructure. On the other hand they are likely to be lowest for crop and resource management, which are more likely to involve field work and adaptation to local environmental conditions (Byerlee and Traxler 2001).[14] Traditional plant breeding and some forms of livestock research might fall in between. More generally, research with substantial economies of scale is more likely to be accompanied by the potential for higher spillovers than research with lower economies of scale. In fact, it may have to have high spillovers to pay for itself in a social sense. These relationships are depicted graphically in Figure 3.

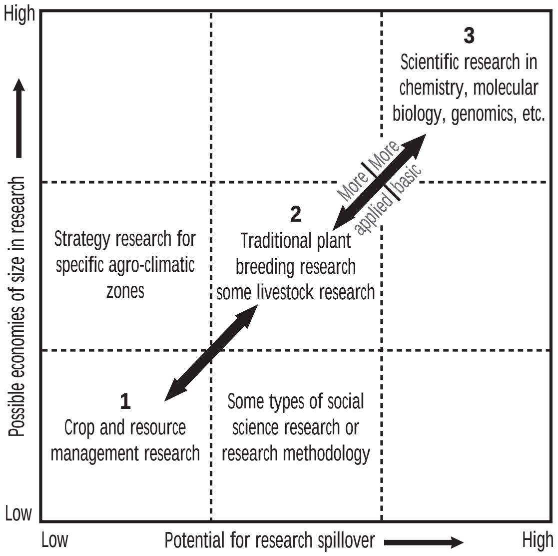


Figure 3. Illustrative categorization of agricultural research activities in terms of possible economies of size and spillover.

Source: Adapted from Byerlee and Traxler (2001).

Note: The principal changes in adaptation have been: 1) inclusion of an additional row and column which allow the insertion of a new box 2; 2) rephrasing of the remaining boxes and the axes; and 3) providing for a two-way relationship between the diagonal boxes and distinguishing between more basic and more applied research. Biotechnology, depending on the degree to which it is basic or applied, might fall between boxes 2 and 3 or in box 3. Some forms of strategic research for agroclimatic zones might fall in box 2.

Byerlee and Traxler (2001) go on to consider a third important factor: market size, or economies of scale in technology use. This might be conceptually viewed as a variant of the two previous variables, or as a third dimension. In its simplest form, it means that the more widely a technology is adopted, the more significant the payoff from the research. This has clearly been the case for public breeding programs for wheat and rice, which tend to be raised in similar agroecological zones (often irrigated) over many areas of the world. And it has been facilitated where the centers breed for broad adaptability. Where this is the case, market size can become the dominant determinant of research efficiency.

But there is more to the process. This comes about when it is possible to develop a feedback loop with users of the technology at the country level. The combination of being able to tap into advanced research in developed countries, to draw on centralized genebanks at headquarters, and interact with a large group of collaborators at the country level adds a further and very significant note of efficiency for the whole process. As Anderson (1998) has noted, the importance of international agricultural research derives in part from "the productivity-boosting collegiality and cost-cutting benefits thereof of sharing information and materials."[15] These complementary two-way relationships between the contributors to the public goods sector (as reflected in the horizontal relationships suggested in Figure 1) may be of major importance in stimulating research productivity.

---

[13] Schumpeter (1942) argued that there are increasing returns in R&D both with respect to size of research establishment and firm, but this is difficult to prove and it has been argued that the tests employed through the early 1970s were inappropriate (Fisher and Temin 1973). It would be useful to know of more recent studies relating to industry.

[14] On the other hand, variable costs (such as logistics) for some forms of fieldwork–such as multilocation trials or systems research–can be quite high.

[15] It has also been suggested that this process might help identify problems whose solution would help expand the market.

Public-Private-Philanthropic Relationships

The primary characteristics of science and research influence the nature of relationships between the public and private sectors. This is perhaps most immediately seen in the case of intellectual property rights (IPR). It has been suggested that scientific research (and to some extent technological research) is inherently a public good. Hence, private firms engaging in such research and wishing to keep it from becoming a public good, at least for a while, make use of IPR. The public sector may also make use of IPR protection, but often, paradoxically, for a different reason—to protect the good in order to keep it in the public sector. There may be tension between the public and private sectors in these respects, but there also may be cooperative arrangements such as licensing and others to be noted (John Barton, Stanford University Law School, personal communication).

The two sectors may have some other similarities. Large, multilateral firms, for instance, have the financial resources to carry our centralized research that is verified and adapted in field trials elsewhere. The ability to market in more than one country is every bit as important for the private sector (for further information see Pray and Fuglie, forthcoming). Hence the combination of these and other factors may sometimes lead the public and private sectors into converging paths.

Both sectors, however, may face somewhat different combinations of problems in achieving these aims. The public sector increasingly has difficulties with funding and IPR. The private sector may not have as many complications in these areas, but may face other formal or informal barriers to entry in some nations (see, for example, Gisselquist and Grether 2000; Tripp and Pal 2001). In this case, the public system may benefit from its contacts with national systems and be able to transcend national boundaries. The private sector may reach more into the commercial sector of the farming community and the public sector into the lower income portion. Both may face complications associated with government regulations and / or public resistance to genetic engineering, but so far these have been greater problems for the private sector, in part because of the nature of its products. However, the prospect that some public goods might become "regulated public goods" is in sight (Sam Dryden, CGIAR Private Sector Committee, personal communication).

In the best of circumstances, the two groups can complement each other in important ways. Although the private sector is constrained by the need to make profits, and hence looks more to developed than developing countries, a degree of market segmentation may be possible. This can mean continuing, as usual, in the developed countries but taking a different policy towards countries where there is little prospect for a significant commercial market. The latter approach is, of course, sometimes encouraged by the opportunities for improving public relations, a matter or particular importance for biotechnology firms. These admirable gestures, however, cannot be counted on in advance, may have some strings attached, and may require further development and testing by public research organizations (golden rice is a case in point).[16] [17]

There is one other important category of participants in the research process: foundations and private philanthropy. These groups have made substantial increases in their overall funding for research.[18] Rockefeller continues its interest in biological research, and has played a vital role. Ford has largely moved to the social science arena. New actors have come on the scene—particularly the Gates Foundation—but so far have shown little interest in research in agriculture and natural resources. Still, they have come close, especially the immense investment made by the Gates Foundation in health. The recent donor of US$ 100 million to Johns Hopkins University for research on malaria wanted to "…make a real difference in the world"[19]—a sentiment which may have broader appeal.

---

[16] For a recent example, see the discussion about the unraveling of the rice genome by a private firm: Pollack (2001a); Regaldo (2001). A more general account of challenges faced in interaction is provided in Pollack (2001b).

[17] I have attempted to summarize the major public-private relationships discussed in this and the previous paragraph in graphic form in the Annex. A market context is utilized. The resulting diagram is more complex than I would like (and could be even more so), but may be of interest to those who are partial to graphic presentation and may stimulate some further ideas.

[18] "Philanthropy's rising tide lifts science." *Science*, October 8, 1999, Vol. 286, pp. 214-233.

[19] "Johns Hopkins lands gift of $100 million." *The Washington Post*, May 7, 2001, pp. A1.

Some Policy Questions for the CGIAR

Operating an international organization devoted to the production of IPGs or GPGs is a very complex process. It necessarily involves some complicated policy issues and questions. Although the CGIAR is, in many ways, a prime example of an international or global public goods provider, the system has not always acted in a way to suggest that it was fully aware of this. This is often because, as a public organization, it either tries to respond to emerging needs or is more directly influenced by the views of its donors or advisors. Sometimes, as might be expected, these views differ. At other times the group has been influenced by current styles, fancies, and fads. The latter are generally well intentioned, but seldom are measured in terms of their possible effect—positive or negative—on the ability of the system to produce GPGs. Some may be better suited for regional or local action or humanitarian programs than for international research and development centers. Often the R&D programs can make a substantial contribution, but it may not be in a very obvious or immediate way

Examples of indirect effects

Consider two categories of examples from the past decade that illustrate the geographic dimension and the role of indirect benefits. In the case of *natural resources*, the CGIAR has taken some obvious moves to expand its work in this area, most notably by setting up or adopting four centers that deal directly with these issues (CIFOR, ICRAF, IWMI, and ICLARM).[20] Other centers deal with some of these issues as components of their programs. This type of work is generally long-term and regional in nature and is fairly difficult to assess the payoff in terms of global benefits.

One example is the adoption of the concept of an ecoregional approach to natural resources. In theory this makes sense: it should be possible to develop technologies that would spill over from one ecoregional zone to another (see McCalla 1994). Some ecoregional projects were initiated about a decade ago, and eight system-wide programs were reviewed by TAC in the late 1990s. It has always been difficult to determine how much spillover from zone to zone has been achieved. Significantly, one of the recommendations of the TAC study is that research should be organized around “major problems…that are of international relevance” and that “…it should provide for its progress to be measured against specific performance indicators” (Henzell et al. 2000). What is not mentioned in the TAC report is that, in some cases, these programs came with a stiff opportunity cost within the center—in some cases breeding programs, which generally rank well in terms of spillovers, were shrunk to pay for them.[21]

This leads to the question of the effect of more general productivity-enhancing technological change in agriculture on natural resources. Both negative and positive effects could be envisaged. A recent review of 140 economic studies of deforestation suggested that the immediate effect of technological change was indeterminate and that the indirect effects generally were positive (they reduced deforestation) (Angelsen and Kaimowitz 1999; see Angelsen and Kaimowitz 2001). Another approach is to estimate the effect of increasing crop productivity on reducing the land area needed to produce these crops and thus saving marginal and forested land from the plow. Recent reviews suggest significant land saving figures in the range of 200 million hectares (nearly 500 million acres) (see, for example, Victor and Ausubel 2000; Nelson and Maredia 2000).[22]

More recently, *poverty alleviation* has come to the fore and somewhat the same pattern has emerged: an admirable goal with global potential but one that has tended to be looked at in subregional or local terms—tasks that should be carried out by national or regional programs. These could divert the CGIAR away from its comparative advantages in terms of economies of size in research, spillover potential, and economies of market size. Instead, it could, in some instances, be diverted into gap filling arising from shortfalls in national programs. And, as in the case of natural resources, the CGIAR is already making enormous but under-appreciated contributions to poverty alleviation

---

[20] CIFOR = Center for International Forestry Research (Indonesia); ICRAF = International Centre for Research in Agroforestry (Kenya); IWMI = International Water Management Institute (Sri Lanka); ICLARM = International Center for Living Aquatic Resource Management (Malaysia).

[21] For example, from 1992/93 to 1998/99, the proportion of the overall CGIAR budget spent on germplasm enhancement and breeding dropped from 25.25% to 17.70% (CGIAR 1994; 1999).

[22] There may be some offsetting negative consequences, such as salinization, but it is difficult to sort out the specific impacts of agricultural research from the effects of more general intensification (Maredia and Pingali 2001).

by increasing productivity. In this case, the result is lower food prices for staple food crops and is especially important for the poor who spend a large portion of their meager incomes on food. There are also positive spin-off economic effects for early adopters of new technologies, for local employment, and for local communities.

A recent report on poverty prepared under the auspices of the International Fund for Agricultural Development (IFAD) states that, "The anti-poverty record of the Green Revolution was excellent." It goes on, however, to note that, "From 1980 the CGIAR moved away from breeding for yield, especially yield potential, towards such issues as environment, gender and distribution, and towards less promising crops and areas. Yet this has probably helped to reduce the growth in the yield of staples even for lead areas of the Green Revolution, and has been ineffective in delivering growth to some of the areas where the poor are increasingly concentrated." "*Research must now be refocused on yield*" (IFAD 2001).

Funding considerations

Other actions can have unintended effects. One is a gradual but accelerating shift from unrestricted or institutional (U/I) financial support to restricted or targeted (R/T) support. U/I funding supports the basic longer-term research operations of the centers, including genebanks. The R/T category is usually for more specific programs or projects that may be shorter term, more localized, and more applied in nature. Although the level of institutional (U/I) funding held relatively steady in dollar terms from 1994 to 1998, it declined rather sharply in 1999 and again in 2000 (a drop of US$ 41.8 million or 20.3% over the two years). Furthermore, the U/I proportion of total funding dropped from 60.6% to 49.5% from l998 to 2000.[23] Preliminary data for 2001 suggest a further decline in the U/I proportion to 22.8%.[24]

If this process continues, it could—depending on the nature of the earmarking—result in a further decline in the funding which is readily available for the "heartland" research activities of the centers.[25] This in turn could well lead to an imbalance in the nature of the scientific work and lessen the global dimension. There are also less obvious transactions costs in terms of scientist time diverted to securing and reporting on restricted projects. [26] Since the special strength or comparative advantage of the CGIAR is at the global level, this shift is a matter of some concern and needs to be examined more closely.[27]

A somewhat different funding question relates to the degree to which the costs of research should be borne by the beneficiary countries. The problem here is that the primary intended beneficiaries are the poor nations who, by definition, are in the weakest position to pay. One early view in the CGIAR was that if these countries could muster some additional funding for research, they should spend it on their own national programs, which in turn would facilitate their ability to utilize GPGs. And though a number of developing countries have joined the CGIAR in recent years, generally with fairly modest contributions, their funding is almost always though the ministries of agriculture and they are represented by that agency; hence, a domestic opportunity cost may be involved.

---

[23] Compiled from CGIAR Financial Reports 1994 to 2000. By comparison, R/T funding increased by US$ 33.3 million from 1998 to 2000; similarly, the R/T proportion increased from 39.4% to 50.5%. It is sometimes difficult to draw a sharp line between the two categories, especially when the restrictions or targeting are very mild or essentially involve placing a country flag on an existing center program.

[24] "2001 Resource Monitoring Report", 19th Meeting of the CGIAR Finance Committee, CGIAR Secretariat, May 2001, Annex 1. Much of the drop represents a change in the classification of the contribution of a major donor that generally falls in the "country flag" category.

[25] Not all donor restrictions fall into this category. For example, USAID has a very light earmark, not in the R/T category, calling for 8% of its funding to be used for scientific collaboration with US universities (and through them with other US research institutions); the centers select the institutions and topics. The program has been very well received by both sides and appears to be quite successful. The French have long provided part of their contribution on an in-kind basis in the form of scientists stationed at the centers who have worked on advanced subjects such as apomixis. There may be other such cases.

[26] Some of these issues have been pursued at length in the debates about formula vs. competitive funding of domestic agricultural research in the US.

[27] The shift may partly reflect the desire of some donors for more specific program accountability. From the organizational point of view, the process might be viewed as a variant of 1) the fallacy of composition, whereby what seems good from an individual point of view may not be good for the group (see Hardin 1982), or 2) of the classic problem of maintaining the commons (see Hardin 1968). One might also wonder if is sometimes more of a risk-minimizing strategy (in terms of maintaining funding within the donor organization) than an effort to maximize social returns on investment.

On the other hand, it might be argued that some of the larger countries that have benefited the most from the CGIAR should contribute more, or that a greater portion of the cost of regional programs should be carried locally.[28] Another dimension is that the secondary benefits have accrued to at least some of the donor nations. This has been particularly true of the United States in the case of wheat and rice. The benefits to both sets of nations have recently been studied in some detail and will soon be published.[29]

Balancing large and small countries. While a broad market for public goods can play a major role in determining the public value of the good, this is not merely a matter of counting countries: the actual extent to which the good is adopted may be a telling statistic. A technology that is widely adopted in a large country such as China or India may have considerably more overall public good impact than a technology that is adopted in a larger number of smaller countries.

The related issue that has arisen in the CGIAR is the degree to which its centers should assist larger countries when they represent the bulk of production and have relatively well-developed national research programs (pigeon peas in India and sweet potatoes in China have been recurrent issues). In some cases this is an easy call, in others it is more difficult. The easy call arises when a center is able to make a specific contribution to a large country where it has the potential for widespread impact, at relatively low cost to the center. This happened recently when the International Potato Center (CIP) was able to assist China to adapt a simple and low cost procedure to eliminate viruses.[30] Moreover, in any large system in a poor country (as well as perhaps elsewhere) there are components that may not have been well supported, have been isolated from the mainstream of science, or have had limited access to GPGs and which could benefit from contact with an outside center (Hubert Zandstra, Director General, CIP, personal communication). The more difficult task is to assess the tradeoffs and to know where to draw the line.

Thus the reach to develop global public goods should not obscure the potential for equally large social gains through more limited efforts, in terms of number of countries, where the opportunity for a low-cost targeted contribution and / or widespread use is great. This dimension has received some attention by TAC but merits further thought (see CGIAR 2000b).

Public-private sector issues. There is some question about the degree to which the nature of the demand for agricultural GPGs may change because of 1) increased research activity by the private sector, 2) increased use of IPR, and 3) increased constraints on the international exchange of plant germplasm. Some suggest that the first factor may lessen the need (or demand) for genetic improvement by the public sector and that the second may complicate the public sector role and lessen its ability to provide (supply) GPGs. I have some doubts about how far the private sector will increase its research efforts unless hybrids begin to replace open-pollinated varieties to a significant extent, which doesn't seem very likely in the poor or most disadvantaged areas. Moreover, the public sector research programs are a source of parent materials that can be finished off and sold by local seed companies, many of which have limited research resources and capacity (Donald Duvick, email, April 17, 2001; see Dalrymple and Srivasta 1994:191-195). Increasing complications associated

---

[28] Smith (2000:788) wrote in 1776 that, "Even those public works which are of such a nature that they cannot afford the revenue for maintaining themselves, but of which the conveniency is nearly confined to some particular place or district, are always better maintained by a local or provincial revenue, under the management of a local and provincial administration, than by the general revenue of the state, of which the executive power must always have the management."

[29] The contribution of CGIAR crop varieties to developing nations has been analyzed in a comprehensive study headed by Prof. R.E. Evenson and involving the centers; it was sponsored by the TAC Standing Panel on Impact Assessment (SPIA). The most recent summary of the findings is provided in Evenson and Gollin (2001). A book by the same authors titled "Crop Genetic Improvement and Agricultural Development" will be published in late 2001 by CABI. A study by Philip Pardey, Julian Alston, and Connie-Cha Chang tentatively titled "Donor and Developing-Country Benefits From International Agricultural Research: A Double Dividend?" is nearing completion at the International Food Policy Research Institute and is expected to be published in late 2001 or early 2002.

[30] The process was initially adopted in two provinces on 800,000 ha (2 million acres) and could be extended to all regions in the country (Fuglie et al. 1999).

with the second and third points, or other forms of regulation brought about by health, safety, or environmental concerns, seem a more likely possibility over time. Further study would be desirable on both points.[31]

These factors could influence the balance of activities within the public sector. If the private sector moves more into genetic improvement in the future, should the public sector redirect more of its activities into crop management or natural resources which are less likely to draw private sector investment?[32] The problem for the CGIAR is that genetic improvement is the area in which the greatest GPG benefits can be demonstrated, in contrast with the other two areas where spillovers are more likely to be less (Figure 3) and the benefits are of an even longer-term nature and are much more difficult to measure. To continue to attract financial support, the CGIAR must be able to carry a sufficient array of activities that show demonstrable payoffs so that it can also carry other important programs where it is more difficult to demonstrate payoffs. In this sense, the public sector may not be so different from the private sector: both need to show a positive overall return on investment.

Proposal for global challenge programs. During International Centers Week in October 2000 (ICW00), the CGIAR decided to initiate a program of change. Two of the challenges outlined by the CGIAR Chair were "Maintaining science and research at the Centers at the highest levels" and "Strengthening the CGIAR's position as a producer of global public goods" (CGIAR 2000a).[33] A Change Design and Management Team (CDMT) was established and reported to the Mid-Term Meeting of the CGIAR in May 2001 (MTM01). The most important proposals in terms of these challenges were: 1) the establishment of Global Challenge Programs (GCPs) alongside the regular research activities of the Centers, and 2) the transformation of TAC into a Science Council. The basic idea was to facilitate the CGIAR's ability to take on major global challenges with a wider range of partners and widen the provision of scientific knowledge. "The impact, significance, and visibility of the CGIAR research agenda could be substantially elevated and the CGIAR's own meetings could increasingly focus on higher-level strategic issues…" (CGIAR 2001). Together, the two proposals could provide an important stimulus for science-based GPGs.

So far, so good, but there was a significant intersection with another outcome of ICW00: the approval of a recommendation to implement testing of a regional approach to research planning. While the original proposal called for a test in one region for a couple of years, it was evident even before MTM01 that the process had attained a great deal of momentum in many regions.[34] This development evidently did not go unnoticed by the CDMT team: GCPs were defined somewhat ambiguously as being "global, regional, or *subregional* in focus: the challenge should be global; the applications may well be *very local."* A subsequent communication from the Chairman to the membership dropped global from the title and referred to "Programs of global and regional importance…to resolve problems that have *local* applications and are of universal concern and importance." In the discussions at MTM01, there was significant support for the global dimension (especially in the case of genebanks), but some donors and other groups wanted the regional dimension raised in importance and others would have just as soon seen global

---

[31] The TAC Standing Committee on Priorities and Strategies (SCOPAS) has been considering initiating a study of "International Public Goods in an Era of Intellectual Property Rights". There is another, larger, dimension that might also be worthy of consideration. A study of the relative effects of public and private agricultural research in the US over the period from 1951 to 1983 found that private research had a larger impact in the short run and that public research had a larger impact in the longer run. "This suggests that a substitution of current R&D funding from public to private would increase productivity in the short term (0-10 years), but would tend to reduce the rate of progress in the longer term (beyond 15 years)" (Chavas et al. 1997). It is uncertain whether the same relationship would be found for a more recent period or in the future, given the changing nature of some research.

[32] Herdt (2001) has recently advocated that the CGIAR devote more attention to crop management research as well as to "…focusing plant breeding on developing specific traits valuable for regions and crops the private sector neglects." The CGIAR does considerable research for neglected areas and could do more if donors were willing to provide the funding.

[33] In his closing statement to the meeting, the CGIAR Chair said, "…the global public goods element must always be present."

[34] TAC perceived the relative role of the regional programs as follows: "In addition to regional perspectives, the CGIAR is pursuing objectives at the global level, which are not simply the aggregation of regional research needs." Thus "…within a region, the CGIAR will be pursuing objectives that are partly, and potentially largely, coincidental with national and regional objectives, but also partly distinct" (Janvry and Kassam 2001).

dropped.[35] Bottom-up participatory planning was also emphasized by some, although its role at the global level is somewhat obscure. The final brief summary of the meeting referred only to the "…implementation of Challenge Programs" (RAFI 2001:10).[36] *Sic transit gloria mundi?*

While the deliberations on the GCP program might be viewed as being diluted by regional or even local interests, and hamstrung by process proposals, there were also more global perspective. The group was provided excellent reports on the impact of past research programs (Evenson and Gollin 2001; Nelson and Maredia 2000; Maredia and Pingali 2001)[37] and massive global challenges (climate change, water, livestock diseases) that promise to expand in the future. Many participants expressed the need for additional resources for GCPs so that they would not have to be funded at the expense of existing core activities of the centers. And the group decided to transform TAC into a Science Council.

It was almost a tale of two different meetings. But it was illustrative of both the performance of, and promise for, GPGs as well as the perils of trying to obtain adequate public funding for them in the face of a host of other interests. Still, the elements for a greater global focus remain. It will, however, be a challenge to see that they are realized.

Concluding Remarks

The most important problems of our time are global in nature and need substantial involvement by the public sector. This situation will, if anything, increase in the future. The concept itself offers a generalized framework or umbrella for a fairly wide array of activities. This may facilitate communication and interaction between a reasonably diverse array of groups and programs. It also might provide a common point for communicating with a wider lay audience.

In retrospect, it is curious that all of this has taken so long to unfold. As Sachs (2000:212) stated in his speech to the CGIAR in October 2000, "…international public goods are not just a nice thing that we need to add on. They are the fundamental thing that's been missing from our template for the past 30 years." Yet they have been produced by the national public agricultural research systems for well over a hundred years. The global dimension is more recent, but the CGIAR centers have been at the heart of it. Still, the concept itself has not been given serious attention in the agricultural community until recently, and even then there might be some question as to how well it has taken root.

But while research of the sort sponsored by the CGIAR was one of the earliest and perhaps most successful efforts to produce GPGs, it is now most certainly not the only one. There is plenty of company, especially in the health field.[38] And though there are few institutional counterparts to the CGIAR, the most rapid increase in GPG funding of research has been in other areas. While agricultural research fits this classic concept, so do others. It is necessary to keep running to stay even.

Thus the CGIAR is in the paradoxical position of needing to catch up with some other players in an area in which it was a pioneer and is still a major player. Whether it will be able to do so is somewhat uncertain, both for internal and external reasons. Internal factors include a combination of stagnation in overall donor funding combined with a shift toward restricted funding. This shift is likely to lessen core or "upstream" research activities in favor of more localized development projects. External factors include increasing pressure from some groups to shift emphasis from global to regional or local goods and control.

Since most of the funding for the CGIAR is provided by international and national development

---

[35] One Civil Society organization, though tacitly accepting the concept of IPGs, would limit research activities almost entirely to the regional level: "If some IARCs offer goods that are important to more than one region, the other region(s) can contact the host region for access to its services" (CDMT Report 2001). A statement initiated by the NGO Committee of the CGIAR stated that "…the CGIAR needs to shift the governance and implementation of agricultural research and development activities to regional structures" (CSO 2001). The same group also proposed in a press statement that the CGIAR should "…evolve from commodity- to ecoregional-based institutes…"

[36] Email from Ian Johnson, CGIAR Chair, to CGIAR membership, May 4, 2001 "Report of Working Group 1, Challenge Programs", May 23, 2001 (verbal version); personal observations; and "Summary of Main Decisions", May 25, 2001, pp. 1.

[37] In addition, a preliminary report was presented on a set of country case studies on the effects of research on the alleviation of poverty and related matters conducted under the leadership of the International Food Policy Research Institute. The overall program of impact assessment is outlined in TAC (2001).

[38] "The cure hunters: dispatches from the frontiers of global medicine." *The New York Times,* May 6, 2001, Section 6.

organizations where even science for development may hold a tenuous position, these shifts, where they occur, are understandable and difficult to resist.[39] What the CGIAR really needs—at a time of unparalleled global scientific challenge and opportunity—is increasing support from more general sources of public scientific funding. These sources exist at the national level in many countries—such as the National Science Foundation or the National Institutes of Health in the United States—but not in comparable form at the international level.[40] However, even these programs do not provide institutional support, but are directed to competitive grants. Some further mechanism may be needed.

In these respects, then, the CGIAR shares the classic funding problem faced by any GPG activity. It has the capacity to make important contributions to the poorer members of society in developing nations, but is increasingly constrained by the level and conditions of existing funding. This is particularly frustrating because the overall level of research funding needed is not great (the current CGIAR budget is about US$ 330 million a year)—in 1995/96 it represented slightly less than 3% of all public funding for agricultural research in developing nations (Phil Pardey, IFPRI, personal communication, May 31, 2001).[41]

Given these circumstances, it is, I think, vital that the CGIAR System, and particularly its donors, give the concept of global public goods a more prominent place in its hierarchy of values, priorities, and programs. It is also vital that the system finds additional support and funding from organizations and donors that are more science-oriented than most development assistance agencies. The implementation of a Science Council could play a significant role in furthering both steps.

The CGIAR is an incredibly important and yet fragile enterprise. It wrestles with some of the world's most important problems as far as the poor and hungry are concerned. But its global public goods nature is at once its major strength and its major weakness. Maintaining both the CGIAR System and its essential GPG qualities is indeed a global challenge. Much depends on how well this challenge is met.

Acknowledgements

Helpful review comments on various earlier versions were provided by Jock Anderson, John Barton, Derek Byerlee, Sam Dryden, Donald Duvick, Robert Evenson, Curtis Farrar, Keith Fuglie, Amir Kassam, Michel Petit, Francisco Reifschneider, Meryl Williams, Donald Winkelmann, and Hubert Zandstra. The views expressed here are my own and not necessarily those of my employers.

References

Anderson, J.R. 1997. Development and the Agricultural Knowledge System: National and International Imperatives. Snyder Memorial Lecture, Purdue University, March 6, 1997, pp. 4.

Anderson, J.R. 1998. Selected policy issues in international agricultural research: on striving for international public goods in an era of donor fatigue. *World Development*, June 1998, Vol. 26, No. 6, pp. 1149.

Angelsen, A., and D. Kaimowitz. 1999. Reducing the causes of deforestation: lessons from economic models. *The World Bank Research Observer*, February 14 (1):82, 84-85, 87, 91.

Angelsen, A., and D. Kamowitz (eds.). 2001. *Agricultural Technologies and Tropical Deforestation*, CABI Publishing in association with the Center for International Forestry Research (CIFOR). 422 pp.

Baum, W.C. 1986. *Partners Against Hunger: The Consultative Group on International Agricultural Research*, pp. 27-53. Published for the CGIAR by the World Bank, Washington, DC.

Byerlee, D., and G. Traxler. 2001. The role of technology spillovers and economics of size in the efficient design of agricultural research systems. In: J.M. Alston, P.G. Pardey, and M.J. Taylor (eds.), *Agricultural Science Policy: Changing Global Agendas*, pp. 161-186. John Hopkins University Press.

CGIAR (Consultative Group on International Agricultural Research). 1994. *Financial Report*, Tables III-5&6. CGIAR Secretariat, World Bank.

---

[39] I reviewed, anonymously, the early experiences of the US government in international agricultural research in some detail in "Global Agricultural Research Organization" in *Supporting Papers: World Food and Nutrition Study*, Vol. V (Study Team 14, Agricultural Research Organization), National Academy of Sciences, Washington, DC, 1977, pp. 91-127. For some more recent comments, see Dalrymple (2000: 29-30).

[40] There is an International Foundation for Science [www.ifs.se/] but it has rather limited resources and is oriented to relatively small grants to developing country scientists. International center scientists may participate in grant proposals submitted by US groups and institutions to, say, NSF, and one IRRI scientist was recently part of such a proposal, but it is difficult to think of other examples (Ron Cantrell, Director General of IRRI, personal communication, May 24, 2001). One basic problem is that CGIAR centers are applied research organizations, whereas grants are usually for more advanced research. Still, the Centers may have something to bring to the table in the form of human or genetic resources or their locations and contacts in subtropical and tropical zones.

[41] The actual figure as currently tabulated is 2.8%. This represents a decline from a figure variously placed at about 5% in 1980 (TAC 1986) and 4.3% for the 1981-85 period (Gryseels and Anderson 1991). If comparisons were made in terms of numbers of researchers, the proportion would be much lower: Anderson has placed the CGIAR proportion at 0.4% (Anderson 1997).

CGIAR (Consultative Group on International Agricultural Research). 1999. *Financial Report*, pp. 47, Table III-2. CGIAR Secretariat, World Bank.

CGIAR (Consultative Group on International Agricultural Research). 2000a. *Summary of Proceedings and Decisions, CGIAR International Centers Week, Washington, D.C., October 23-27, 2000*, pp. 22-25, 48-49. CGIAR Secretariat, World Bank.

CGIAR (Consultative Group on International Agricultural Research). 2000b. Priorities and Strategies for Resource Allocation During 1998-2000 and Center Proposals and TAC Recommendations, pp. 30. TAC Secretariat, FAO, Rome.

CGIAR (Consultative Group on International Agricultural Research). 2001. Designing and managing change in the CGIAR: Report to the Mid-Term Meeting 2001. Change Design and Management Team, April 2001, pp. 6-7, 9-11.

Chavas, J.-P., M. Alber, and T.L. Cox. 1997. An analysis of the source and nature of technical change: the case of U.S. agriculture. *The Review of Economics and Statistics,* August 1997 79(3):482-493.

Cornes, R. and T. Sandler. 1996. *The Theory of Externalities, Public Goods, and Club Goods,* pp. 4. 2nd ed. Cambridge, UK: Cambridge University Press.

CSO (Civil Society Organizations). 2001. Declaration for Durham. May 2001.

Dalrymple, D.G. 2000. The role of public agricultural research in international development. In: *The Warren E. Kronstad Honorary Symposium, 1999*. Oregon State University, Extension Service Special Report 1017. [www.css.orst.edu/News/Publicat/Kronstad/Default.htm].

Dalrymple, D.G., and J.P. Srivastava. 1994. Transfer of plant cultivars: seeds, sectors and society In: J.R. Anderson (ed.), *Agricultural Technology: Policy Issues for the International Community*, pp. 191-195. CAB International.

David, P.A. 2001. The political economy of public science. In: H. Lawton Smith (ed.), *The Public Regulation of Science and Technology*. Routledge Press (in press).

Evenson, R.E. and D. Gollin. 2001. The Green Revolution at the end of the twentieth century. CGIAR MTM 2001, Doc. SDR/TAC:IAR/01/12, May 2, 2001. TAC Secretariat, Rome. 22 pp.

Evenson, R.E., and D. Gollin. Crop Genetic Improvement and Agricultural Development. CAB International (in press).

Fisher, F.M., and P. Temin. 1973. Returns to scale in research and development: what does the Schumpeterian hypothesis imply? *Journal of Political Economy* 81(1):56-70.

Fuglie, K.O., and D.E. Schimmelpfenning (eds.). 2000. *Public-Private Collaboration in Agricultural Research*, pp. 219-321. Iowa State University Press.

Fuglie, K.O., Liming Zhang, L.F. Salazar, and T.S. Walker. 1999. *Economic Impact of Virus-Free Sweetpotato Planting Material in Shandong Province, China.* CIP press release, February 13, 2001 [www.futureharvest.org].

Gerard, C.D., M. Ferroni, and A. Moda. (eds.). *Global Public Policies and Programs: Implications for Financing and Evaluation.* Proceedings of a Workshop Organized by UNDP and the World Bank, July 11-12, 2000. Washington, DC: World Bank, OED (forthcoming).

Gisselquist, D., and J.-M. Grether. 2000. An argument for reregulating the transfer of agricultural technologies to developing countries. *The World Bank Economic Review,* January 14(1):111-127.

Gryseels, G., and J.R. Anderson. 1991. International agricultural research. In: P.G. Pardey, J. Roseboom, and J.R. Anderson (eds.), *Agricultural Research Policy; International Quantitative Perspectives*, pp. 312. Cambridge, UK: Cambridge University Press.

Hardin, G. 1968. The tragedy of the commons. *Science*, December 13, 1968 162:1243-1248.

Hardin, R. 1982. *Collective Action*. Published for Resources for the Future by the Johns Hopkins University Press.

Henzell, T., D. Byerlee, and N. Mateo. 2000. *Review of Systemwide Programmes with an Ecoregional Approach*. TAC Secretariat, FAO, Rome. 38 pp.

Herdt, R.W. 2001. Changing Priorities for International Agricultural Research. Fifth Distinguished Economics Lecture, CIMMYT, Mexico. Mexico, D.F.:CIMMYT.

IFAD (International Fund for Agricultural Development). 2001. *Rural Poverty Report 2001: The Challenge of Ending Rural Poverty*, pp. 135-136. Oxford, UK: Oxford University Press.

Janvry, A. de, and A. Kassam. 2001. Regional approach to research [priority setting] for the CGIAR and its partners, pp. 16. CGIAR MTM:SDR/TAC:IAR/01/09. TAC Secretariat, FAO, Rome.

Kanbur, R., and T. Sandler, with K.M. Morrison. 1999. *The Future of Development Assistance: Common Pools and International Public Goods*. Overseas Development Council, Policy Essay No. 25, pp. 70-71. Washington, DC: ODI.

Kaul, I., I. Grunberg, and M. Stern (eds.). 1999. *Global Public Goods: International Cooperation in the 21st Century*. Oxford, UK: Oxford University Press. 546 pp.

Kindelberger, C.P. 1986. International public goods without international government. *American Economic Review* 76(1):8.

Maredia, M.K., and D. Byerlee (eds.). 1999. *The Global Wheat Improvement System: Prospects for Enhancing Efficiency in the Presence of Spillovers*. CIMMYT Research Report No. 5. Mexico, D.F.: CIMMYT. 130 pp.

Maredia, M., and P. Pingali. 2001. Environmental impacts of productivity-enhancing crop research: a critical review, pp. 19. [CGIAR/MTM, Doc. SDR/TAC:IAR/01/14, May 2, 2001]. TAC Secretariat, FAO, Rome.

McCalla, A.F. 1994. Ecoregional Basis for International Research Investment. In: J.R. Anderson (ed.), *Agricultural Technology: Policy Issues for the International Community*, pp. 96-105. CAB International.

Mokyr, J. 1990. *The Lever of Riches: Technological Creativity and Economic Progress*, pp. 296. Oxford, UK: Oxford University Press.

Nelson, M., and M. Maredia. 2000. Environmental impacts of the CGIAR: an initial assessment, pp. 36-37, 47. Agenda Item 2, ICW 1999. TAC Secretariat, CGIAR, Rome.

Olson, M. 1971. *The Logic of Collective Action; Public Goods and the Theory of Groups,* pp. 14. Harvard University Press.

Pardey, P., J. Alston, and C.-C. Chang. Donor and Developing-Country Benefits From International Agricultural Research: A Double Dividend?" (forthcoming).

Pollack, A. 2001a. Rice genome called a crop breakthrough. *The New York Times*, January 27, 2001, pp. 8.

Pollack, A. 2001b. The Green Revolution yields to the bottom line. *The New York Times*, May 15, 2001, pp. D1.

Pray, C., and K. Fuglie. *The Private Sector and International Agricultural Technology Transfer in Developing Countries: Case Studies*…. U.S. Department of Agriculture, Economic Research Service, Agricultural Economics Report. (forthcoming).

RAFI (Rural Advancement Fund International). 2001. In search of common ground. II. CDMT—can dinosaurs make teammates? RAFI, Winnipeg. RAFI Communique #7, May/June 2001, pp. 14-17.

Regaldo, A. 2001. Syngenta sequences the genome of rice... *Wall Street Journal*, January 26, 2001, pp. B6.

Rosenberg, N. 1982. *Inside the Black Box: Technology and Economics,* pp. 258. Cambridge, UK: Cambridge University Press.

Rutton, V.W. 2001. *Technology, Growth, and Development: An Induced Innovation Perspective.* Oxford, UK: Oxford University Press.

Sachs, J. 1999. Helping the world's poorest. *The Economist*, August 14, 1999, pp. 17-20;

Sachs, J. 2000. A new map of the world. *The Economist*, June 24, 2000, pp. 81-83.

Samuelson, P. 1954. The pure theory of public expenditure. *Review of Economics and Statistics* 36(4):387-389.

Samuelson, P. 1955. Diagrammatic exposition of a theory of public expenditure. *Review of Economics and Statistics* 37(4):350-356.

Schumpeter, J. 1942. *Capitalism, Socialization, and Democracy*. New York, NY: Harper & Row.

Smith, A. 2000. *The Wealth of Nations*. The Modern Library.

TAC (Technical Advisory Committee). 1987. TAC Review of CGIAR priorities and future strategies, December 1986. In: *CGIAR Priorities and Future Strategies*, pp. 21. TAC Secretariat, FAO, Rome.

TAC (Technical Advisory Committee). 1992. A possible expansion of the CGIAR. In: *Expansion of the CGAR System,* pp. 43. TAC Secretariat, FAO, Rome.

TAC (Technical Advisory Committee). 2001. Report from TAC's Standing Panel on Impact Assessment (SPIA) to MTM 2001. (CGIAR MTM: SDR/TAC:IAR/01/05). TAC Secretariat, FAO, Rome.

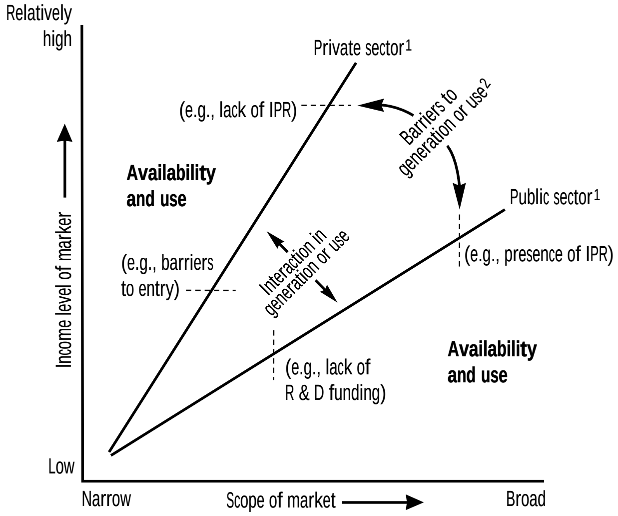
Tripp, R., and S. Pal. 2001. The private delivery of public crop varieties: rice in Andhra Pradesh. *World Development* January 29 (1):103-117.

Victor, D.G., and J.H. Ausubel. 2000. Restoring the forests. *Foreign Affairs*, November-December 2000, Vol. 79, No. 6, pp. 127-144.

Winkelmann, D.L. 1994. A View of quintessential agricultural research. In: J.R. Anderson (ed.), *Agricultural Technology: Policy Issues for the International Community*, pp. 85-89. CAB International.

World Bank. 2001. Effective use of development finance for international public goods. In: *Global Development Finance 2001: Building Coalitions for Effective Development Finance, Analysis and Summary Tables,* pp. 120. Washington, DC: World Bank.

Annex



Conceptual relationship of factors influencing availability and use of research-based public and private sector goods.

[1] The sector lines displayed show only one of many possible configurations. In this perhaps extreme case, clear market segmentation is presumed, with 1) the private sector providing more elite goods (probably incorporating intellectual property rights, IPR) for wealthier commercial farmers, and 2) the public sector providing more ordinary goods which are less profitable for the private sector and which reach more broadly across the market. In other cases, the sector lines might be curved, closer together, congruent, overlapping, or fuzzy. Certain private sector firms could, for instance, be more like the public sector and vice versa, at least for a portion of their activities. The area between the public and private sector lines might be viewed as the portion of the potential market not adopting the research-based good.

[2] The limitations, more generally, could take a variety of forms such as political, legal, biological, or environmental. Public resistance to products perceived to be the product of genetic engineering has been an increasingly important barrier. The positioning of the barrier may vary by sector and for individual components. Some may be common to both sectors.

Growth in Wheat Yield Potential in Marginal Environments

M.A. Lantican, P.L. Pingali, and S. Rajaram

Introduction

Wheat yield potential in favorable environments is well documented. Semidwarf spring wheat varieties have been widely adopted in these areas and have contributed greatly to increased yields. However, in marginal environments technological progress and increases in wheat productivity appear to have been limited, despite the relatively large area of marginal cropping land in the developing world. About one-third of the bread wheat area and nearly three-quarters of the durum wheat area in the developing world are located in marginal environments (Byerlee and Morris 1993). Since crops grown in these environments experience severe drought stress during the growing season, farmers' yields are generally low.

Empirical evidence presented in this paper, however, indicates that substantial progress in shifting the wheat yield frontier in marginal environments has been made over the past two decades. Wheat yield improvements in marginal environments firstly resulted from spillovers from favorable environments and, more recently, from breeding efforts targeting drought and high temperature environments. This paper provides empirical estimates of 1) the rate of increase in wheat yield potential according to mega-environment, 2) the crossover and spillovers of varieties and germplasm from favorable to marginal environments, and 3) the increase in production and productivity at the farm level according to the wheat growing environment.

Materials and Methods

Data sources

Yield data used in the study were taken from 19 yield nurseries of the Elite Spring Wheat Yield Trial (ESWYT) grown in 246 locations in 65 countries between 1979 and 1999. In addition, data from 30 yield nurseries of the International Spring Wheat Yield Nursery (ISWYN) grown in 411 locations in 82 countries between 1964 and 1995 were also used. Data on spring wheat varieties planted in 1990 and 1997, including pedigrees, year of release, area planted, and targeted ME, were obtained from the CIMMYT Wheat Impacts database.

The ISWYN was designed to test adaptation of advanced spring lines and varieties under a wide range of latitudes, climates, day lengths, fertility conditions, water management regimes, and exposure to disease complexes. The purpose of the experiments was to study the performance of some of the most important varieties and materials from the world's major wheat growing areas under different environmental conditions. The ESWYT, on the other hand, was designed to test the adaptation of high yielding, disease resistant, advanced lines bred by CIMMYT in limited locations around the world. The most promising ESWYT materials are further tested in ISWYN (CIMMYT 1979).

Analysis

ISWYN data were grouped into two time periods: the Green Revolution (1964-78) and post-Green Revolution (1979-95). All ESWYT data were grouped into the post-Green Revolution period (1979-99). The three highest wheat yields for each location in each year were averaged. The locations were then grouped according to mega-environment. A mega-environment (ME) is a broad, frequently transcontinental, but not necessarily contiguous, area occurring in more than one country, with similar biotic and abiotic stresses, cropping system requirements, consumer preferences, and, possibly, volume of production (Pingali and Rajaram 1999). Mega-environments are useful for defining breeding objectives because each one covers millions of hectares that are relatively homogeneous for wheat production (Dubin and Rajaram 1996).

Our analysis focused on four spring wheat mega-environments: ME1, ME2, ME4, and ME5. ME1 (low rainfall, irrigated) and ME2 (high rainfall) represent favorable environments, while ME4 (low rainfall, drought) and ME5 (high temperature) represent marginal environments. Wheat yield growth rate (%) for each mega-environment in the ESWYT and ISWYN was estimated using the following log-linear regression model:

$$\ln (Y) = \alpha + \beta X + \varepsilon$$

where:
α = constant;
$\ln(Y)$ = natural logarithm of Y, which is the average of the highest three yields per location;
X = time (yr);
ε = error term.

This function describes the variable Y, which exhibits a constant proportional rate of growth ($\beta>0$) or decay ($\beta<0$). β may also be interpreted as the annual percentage change in Y.

To determine the effects of wheat breeding research on productivity, wheat production increases from 1990 to 1997 were estimated using CIMMYT Wheat Impacts data based on 1) additional area under improved wheat production and 2) yield increases due to variety replacement. The following formula was used to estimate the production increases[1] due to additional area sown to modern varieties (MVs):

$$\Delta Q = (MV_1 - MV_0)\, Y_0 e^{gt}$$

where:
MV_1 = area sown to MVs in 1997;
MV_0 = area sown to MVs in 1990;
Y_0 = yield in 1977, according to Byerlee and Moya (1993);
e = exponential term;
g = annual rate of yield gain;
t = time period.

Rate of yield gain (g), used to estimate production increases, was based on growth rates obtained from the analysis of the ESWYT and ISWYN data. To estimate yield increases due to the replacement of older MVs with newer MVs, a replacement factor (r) was first calculated based on variety turnover. Yield increases due to variety replacement were then estimated using the following formula:

$$\Delta Q = MVrY_0 e^{gt}$$

where:
MV = area sown to MVs in 1997;
r = replacement factor (based on variety turnover);
Y_0 = yield in 1977, according to Byerlee and Moya (1993);
e = exponential term;
g = annual rate of yield gain due to replacing older MVs with newer MVs;
t = time period.

A comparison of results was made between mega-environments in both the ESWYT and ISWYN.

Growth in Wheat Yield Potential

Wheat yield growth rates generated from the ESWYT data, encompassing the post-Green Revolution period (1979-99), showed a faster rate of yield increase in marginal environments than in favorable environments. The highest increase in wheat yield potential among the four mega-environments was measured in ME4, which had a yield gain of about 3.5% per year or 88 kg per year (Table 1). ME5 showed a yield gain of 2.1% per year or 46 kg per year. The favorable environments, ME1 and ME2, sustained a 1% per year increase in wheat yield potential, or 53.5 kg per year and 62.5 kg per year, respectively. Figure 1 shows an increasing trend in average wheat yield potential for both favorable and marginal environments. These results confirm the findings of Trethowan (2001), who demonstrated a yield increase over time in both low and intermediate yielding environments.

To confirm that these high rates of yield growth and yield potential in marginal environments were indeed possible, we conducted the same analysis using the ISWYN data (1964-95). The same trend resulted—growth rates in wheat yield potential in marginal environments were higher and increasing at a faster rate than those in favorable environments, particularly during the post-Green Revolution period (Table 2). In fact, the results implied that the yield growth rates in marginal environments were at least double those in favorable environments during this period. The rates

---

[1] In estimating the production increase due to wheat area expansion, South Africa and China were excluded to avoid biased estimates. This is because South Africa was not included in the 1990 Wheat Impacts Survey, and only four wheat-producing provinces in China were included. In contrast, the total wheat area of both of these countries was included in the 1997 Wheat Impacts Survey. If both China and South Africa were to be included in the estimation of production increases due to area expansion, there would be a huge difference in MV area, and thus, very high and biased production increases.

Table 1. Trends in wheat yield growth rate according to mega-environment, Elite Spring Wheat Yield Trial, 1979-99.

Mega-environment	Growth rate (%/yr)	Growth (kg/yr)
ME1: Irrigated	0.82	53.5
ME2: High rainfall	1.16	62.5
ME4: Drought prone	3.48	87.7
ME5: High temperature	2.10	46.1

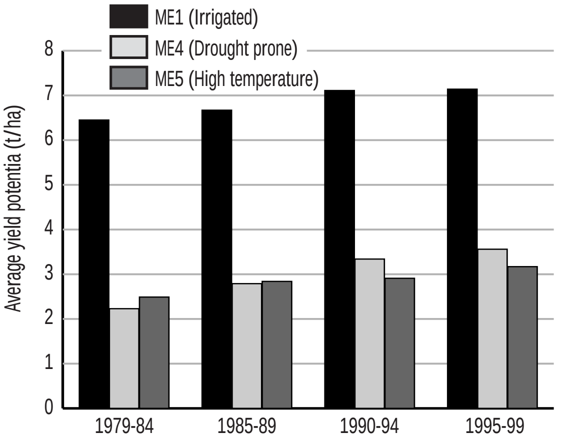


Figure 1. Average wheat yield potential according to mega-environment (ME) and period, Elite Spring Wheat Yield Trial, 1979-99.

Table 2. Rate of growth (%/yr) in wheat yield according to mega-environment (ME), International Spring Wheat Yield Nursery, 1964-95.

Period	ME1 Irrigated	ME2 High rainfall	ME4 Drought prone	ME5 High temperature
1964-78	1.22 (71.60)	1.72 (81.50)	1.54 (32.40)	1.41 (34.90)
1979-95	1.32 (84.60)	1.71 (92.80)	2.75 (70.50)	2.53 (72.30)

Note: Figures in parentheses are growth in kg/yr.

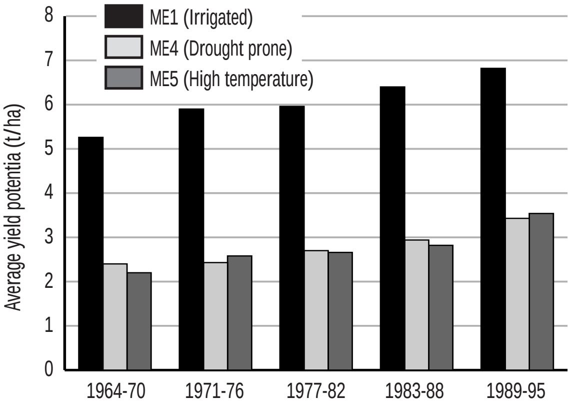


Figure 2 . Average wheat yield potential according to mega-environment (ME) and period, International Spring Wheat Yield Nursery, 1964-95.

of wheat yield gain in ME4 and ME5 during 1979-95 were 2.75% per year (70.5 kg/yr) and 2.5% per year (72.3 kg/yr), respectively (Table 2). It is possible that the yield growth rate for ME4 could have been even higher if the ISWYN data (1979-95) had encompassed the same number of years as the ESWYT data (1979-99).

The average wheat yield potential in ISWYN locations showed an increasing trend similar to that in ESWYT locations (Figure 2). The average wheat yield potential in the three mega-environments increased over time, with the highest occurring in ME1.

To further our understanding of wheat production in marginal environments, we also determined the rates of adoption of modern varieties (MVs), crossover and spillovers from favorable to marginal environments, and production increases from wheat breeding research based on the CIMMYT Wheat Impacts database.

Adoption Rate of Modern Varieties

In the 1990 Global Wheat Impacts Study (Heisey et al. 1999), the adoption of MVs in marginal environments was generally lower than in favorable areas. However, in the 1997 study, the adoption rate had increased and was similar for favorable and marginal environments. Between 1990 and 1997, adoption rates of ME1, ME2, and ME4 varieties in the developing world increased, except in sub-Saharan Africa, which was represented by only four MVs planted in Sudan in ME5 (Table 3).

Table 3. Adoption (%) of modern wheat varieties according to mega-environment (ME) and region, 1990 and 1997.

Year/region	ME1 Irrigated	ME2 High rainfall	ME4 Drought prone	ME5 High temperature
1990				
Sub-Saharan Africa	95.8	60.3	93.8	100.0[1]
West Asia/North Africa	85.6	59.5	67.6	-
Asia	88.6	99.6	82.1	99.8
Latin America	96.8	89.8	90.6	66.3
1997				
Sub-Saharan Africa	100.0	57.5	99.4	80.0
West Asia/North Africa	85.8	79.6	79.3	-
Asia	99.8	98.3	92.7	100.0
Latin America	100.0	95.9	99.0	95.1

[1] Represented by only four modern wheat varieties planted in Sudan.

Source: CIMMYT Economics database.

The adoption rate of ME1 varieties was very high in all regions. For sub-Saharan Africa, only ME2 had a lower adoption rate relative to the other mega-environments. In contrast, MV adoption rates in West Asia and North Africa (WANA) were lower for all four mega-environments relative to the other regions. This is possibly due to the relatively large area of landraces still cultivated in the region: landraces cover slightly less than 20% of the spring durum area in WANA (Heisey et al. 1999).

The MV area is congruent with the MV adoption rate (according to ME) for each region. The big difference in MV area between 1990 and 1997 for Asia and sub-Saharan Africa, particularly for MEs 1 and 4, was partly due to the inclusion of South Africa and China in 1997 (Table 4). During this year, about 42 million hectares of MVs were planted in ME1 and about 12 million ha were planted in ME2 (Table 4). The relatively larger area planted in WANA in 1997 could be associated with the slight increase in MV adoption rate in the region from 67.6% in 1990 to 79.3% in 1997.

Crossover and Spillovers from Favorable to Marginal Environments

Crossover occurs when the same variety is planted in both favorable and marginal environments during the same period. This means that ME1 or ME2 materials are used in other MEs without further breeding. Spillover, on the other hand, is when ME1 or ME2 materials are used in breeding varieties for either ME4 or ME5. In breeding for marginal environments, the use of ME1 materials as both parents in a cross could be considered a direct transfer or spillover. An indirect or adaptive transfer would use ME1 material as one parent, combined with a drought-resistant or heat-tolerant (non-ME1) parent to breed for either ME4 or ME5.

Using the CIMMYT Wheat Impacts database, crossover from favorable to marginal environments was determined by identifying the wheat varieties planted in both ME1 or ME2 and ME4 or ME5 in 1997. Spillover was determined by carefully checking the pedigrees of wheat varieties planted in ME4 and ME5 in 1990 and 1997 for any ME1 or ME2 material.

Crossover

As shown in Table 5, 19.5% of the total MV area in ME4 and ME5 was crossovers from ME1 and ME2. Crossover varieties were released from 1973 to 1986 and a total of about 3 million ha was planted to them. Among these varieties, HD 2285 and Sonalika covered the largest area (1.1 million ha each) for ME4 and ME5 in 1997. Sonalika (an Indian variety originally bred in Mexico by CIMMYT) matures very early and thus can escape heat exposure (Morgounov 1995). There were also three crossover durum varieties: Mexicali, Cocorit, and Waha. The adoption of hallmark cultivars such as Mexicali 75 and Cocorit 71 reflects the international reach of CIMMYT's durum breeding program (Pfeiffer et al. 2001).

Table 4. Area (000 ha) planted to modern wheat varieties according to mega-environment (ME) and region, 1990 and 1997.[1]

Year / region	ME1 Irrigated	ME2 High rainfall	ME4 Drought prone	ME5 High temperature
1990				
Sub-Saharan Africa	120	1,168	75	296
West Asia/North Africa	4,938	1,692	2,335	-
Asia	22,020	369	1,702	5,978
Latin America	1,791	5,203	636	32
Total	28,869	8,430	4,748	6,306
1997				
Sub-Saharan Africa	823	790	181	241
West Asia/North Africa	6,411	1,852	4,816	-
Asia	33,749	2,965	4,771	4,536
Latin America	912	6,362	561	536
Total	41,895	11,969	10,329	5,314

[1] Improved tall varieties included.

Source: CIMMYT Economics database.

Table 5. Wheat varieties planted in ME1 (irrigated) or ME2 (high rainfall) as well as ME4 (drought prone) or ME5 (high temperature), 1997.

	Area (000 ha)	
Variety[1]	ME1 and ME2	ME4 and ME5
Pavon F76 (1976)	208.8	27.8
Mexicali (1978)	13.5	52.3
Cocorit (1975)	13.3	54.8
Veery (1985)	1,798.6	130.5
Debeira (1982)	3.9	169.0
Waha (1986)	5.8	345.7
Sonalika (1973)	5.5	1,127.5
HD 2285 (1985)	8.1	1,137.0
Total area	2,057.5	3,044.5

[1] Figures in parentheses are dates of release.

Note: Crossover = 19.5% of the total modern variety area in ME4 and ME5.

In the CIMMYT Wheat Impacts database there are also varieties targeted at either ME1 or ME2 as well as at ME4 or ME5 as alternatives. Hence, it is possible that for the last three or so years, the number of crossover varieties, as well as their cultivated area, could have increased.

Spillover

Direct spillovers from ME1 and ME2 decreased slightly from about 16.9% of cultivated area in 1990 to 12.5% in 1997 (Figure 3). The area planted to varieties specifically targeted at MEs 4 and 5 (i.e., no ME1 or ME2 materials were used in breeding these varieties) increased by 6.6% in 1997. Indirect spillovers, where ME1 material was used as one of the parents in breeding varieties for MEs 4 and 5, were approximately equal in 1990 and 1997. The CIMMYT Wheat Program uses this system for breeding for drought tolerance, where yield responsiveness is combined with adaptation to drought. Wheat production in WANA has benefited greatly from such spillover research.

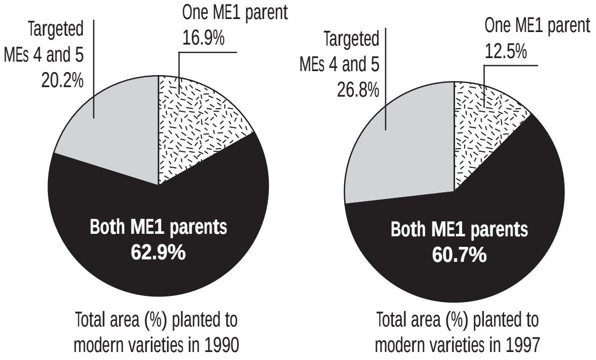


Figure 3. Effect of ME1 (irrigated) and ME2 (high rainfall) spillovers on yield potential in ME4 (drought prone) and ME5 (high temperature), 1997.

Therefore, over time more breeding efforts have been targeted towards MEs 4 and 5 (Figure 3).

The international wheat research system plays a key role in maximizing the spillover benefits of research in marginal environments across countries. Maredia (1993) and Maredia and Byerlee (1999) estimated a “spillover matrix” based on ISWYN data, which indicated large global research spillovers for wheat.

Effects of Breeding on Wheat Production

There are two sources of production increases from wheat breeding research: 1) increases due to additional area planted to MVs, and 2) increases due to the replacement of older MVs with newer MVs. Although details of the estimation of production increases have already been discussed in the Methodology section of this paper, it is worth repeating that South Africa and China were excluded from the estimations due to the expansion in MV area in these countries, which would have produced biased results.

The total wheat production increase due to MV area expansion and variety replacement in favorable and marginal environments was about 38 million tons. Of this, 27.2 million t of additional production was attributed to favorable environments, while marginal environments contributed 10.7 million t. Of the total increase in wheat production (favorable and marginal areas combined), 22.8 million t resulted from the expansion in MV area, while 15.2 million t resulted from increased yields through variety replacement.

Production increases due to area expansion

Of the 22.8 million t attributed to the increase in MV area during 1990-97, 8.84 million t was produced in marginal environments. Asia and WANA contributed about 5.6 million t and 4.3 million t of additional wheat, respectively, from ME4 in 1990-97 (Table 6). These two regions were also the main contributors of additional wheat production from ME1 due to increased MV area.

Some countries or regions, however, were not able to benefit from the increase in wheat yield potential due to a reduction in their wheat areas in 1997. In Latin America, 0.19 million t and 4.95 million t of wheat production were lost in ME4 and ME1, respectively, due to the reduction in MV area in Brazil and Mexico

Table 6. Production increase / decrease (million tons) in 1990-97 due to addition / reduction in modern variety area according to region and mega-environment (ME).

Mega-environment	Sub-Saharan Africa	West Asia / North Africa	Asia	Latin America	All
ME1: Irrigated	(0.06)	5.77	8.47	(4.95)	9.23
ME2: High rainfall	(0.66)	0.49	0.96	3.89	4.68
ME4: Drought prone	0.19	4.31	5.60	(0.19)	9.93
ME5: High temperature	(0.10)	na	(1.98)	1.00	(1.08)
Total increase / decrease	(0.63)	10.58	13.05	(0.25)	22.80

Note: Figures in parentheses represent a production decrease.

in 1997. The declining international price of wheat in 1997 may have influenced these and other countries to reduce their wheat area. In ME5, 0.10 million t of wheat production was lost in sub-Saharan Africa because of the reduction in MV area in Sudan (which represents all of the ME5 area in this region) in 1997. Similarly in ME1, Zimbabwe and Nigeria (sub-Saharan Africa) had smaller MV wheat areas in 1997 compared to 1990.

Additional production due to variety replacement

The total additional wheat production due to variety replacement was 15.2 million t (Table 7). Factors affecting the rate of variety replacement in wheat are discussed from a theoretical perspective by Heisey and Brennan (1991) and empirically by Heisey (1990), Alemu Hailye et al. (1998), Regassa Ensermu et al. (1998), and Hailu Beyene et al. (1998). Moreover, Byerlee (1994) concluded that the continuous release of newer generations of MVs in areas already sown to MVs has contributed significantly to increased productivity. Production increases due to the replacement of older MVs with newer MVs were very high in ME1 in Asia (about 7.2 million t) and ME2 in Latin America (2.4 million t) (Table 7). However, despite the fact that farmers in developing countries have widely adopted improved varieties, the rate at which older improved varieties are replaced by newer improved varieties remains unacceptably slow (see Heisey et al. 1999). The total increase in wheat production due to variety replacement in marginal environments was 1.85 million t.

For ME5, Asia had a wheat production increase of about 0.4 million t due to variety replacement. West Asia and North Africa, the world's most drought-prone area, had the highest production increase of 0.64 million t for ME4 due to replacement of older MVs with newer MVs (Table 7). Most of the production increases in WANA's marginal environments may have resulted from work conducted by CIMMYT in conjunction with ICARDA on improving wheat production. The CIMMYT/ICARDA Joint Dryland Wheat Program for the region seeks to increase wheat productivity by developing spring bread wheats and durum wheats that are better adapted to the WANA region (CIMMYT 1997).

Table 7. Production increase (million tons) due to replacement of older modern varieties (MVs) with newer MVs according to region and mega-environment (ME), 1990-97.

Mega-environment	Sub-Saharan Africa	West Asia/ North Africa	Asia	Latin America	All
ME1: Irrigated	0.31	1.63	7.19	0.42	9.54
ME2: High rainfall	0.09	0.41	0.88	2.43	3.80
ME4: Drought prone	0.02	0.64	0.43	0.20	1.29
ME5: High temperature	0.03	na	0.43	0.11	0.56
Total production increase	0.44	2.68	8.92	3.15	15.19

Conclusions

Substantial progress has been made in shifting the wheat yield frontier in marginal environments. Evidently, the growth in wheat yield potential in marginal areas has increased at a faster rate than in favorable environments, particularly during the post-Green Revolution period. Wheat yield gains in marginal environments have resulted firstly from spillovers from favorable areas, and more recently from targeted wheat breeding for drought and warmer environments.

Using either ESWYT or ISWYN data has revealed an increasing trend in average wheat yield potential in both favorable and marginal environments. The high rates of yield gains and the increasing yield potential show the huge promise for improving wheat yield productivity in marginal environments. Overall, marginal environments contributed a total of 10.7 million t of additional wheat due to MV area expansion and yield increase from the replacement of older MVs with newer MVs. Of this figure, 8.84 million t can be attributed to the area expansion effect and 1.85 million t to the yield increase effect. Since it is unlikely that the anticipated gains in high potential environments will meet the projected increase in wheat demand over the next 20 years, any improvement in wheat productivity in marginal environments will contribute enormously to the food security of the poor in these areas.

References

Beyene, Hailu, H. Verkuijl, and W. Mwangi. 1998. *Farmers' Seed Sources and Management of Bread Wheat in Wolmera Woreda, Ethiopia*. Mexico, D.F.: CIMMYT and IAR.

Byerlee, D. 1994. *Modern Varieties, Productivity, and Sustainability: Recent Experience and Emerging Challenges*. Mexico, D.F.: CIMMYT.

Byerlee, D., and M. Morris. 1993. Research for marginal environments: Are we underinvested? *Food Policy* 18(3):381-393.

Byerlee, D., and P. Moya. 1993. *Impacts of International Wheat Breeding Research in the Developing World, 1966-1990*. Mexico, D.F.: CIMMYT.

CIMMYT (International Maize and Wheat Improvement Center). 1979. *Instructions for the Management and Reporting of Results for Wheat Program International Yield and Screening Nurseries*. Mexico, D.F.: CIMMYT.

CIMMYT (International Maize and Wheat Improvement Center). 1997. *CIMMYT in 1996-97. Widening the Circle of Partnerships*. Mexico, D.F.: CIMMYT.

Dubin, H.J., and S. Rajaram. 1996. Breeding disease-resistant wheats for tropical highlands and lowlands. *Annual Review of Phytopathology* 34:503-526.

Ensermu, Regassa, W. Mwangi, H. Verkuijl, M. Hassena, and Z. Alemayehu. 1998. *Farmers' Wheat Seed Sources and Seed Management in Chilalo Awraja, Ethiopia*. Mexico, D.F.: IAR and CIMMYT.

Hailye, Alemu, H. Verkuijl, W. Mwangi, and Asmare Yellew. 1998. *Farmers' Wheat Seed Sources and Seed Management in Enebssie Area, Ethiopia*. Mexico, D.F.: IAR and CIMMYT.

Heisey, P.W. (ed.). 1990. *Accelerating the Transfer of Wheat Breeding Gains to Farmers: A Study of the Dynamics of Varietal Replacement in Pakistan*. CIMMYT Research Report No. 1. Mexico, D.F.: CIMMYT.

Heisey, P.W., and J.P. Brennan. 1991. An analytical model of farmers' demand for replacement seed. *American Journal of Agricultural Economics* 73:1044-1052.

Heisey, P.W., M.A. Lantican, and H.J. Dubin. 1999. Assessing the benefits of international wheat breeding research: An overview of the Global Wheat Impacts Study. In: P.L. Pingali (ed.), *CIMMYT 1998-99 World Wheat Facts and Trends. Global Wheat Research in a Changing World: Challenges and Achievements*. Mexico, D.F.: CIMMYT.

Maredia, M.K. 1993. The Economics of International Agricultural Research Spillovers: Implications for the Efficient Design of Wheat Improvement Research Programs. PhD dissertation. Michigan State University, Department of Agricultural Economics, East Lansing.

Maredia, M.K., and D. Byerlee (eds.). 1999. *The Global Wheat Improvement System: Prospects for Enhancing Efficiency in the Presence of Spillovers*. CIMMYT Research Report No. 5. Mexico, D.F.: CIMMYT.

Morgounov, A. 1995. Bread wheat breeding for heat tolerance. In: S. Rajaram and G.P. Hettel (eds.), *Wheat Breeding at CIMMYT: Commemorating 50 Years of Research in Mexico for Global Wheat Improvement*. Wheat Special Report No. 29. Mexico, D.F.: CIMMYT.

Morris, M.L., H.J. Dubin, and T. Pokhrel. 1992. Returns to Wheat Research in Nepal. CIMMYT Economics Working Paper 92-04. Mexico, D.F.: CIMMYT.

Pfeiffer, W.H., K.D. Sayre, and T.S. Payne. 2001. Increasing durum wheat yield potential and yield stability. In: *Research Highlights of the CIMMYT Wheat Program, 1999-2000*. Mexico, D.F.: CIMMYT.

Pingali, P.L., and S. Rajaram. 1999. Global wheat research in a changing world: Options for sustaining growth in wheat productivity. In: P.L. Pingali (ed.), *CIMMYT 1998-99 World Wheat Facts and Trends. Global Wheat Research in a Changing World: Challenges and Achievements*. Mexico, D.F.: CIMMYT.

Trethowan, R.M. 2001. Breeding for marginal environments. In: *Research Highlights of the CIMMYT Wheat Program, 1999-2000*. CIMMYT: Mexico, D.F.

The Complexity of Breeding Improved Wheat Cultivars for the Great Plains Region of the USA

A. Klatt

Description of the Region

The hard winter wheat region of the central and southern Great Plains includes southern South Dakota, Nebraska, most of Kansas (except a small area in the east), Oklahoma, the eastern plains of Colorado, and the High Plains and Rolling Plains of Texas. Some hard winter wheat is grown in North Dakota, Montana, Wyoming, and Utah, but the total area is quite limited. The region has traditionally grown hard red winter wheat (HRWW), but recently white seeded varieties have been released.

Production factors

Winter temperatures increase from north to south, and the level of winterhardiness is a very important factor for varietal selection. Rainfall decreases from east to west, with total annual rainfall ranging from more than 1000 mm in parts of the east down to about 300 mm in the west. Rainfall distribution is highly variable within and between years. Elevation generally increases from east to west. At higher elevations, night temperatures decrease and grainfilling duration increases (Peterson 1992). Leaf rust is endemic throughout the region, but generally is most severe in north Texas and central Oklahoma and Kansas. Stem rust can affect production in Nebraska and South Dakota. Scab can be a production factor in the east of the region, and various foliar, viral, and root and crown diseases are also common in the region.

Cultural practices

In some of the drier regions, a wheat-fallow system is still used, resulting in one crop in every two years; however, in many parts of the Great Plains, wheat is grown on an annual basis without crop rotation. Despite this, the area of summer crops such as soybeans, corn, sorghum, and sunflowers is increasing, especially in the central part of the region where summer rains are more reliable. These summer crops are being grown following wheat or in a three-crops-in-two-years rotation. Tillage systems vary from no-till to conventional moldboard plowing. Sweep plows are commonly used to control weeds and volunteer wheat in the fallow, leaving some residue on the surface to reduce wind and water erosion.

Fertilizers

Nitrogen is the most common limiting nutrient and phosphorus is required in parts of the region, whereas potassium is seldom limiting. In the drier areas, any nitrogen is normally applied pre-planting; in the more humid areas, nitrogen may be applied prior to planting followed by a top-dressing in the early spring. Low pH soils (>5.5) are a limiting factor in some areas of the southern Great Plains (Carver and Ownby 1995).

Weed control

Weeds are a problem throughout the region. Broad leaf weeds are commonly controlled with herbicides. Grassy weeds are increasing, especially *Bromus* spp., and, although new herbicides are now available to control most grassy weeds, their costs are high compared to the current grain value. Fungicides are not commonly used in the region to control foliar diseases. Insecticides are used, as needed, to control insect pests, most commonly greenbugs.

Dual-purpose management system

An important management system in the southern Great Plains is dual-purpose wheat, i.e., forage plus grain. In a typical year, as much as 50-60% of the wheat in Texas, Oklahoma, and the extreme southern part of Kansas is grown under the dual-purpose system. In this system, wheat is planted early (late August to mid September) to produce significant vegetative growth (forage) by the fall. Due to mild winter temperatures, some vegetative growth continues throughout the winter. Grazing with cattle begins in mid to late November and continues until the very early jointing stage, which normally occurs in late February to mid March, depending on the area and the year. The wheat is then allowed to grow and produce grain. With good management, grain yield is reduced by only 10-20% under this system and most of the reduction is due to early seeding and not to grazing (Carver et al. 2001). Moreover, significant income is derived from the (approximately) 100 days of grazing. Some producers use the wheat as a full-season forage crop (graze-out), especially if cattle prices are high and wheat prices are low. Wheat sown for grain only is normally seeded in October or early November.

History of Varieties

Early history

Winter wheat was first introduced into the region in the 1830s, but the varieties grown were primarily soft red winter wheats and were poorly adapted, lacking winterhardiness, disease resistance, and drought tolerance (Salmon et al. 1953). Mennonite settlers introduced the cultivar Turkey in the 1870s, and this marked the beginning of hard red winter wheat (HRWW) production in the USA. Its spread throughout the region was slow, but by the late 1890s and early 1900s it was the predominate variety. Turkey was a landrace (heterogeneous population) and many important cultivar selections were derived from it, including Kanred, Blackhull, Early Blackhull, Nebraska No. 60, Cheyenne, and Nebred (Quisenberry and Reitz 1974). Turkey and its derivatives occupied more than 90% of the HRWW region during the 1910s, 1920s, and 1930s. In 1919, it occupied 99% of the HRWW region and 30% of the total US wheat area. Turkey continued to be the predominant variety until the early 1940s.

1940s and 1950s

Tenmarq became the leading variety in the HRWW region in 1944, with Turkey occupying second place (Clark and Quisenberry 1948). Significant cultivar changes occurred in the region in the late 1940s, primarily due to the need for better disease resistance, especially to stem rust. The area under Tenmarq and Turkey decreased dramatically, and Pawnee, Comanche, Triumph, and Wichita became the leading varieties (Bayles and Clark 1954). These continued to be the predominant varieties in the 1950s and early 1960s. All were derived from Turkey or from crosses involving selections from Turkey (Salmon and Reitz 1957). Pawnee was primarily grown in the northern section of the region, and Triumph and Wichita were popular in the southern and central parts (Reitz and Briggle 1960). Wichita and Triumph were still the most popular varieties in the region in 1964. Triumph and its derivatives occupied more than 25% of the total wheat area in the region in the late 1950s and early 1960s (Reitz and Briggle 1966). It was successful because of its very early maturity, good yield, and its ability to grainfill under adverse conditions (Cox 1991). Due to these characteristics, it has been used as a parent in crossing programs around the world.

1960s and 1970s

Scout was released in the mid 1960s and was the predominant variety in the late 1960s and during the 1970s. By 1974, Scout, selections from Scout, and its backcross derivatives, occupied 35% of the HRWW region. Their popularity was due to good disease resistance, high yield potential, good quality characteristics, and broad adaptation. In 1969, the HRWW region constituted almost 60% of the total wheat area in the US (Reitz and Lebsock 1972).

The first semidwarf HRWW was released by Dr. K.B. Porter of Texas in 1966 (Cox 1991). It was primarily sown in the irrigated areas of Texas and Oklahoma, but never occupied an extensive area. In 1974 it reached its peak and was grown on more than 600,000 hectares (4.2% of the region) (Reitz and Hamlin 1978).

Centurk, TAM 101 (another semidwarf variety from Texas), and Scout and its derivatives were the leading varieties in 1979; Triumph and its derivatives continued to occupy 9% of the region (Briggle et al. 1982).

1980s: dominance of semidwarfs

Newton, a semidwarf from Kansas, became the leading variety in 1984 (Dalrymple 1988). It was derived from the cross Bluebird sib / Scout, and this marked the first significant appearance of CIMMYT germplasm in the HRWW region (Cox 1991). Newton remained the leading variety throughout most of the 1980s, while other significant varieties included TAM 105, Vona (semidwarf from Colorado with CIMMYT germplasm), and TAM 101. Thus, the four leading varieties in 1984 were semidwarfs, which signaled a dramatic change in the cultivars of the HRWW region (Dalrymple 1988).

New virulences of leaf rust in the mid 1980s caused dramatic shifts in cultivars sown in the late 1980s. By 1989, Pioneer 2157, TAM 107, and Chisholm were the leading cultivars. TAM 107 predominated in the drier west, and Chisholm was grown primarily in the southern part of the region (W.D. Worrall, T. Miller, and K.B. Porter, personal communication, 2000).[1]

1990s: period of rapid change

In the early 1990s, new races of leaf rust again caused drastic changes in cultivar composition. Karl (and its reselection Karl 92) became the leading cultivar in 1994. Other important cultivars included TAM 107, 2163 (originally developed by Pioneer Hi-Bred Int., but released by the Kansas Agricultural Experiment Station), Tomahawk (AgriPro), and Arapahoe (Nebraska) (W.D. Worrall, T. Miller, and K.B. Porter, personal communication, 2000)[1] . Changes in leaf rust virulence led to significant cultivar changes by 1999, when Jagger became the leading variety. Jagger was derived from the cross KS82W418/Stephens and constituted the first appearance of Pacific Northwest germplasm in the Great Plains. TAM 107 continued to be the second leading variety because of its predominance in the dry west where leaf rust is seldom a problem. Other important varieties included 2137 (Kansas), Karl/Karl 92, Ike, Custer, and Akron (W.D. Worrall, T. Miller, and K.B. Porter, personal communication, 2000).[1]

Contributions from the private sector

It is obvious that public sector breeding programs have released the majority of varieties in the Great Plains; however, the private sector has played a significant role in cultivar development in the region. The most successful variety was Triumph and its derivatives, developed by Joseph Danne, a farmer in central Oklahoma. In the last 20 years, privately developed cultivars have occupied a significant portion of the HRWW region. In 1989, privately developed varieties covered 3.6 million ha in the states of Oklahoma, Kansas, Colorado, and Nebraska, representing 36% of the area in these states. In 1984, 1994, and 1999, the percentage area sown to cultivars of private companies was 10%, 25%, and 16%, respectively (W.D. Worrall, T. Miller, and K.B. Porter, personal communication, 2000).[1] Comparable data for Texas are unavailable, but are probably of similar magnitude. Several private companies have well-financed and aggressive breeding programs that will continue to produce successful varieties for the region.

Yield potential

Average yields in the HRWW region increased from 885 kg/ha in 1869 to only 1,155 kg/ha in 1945. After World War II, fertilizer use increased significantly and average yields rose dramatically. Semidwarf varieties were responsible for significant yield increases in the 1970s and 1980s. Today, more than 90% of the wheat grown in Kansas, Oklahoma, and Texas is semidwarf; the corresponding percentage for Nebraska, Colorado, and South Dakota is slightly lower. It is estimated that yield increases due to genetic improvement averaged 1% per year during 1919-87, with the highest increases occurring in favorable environments with high disease incidence (Feyerherm et al. 1984). Today, average yields in the region vary from just over 2 t/ha in Texas and Oklahoma to approximately 3 t/ha in Kansas and Nebraska.

Breeding Philosophy

In the past, breeders focused on improving yield potential and adaptation to the harsh environmental conditions of the Great Plains. Today, considerably more emphasis is placed on protecting yield potential from biotic and abiotic stresses. The Turkey gene pool dominated breeding efforts until the 1960s, and little use was made of nonadapted or introduced materials in the various breeding programs (Carver et al. 2001). There were some exceptions, particularly related to the incorporation of enhanced disease and insect resistance in the HRWW varieties, however, the total effect on genetic diversity was minimal. The incorporation of semidwarf genes in the late 1960s and 1970s introduced some genetic diversity into the region. Subsequently in the 1980s and 1990s, greater utilization of introduced germplasm from Eastern Europe and the Soviet Union led to further increases in genetic variation and resulted in varieties such as Custer, Tonkawa, Yuma, Arapahoe, Wesley, Siouxland, Yumar, TAM 202, and TAM 301 (Carver et al. 2001). Many breeders within the region continue to exploit the Eastern European and Russian gene pools with considerable success, but the 1B/1R translocation, and its negative impact on quality, present in many of these materials has limited their usefulness.

Selected programs within the region have utilized the CIMMYT spring wheat gene pool, most notably Texas A&M, Colorado, and several private breeding programs. As noted earlier, Newton and Vona are examples of early successes with this germplasm. Also,

---

[1] Colorado Agricultural Statistics Service (1989; 1994; 1999); Kansas Agricultural Statistics Service (1989; 1994; 1999); Nebraska Agricultural Statistics Service (1989; 1994; 1999); Oklahoma Agricultural Statistics Service (1990; 1994; 1999).

several of the privately released varieties have CIMMYT spring wheat in their parentage. In the late 1980s and 1990s, this germplasm was not extensively used due to quarantine restrictions related to Karnal bunt, but more recently there has been renewed interest in the CIMMYT winter and spring wheat gene pools as sources of useful genetic variation for the Great Plains breeding programs.

Breeding for Resistance to Biotic Stresses

Leaf rust

The incorporation of resistance to several biotic stresses is a priority for most breeders in the Great Plains. Leaf rust (*Puccinia triticina*) is prevalent throughout the region but is most damaging in north Texas, Oklahoma, and Kansas. Annual losses in the south of the region are officially estimated at about 5%, but many breeders believe this figure to be higher. In experimental plots, a yield reduction of more than 50% due to leaf rust infection has been measured, and fungicide treatment typically gives a 20-30% yield increase in years of heavy leaf rust infection (unpublished data). Today, all of the predominant varieties in these states are susceptible to leaf rust. New varieties with improved resistance are being multiplied but are not yet widely cultivated.

Breeding for improved leaf rust resistance has traditionally utilized major genes, with (mostly unsuccessful) attempts at pyramiding these resistance genes. Breeders have had success at incorporating new genes for resistance, but the pathogen has been equally successful in developing new virulence for each major gene or gene combination deployed. It is generally agreed that new races originate or multiply in south Texas or northern Mexico and spread northward, reaching central Kansas in one to three years. The incidence of leaf rust is further enhanced by the early sowing of wheat in the fall, especially in the dual-purpose wheat system. Mild environmental conditions during fall promote infection in these early sown fields and greatly increase the amount of potential inoculum. With a mild winter, sufficient early spring moisture, and prevailing southerly spring winds, the inoculum can multiply and rapidly spread northward into Oklahoma and Kansas. Grazing reduces the amount of inoculum, but does not eliminate it.

The widespread use of the dual-purpose management system in the southern Great Plains increases the need for varieties with seedling resistance to leaf rust. Adult plant resistance based on major genes has been the primary resistance mechanism. Several breeding programs have initiated efforts to incorporate the durable leaf rust resistance from the CIMMYT spring wheats (Lr 34 + minor genes), but this effort is several years from completion. Hopefully the incorporation of this gene complex will stabilize leaf rust resistance throughout the region. Breeders are also attempting to identify new leaf rust resistance genes from related species and from the “synthetic” wheats produced by CIMMYT. Most likely the new genes will be major genes, and every effort must be made to guard against the systematic erosion of their utility by the organism. The production of new gene combinations or pyramiding of these genes may also be viable alternatives to controlling leaf rust.

Stem rust

Stem rust (*P. graminis* f.sp. *tritici*) is endemic in northern Kansas, Nebraska, and South Dakota, but generally does not cause significant losses. Programs in these states must be diligent to maintain resistance to stem rust.

Barley yellow dwarf

Barley yellow dwarf (BYD) is prevalent throughout the southern and central Great Plains, and can cause serious losses, especially if infection occurs in the fall (Carver et al. 2001). Again, the dual-purpose system can increase potential losses because wheat sown in the early fall can serve as a host for aphids by providing them with a site for over-wintering. In favorable years, aphids can rapidly build up in the spring and spread BYD throughout the region. Losses of 20-30% are common in heavily infected fields, but average yield losses in the region are generally estimated at less than 5%. No known sources of genetic resistance to BYD are available, but some cultivars show varying degrees of tolerance.

Soilborne mosiac virus and other viral diseases

Soilborne mosaic virus (SBMV) is a significant disease in Oklahoma and Kansas, where it can seriously affect yield and test weight. Extended cool, wet conditions in the fall enhance infection, and symptoms, including leaf yellowing in a mosaic pattern and stunted plants, appear in early spring with the initiation of growth. Genetic resistance is the only known means of controlling the disease and, fortunately, various sources are available (Carver et al. 2001). Many of the wheats from Oklahoma and Kansas have adequate resistance levels. Recently at OSU, 21 randomly chosen spring wheats from CIMMYT were tested and 3 lines were found to have excellent resistance. However, only 6 of 100 winter wheat lines previously selected at CIMMYT showed resistance, and, of these, 2 were from France, 3 were CIMMYT materials crossed to an advanced line from Oklahoma, and only 1 had complete CIMMYT parentage (unpublished data).

Wheat spindle streak mosaic virus (WSSM) is frequently associated with SBMV. Both viruses are transmitted by the same soil fungus and the symptoms appear at the same time, however, WSSM is localized and of lesser economic importance than SBMV.

Wheat streak mosaic is a viral disease transmitted by the wheat curl mite. It is of greatest importance in the western part of the region, particularly in western Kansas. Control is primarily achieved through cultural practices that eliminate volunteer plants in the fallow, which serve as host plants for the mite in the off-season. Genetic resistance does exist, e.g., TAM 107, which was considered resistant but is now susceptible to the prevalent strains (Harvey et al. 1999). New sources of resistance have been identified and are being incorporated into new cultivars.

High Plains disease is a viral disease that is also transmitted by the wheat curl mite. It is primarily found in the High Plains of Texas, normally in association with wheat streak mosaic. High Plains disease was identified in the last decade, and definitive research on the causal agent is underway.

Root and crown rots

Root and crown rots are present throughout the region and appear to be increasing, probably due to the predominant production system of wheat after wheat. The diseases caused by this complex of soilborne pathogens are most prevalent in early seeded fields (e.g., dual-purpose system), soils with a pH above 6.0, and when moisture stress and above-average temperatures occur in the winter months (December to February). Genetic resistance and screening techniques for these pathogens have not been identified and, therefore, breeding programs have not given priority to the problem (Carver et al. 2001). Currently, cultural practices and rotations are the only means of reducing yield losses due to this complex.

Aphids

Aphids (or greenbugs) are present throughout the region and frequently cause severe damage in selected areas. Breeders have diligently tried to develop wheat cultivars with greenbug resistance, but have been largely unsuccessful due to the adaptive advantage of biotype diversity present within greenbug field populations. TAM 110 is the only resistant cultivar grown today and its resistance will most likely be of short duration (Porter et al. 1997).

Several aphid species serve as vectors of BYDV and this is of primary importance. One of these, the bird cherry oat aphid (*Rhopalosiphum padi*), also causes feeding damage, which results in severe stunting of the root system and secondary effects on shoot development. Research is being conducted to develop a rapid screening technique with juvenile plants to assay feeding damage and identify resistant lines and varieties (Carver et al. 2001).

Hessian fly

Hessian fly is present in the region, but is of economic importance only in central and south Texas and eastern Kansas and Nebraska. Resistant cultivars are available, but new biotypes of Hessian fly appear frequently.

Breeding for Resistance to Abiotic Stresses

Drought tolerance

Cultivars with good drought tolerance are needed where rainfall is low and has a highly variable distribution. This characteristic is particularly important in the western part of the region where the annual rainfall is low. Drought is commonplace even in the higher rainfall areas (>600 mm), due to the high frequency of extended periods with little or no rain during the growing cycle. Good drought tolerance has always been a primary breeding objective in all of the region's improvement programs. Cultivars with good tolerance are generally identified by multilocational testing within a state, followed by testing in the regional trials of the Great Plains. The predominant varieties typically have acceptable-to-good levels of drought tolerance. Cultivars Triumph and TAM 107 are recognized as having an exceptional ability to produce reasonable yields and excellent seed under harsh moisture conditions.

High temperature (heat) tolerance

Tolerance to high temperatures is a very desirable varietal trait in the southern part of the region, and is probably associated with drought tolerance. The spring season in the southern Great Plains is typified by widely fluctuating temperatures (daytime highs of 20-37ºC) and frequent days of moderate to strong winds (30-50 km / h). The grainfilling period for this region is May and if winds coincide with moderately high to high temperatures during this period, leaf desiccation can occur and frequently does so, especially if the crop is under moisture stress. Subsequently, grainfilling must rely on the photosynthetic activity of the peduncle, glumes, and awns, which undoubtedly reduces yield. Tolerance to these conditions is being pursued by many breeding programs in the region, primarily by selecting for types that retain their leaves for a longer period of time, i.e., the “stay green” characteristic. Variation does exist and progress is being made. Efforts are also underway to transfer the stay green characteristic from selected CIMMYT spring wheats.

Acid soil tolerance

In the last 10-15 years the area of low pH soils has increased, probably due to fertilizer practices, which have customarily used anhydrous ammonia. Although the level of aluminum saturation is moderate in most cases, it is sufficiently high to warrant the use of varieties with tolerance to acid soils or aluminum. Acid soil tolerance varies among adapted varieties in the region, and producers must be careful to choose the appropriate variety for their conditions. A nontolerant variety grown in acid soils will give poor forage production and reduced grain yield. Genetic variation is available and tolerant varieties are in cultivation (2163, 2180, 2137, and Jagger), but continued selection for this trait is a priority in the Oklahoma and Kansas programs (Johnson et al. 1997).

Important agronomic traits

Other agronomic traits that are important in the region include sufficient winterhardiness (requirements decrease from north to south), appropriate heading date (early, but not too early, to avoid late frosts), appropriate maturity, plant height (semidwarf), good straw strength (to withstand winds), shattering resistance, and high test weight. Efforts are also underway to increase head size by increasing spikelet number and fertile florets per spikelet. In southern areas, however, this objective will be more difficult to realize since the period between anthesis and maturity is normally only 35-40 days (Carver et al. 2001).

Industrial quality

The Great Plains has traditionally grown hard red winter wheat, but recently most programs in the region have also begun developing hard white winter wheats. The earliest and most active program for white wheat development has been in Kansas, but recently Oklahoma and Nebraska have also released white seeded varieties. Several white seeded varieties are being grown by producers, but the area is limited. Initially, the white wheats were developed in response to demand from the international marketplace, but now several domestic buyers are also interested. A problem has emerged related to grain handling facilities, which were originally designed to handle a single class of wheat, but now must adapt to a dual-class production system. Widespread adoption of the white seeded varieties is limited by a lack of post-harvest dormancy (sprouting resistance), and, subsequently, they are recommended for the drier areas in the west of the region (Carver et al. 2001).

All improvement programs must give high priority to industrial quality characteristics in order to meet the standards established for the region. Many promising lines are discarded each year due to unacceptable quality. International buyers of hard winter wheat are now requesting increased consistency in kernel size, even though this characteristic can vary greatly with environmental conditions. Overall milling and baking quality has not declined with the release of higher yielding cultivars or with the introduction of the semidwarf character—a major accomplishment of the various breeders in the region (Cox et al. 1989).

Summary

The southern and central Great Plains is an adverse wheat-growing environment. Lack of moisture limits yield potential in all parts of the region, especially in the arid west. High temperatures and hot dry winds further reduce yield potential in the southern and, sometimes, central parts of the region. Diseases and insects negatively affect yield potential throughout the region, and breeding programs are currently giving priority to the major diseases of their respective areas. Little attention is being given to developing varieties with improved resistance to minor diseases such as septoria, tan spot, helminthosporium leaf spot, and root and crown rots. Resistance to BYD is urgently needed, but effective sources of resistance have not been identified.

Genetic yield gains have been relatively consistent over the last 40-50 years, but average yields remain quite low. Presently, all predominantly grown varieties in the southern Great Plains (Jagger, 2137, Custer, and TAM 107) are susceptible to leaf rust, however, new varieties have been, or are about to be, released from various programs. New varieties include Trego (white), Lakin (white), Stanton, and KS92P0630-4-5 from Kansas; 2174, OK101, and Intrada (white) from Oklahoma; TAM 110 and TAM 400 (AgriPro) from Texas; Millennium, Cougar, and Nuplains (white) from Nebraska; Prairie Red, Yumar, and Prowers 99 from Colorado; Venango (Goertzen); and Thunderbolt and Dumas (AgriPro). These varieties have improved yield potential and many have good leaf rust resistance, which will be advantageous for the southern Great Plains.

It has been difficult to increase genetic variability due to the strict end-use requirements (quality) and specific adaptation required for the Great Plains. Despite these difficulties, some new genetic variability has been introduced into the gene pool in recent years, but additional diversity is still needed. Efforts are underway in several breeding programs to introgress new genetic variability. A cooperative winter wheat breeding effort has been initiated between Oklahoma State University and CIMMYT, and Kansas State University has recently joined the program. The immediate objective is to intercross the CIMMYT winter and spring gene pools with the winter wheats of the southern and central Great Plains. This cooperative program would benefit from the involvement of all of the wheat improvement programs in the Great Plains. Also, CIMMYT's regional winter wheat programs in Turkey, Kazakhstan, and China are slated to be active participants. Discussions are underway to achieve this objective and the initial reaction has been very positive. A close working relationship between the participants in this cooperative research program and national program scientists from the major winter wheat producing countries in the developing world will also be an objective. Obviously, considering the requirements for varietal improvement in the Great Plains, and the expanded mandate of CIMMYT in the winter wheat regions worldwide, this cooperation could prove to be a win-win situation for all parties involved.

References

Bayles, B.B., and J.A. Clark. 1954. Classification of wheat varieties grown in the United States in 1949. *USDA Technical Bulletin* 1083:1-173.

Briggle, L.W., S.L. Strauss, D.E. Hamilton, and G.H. Howse. 1982. Distribution of the varieties and classes of wheat in the United States in 1979. *USDA Statistical Bulletin* 676:1-107.

Carver, B.F., A.R. Klatt, and E.J. Krenzer, Jr. 2001. The North American wheats: U.S. hard winter wheat pool. In: *World Wheat Book* (in press).

Carver, B.F., and J.D. Ownby. 1995. Acid soil tolerance in wheat. In: D.L. Sparks (ed.), *Advances in Agronomy*, Vol 54, pp. 117-173. Academic Press Inc.

Clark, J.A., and K.S. Quisenberry. 1948. Distribution of the varieties and classes of wheat in the United States in 1944. *USDA Circular* 761:1-80.

Cox, T.S. 1991. The contribution of introduced germplasm to the development of U.S. wheat cultivars. *CSSA Special Publication* 17:25-47.

Cox, T.S., M.D. Shogren, R.G. Sears, T.J. Martin, and L.C. Bolte. 1989. Genetic improvement in milling and baking quality of hard red winter wheat cultivars, 1919 to 1988. *Crop Science* 29:626-631.

Dalrymple, D.G. 1988. Changes in wheat varieties and yields in the United States, 1919-1984. *Agricultural History* 62(4):20-36.

Feyerherm, A.M., G.M. Paulsen, and J.L. Sebaugh. 1984. Contributions of genetic improvement to recent wheat yield increases in the USA. *Agronomy Journal* 76:985-990.

Harvey, T.L., D.L. Seifers, T.J. Martin, G. Brown-Guedira, and B.S. Gill. 1999. Survival of wheat curl mites on different sources of resistance in wheat. *Crop Science* 39:1887-1889.

Johnson, J.P., Jr., B.F. Carver, and V.C. Baligar. 1997. Productivity in great plains acid soils of wheat genotypes selected for aluminium tolerance. *Plant and Soil* 188:101-106.

Peterson, C.J. 1992. Similarities among test sites based on cultivar performance in the hard red winter wheat region. *Crop Science* 32:907-912.

Porter, D.R., J.D. Burd, K.A. Shufran, J.A. Webster, G.L. Teetes. 1997. Greenbug (Homoptera: Aphididae) biotypes: selected by resistant cultivars or preadapted opportunists? *Journal of Economic Entomology* 90:1055-1065.

Quisenberry, K.S., and L.P. Reitz. 1974. Turkey wheat: The cornerstone of an empire. *Agricultural History* 48:98-110.

Reitz, L.P., and L.W. Briggle. 1960. Distribution of the varieties and classes of wheat in the United States in 1959. *USDA Statistical Bulletin* 272:1-83.

Reitz, L.P., and L.W. Briggle. 1966. Distribution of the varieties and classes of wheat in the United States in 1964. *USDA Statistical Bulletin* 369:1-68.

Reitz, L.P., and W.G. Hamlin. 1978. Distribution of the varieties and classes of wheat in the United States in 1974. *USDA Statistical Bulletin* 604:1-98.

Reitz, L.P., and K.L. Lebsock. 1972. Distribution of the varieties and classes of wheat in the United States in 1969. *USDA Statistical Bulletin* 475:1-70.

Salmon, S.C., O.R. Mathews, and R.W. Leukel. 1953. A half century of wheat improvement in the United States. *Advances in Agronomy* 5:1-151.

Salmon, S.C., and L.P. Reitz. 1957. Distribution of the varieties and classes of wheat in the United States in 1954. *USDA Agriculture Handbook* 108:1-86.

Frontier Science in the CIMMYT Wheat Program (2001-05)

S. Rajaram

Wheat Breeding in the World Today

Population growth rates in the developing world today are such that demands for food and, in particular, wheat grain, keep rising at a much faster pace than yield increases are being generated. Analysts predict that by 2020, 67% of the wheat consumed in the world will be used in developing countries. In the next 20 years, the world's farmers will have to produce 40% more grain to meet the demand for cereals, wheat among them (Pinstrup-Anderson et al. 1999). In the face of those demands, CIMMYT's wheat breeding strategy has evolved to include several new research thrusts that should speed up the pace of wheat yield gains over the next 20 years and beyond.

CIMMYT's Solid Foundation

Before describing the new methodologies being applied by the Wheat Program today, it is important to note that our "frontier" science, like CIMMYT itself, builds upon a foundation laid down more than 50 years ago by Drs. N.E. Borlaug, E. Wellhausen, and colleagues. Although CIMMYT was founded in 1966, its wheat breeding history harks back to the research conducted by Borlaug at the Office of Special Studies, a joint Mexican Government/Rockefeller Foundation initiative started in 1944. Those efforts culminated in the development of high-yielding, semidwarf wheat varieties that were highly resistant to stem rust, the worst wheat disease at the time.

The breakthrough that produced the new improved varieties was the incorporation into wheat of dwarfing genes that confer short stature and solid stems. Shorter wheats are able to produce more grain in response to fertilizer applications without toppling over under the added weight. Another key advantage of the new semidwarfs was their wide adaptability, a direct result of a novel breeding approach dubbed "shuttle" breeding, initiated and led by Borlaug. In shuttle breeding, two successive cycles of experimental wheat lines are grown in two contrasting environments each year. This alternation eventually causes the lines to become photoperiod insensitive and able to grow in a wide range of environments. These versatile varieties, cropped using fertilizer application and optimum water use technology, ultimately led to the Green Revolution that doubled wheat production levels in many developing world environments.

Maintaining the Momentum

After the initial boost in production in the early years of the Green Revolution, modern semidwarf wheats were disseminated to all corners of the globe, especially in the less developed nations. The semidwarfs continued to evolve, especially due to the introgression of new genetic diversity, the source of many useful traits.

In the 1970s and early 1980s, wheat genetic diversity was greatly expanded by crossing the winter and spring bread wheat genepools. The spring x winter wheat crossing program has been one of the most productive approaches used to develop improved wheat germplasm. In 1972, CIMMYT, in collaboration with Oregon State University (OSU) in the USA, began exploring these vast genepools much more extensively for the improvement of both pools. Crosses between spring and winter materials were made in Mexico. Collaborators at OSU, led by Dr. Warren Kronstad, worked on improving the winter-habit progeny, while CIMMYT breeders, led by this author, developed the spring types.

Those crosses produced the outstanding Veery spring wheats, which provided a yield increase of 15% over the spring wheats that were being grown in the developing world when they were first released. When advanced lines (later dubbed Veerys) derived from the spring x winter wheat cross Kavkaz/Buho//Kalyansona/Bluebird were tested in 73 environments of the 15th International Wheat Yield Nursery (15th ISWYN), their performance was superior to that of any previous high yielding varieties (Figure 1). The main advantages of the Veerys, besides their high yield potential, are resistance to multiple diseases (including leaf and stripe rusts, powdery mildew, and septoria), drought, heat, and cold tolerance, and the ability to use available inputs efficiently in low-input environments and to respond well when more inputs are applied. These superior characteristics, coupled with the Veery's adaptation to a wide range of environments, resulted in their rapid adoption by farmers in developing nations. Today Veery descendants such as Pastor outyield Veery in many environments (Figure 2).

Over the last 25 years, our direct clients, the national agricultural research systems (NARSs) of the developing world, have released at least 500 CIMMYT-derived cultivars, which have had far-reaching impacts and have changed wheat production forever. As an example, in 1970 average wheat yields in the Yaqui Valley and the Indian Punjab were 3 and 1.5 t/ha, respectively. By 2000, they had reached 6 and 4.2 t/ha. These data show not only the stability of the post-Green Revolution varieties, but also that wheat productivity per unit area has continued to increase due to the steady genetic gains in wheat yield potential and better agronomic practices.

Disease Resistance

For the high yielding potential of modern wheats to be realized, it must be accompanied by built-in genetic resistance to diseases. This protection against disease epidemics gives farmers reasonable assurance that they will reap adequate harvests year after year (yield stability).

The rusts

Over the years, CIMMYT wheats have been bred for resistance to all three types of rust (stem, leaf, and stripe), plus fusarium head blight, septoria diseases, barley yellow dwarf, tan spot, and Karnal bunt, among others. About 30 years ago, this author decided to apply the concept of "horizontal" (nonspecific) resistance, which is based on the accumulation of minor genes, in breeding for resistance to leaf and stripe rusts (see data on leaf rust resistance in Figure 3). The methodology paid off, and is still being applied today, not only for the three rusts, but for other diseases as well. Disease resistance genes have also been incorporated from different species, e.g., wheat's wild relatives. As a result of these combined strategies, today most wheat germplasm provided by CIMMYT possesses durable resistance to multiple diseases. Most important for avoiding potentially devastating disease epidemics, CIMMYT makes available to NARSs highly diverse germplasm for use in their breeding programs.

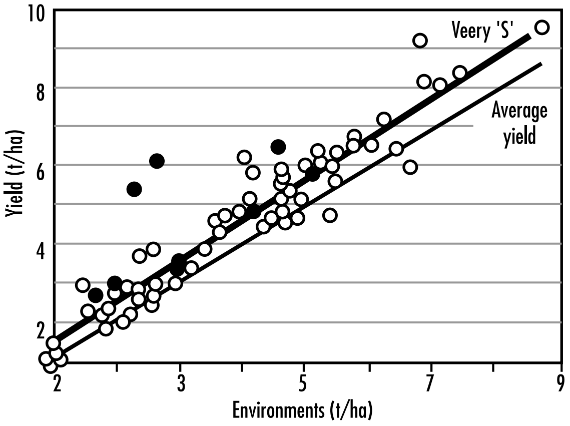


Figure 1. Yield of Veery 'S' in the 73 environments of the 15th International Spring Wheat Yield Nursery.

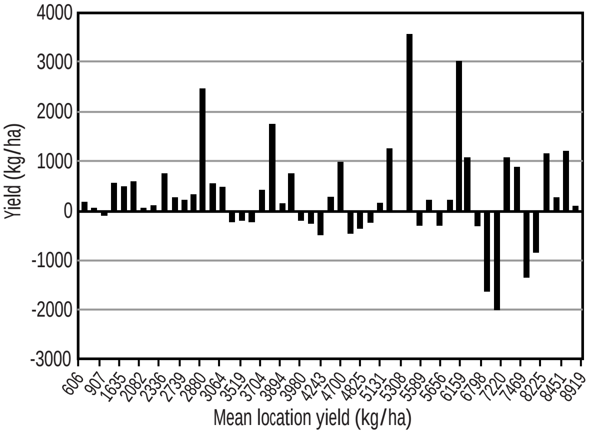


Figure 2. Grain yield difference between Pastor and Seri 82 at 50 locations of the 13th Elite Spring Wheat Yield Trial.

Fusarium head blight

In high rainfall environments, the major wheat production constraints are diseases. Among diseases affecting the spike, fusarium head blight (FHB), induced by various *Fusarium* species, is the number one problem, and seems to be expanding.

CIMMYT/China shuttle breeding program. In the mid 1980s, CIMMYT and China initiated a shuttle breeding and germplasm exchange program focusing

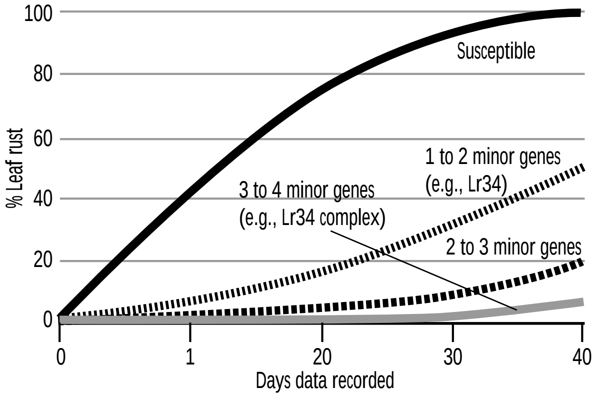


Figure 3. Horizontal resistance to leaf rust.

on incorporating the FHB resistance of Chinese wheats into high yielding CIMMYT germplasm. In the last 15 years, around 700 Chinese commercial varieties, advanced lines, and important FHB resistant wheats (such as Sumai 3, Ning 7840, Shanghai 3, Shanghai 4, Shanghai 5, Suzhou 6, Wuhan 3, and Chuanmai 18) have been sent to CIMMYT. A set of resistant bread wheat lines with good agronomic performance has been developed at CIMMYT through the use of Chinese germplasm.

In general, two types of crosses, Chinese/CIMMYT and Chinese/CIMMYT//CIMMYT, are used in Mexico when using Chinese germplasm to improve wheats for other countries and mega-environments (MEs). However, in CIMMYT crosses directed towards China, crosses are Chinese/CIMMYT//Chinese or sometimes CIMMYT/Chinese//Chinese. Currently, Chinese wheat can be found in the pedigrees of more than 50% of CIMMYT germplasm for high rainfall environments (ME2).

In addition to FHB resistance, Chinese spring wheat also shows good resistance to Karnal bunt, helminthosporium leaf blotch, tan spot, and septoria diseases. A large number of CIMMYT/Chinese crosses are made each year, and many Chinese derivatives are included in CIMMYT's international nurseries. The most outstanding CIMMYT bread wheat crosses under different mega-environments with Chinese germplasm in their pedigrees are presented below. They have shown good adaptation to locations outside Mexico.

ME1-Favorable /ME2-High Rainfall

1. GUAMUCHIL 92 (=CATBIRD=CHUM 18/BAU) (CM 91045-6Y-0M-OY-1M-8Y-0B-0MEX)
2. ARIVECHIL M92 (=LUAN=WUH1/GLEN/4/INIA 66/AG.DI//INIA 66/3/GEN (CM100587-E-0M-0Y-030M-8Y-1Y-0M-0MEX)
3. SHA 3/CBRD (CMSS92Y00595S)
4. WEAVER/WL3926//SW89.3064 (CMSS92Y01054T)
5. NG8675/CBRD (CMSS92Y00639S)
6. SW89.3064/STAR (CMBW91Y01627S)
7. XIANG82.2661/2*KAUZ (CMBW91Y02917M)

ME2-High Rainfall /ME3-Acid Soils

1. SHA4/CHIL (CM 91099)
2. CHIL/CHUM18 (CM92687)
3. XIANG82.2661/2*KAUZ (CMBW91Y02917M)
4. MILAN/SHA 7 (CM97550)
5. CHUM18//JUP/BJY (CM91046)
6. CBRD//VEE#10/2*PVN (CMSS93B01081S)
7. SHA3//SERI// G.C.W.1/SERI (CMBW91Y01596S)
8. HXL8088/DUCULA (CMSS93Y02492S)
9. BR14*2/SUM3//TNMU(CMBW91M02048S)

ME4-Low Rainfall

1. HXL 7573/2*BAU (CMBW91Y03634M)
2. NANJIANG 8646/KAUZ//BCN (CMBW8900966T)
3. HXL8246/KAUZ (CMBW90M2205)

ME5-High Temperature

1. G.C.W 1/SERI (CM86992)
2. SABUF (= SHA3//BUC/FLK) (CM95073)
3. SW8905124*2/FASAN (CMBW91Y03050F)
4. XIANG82.2661/2*KAUZ (CMBW91Y02917M)

Other sources of FHB resistance. The CIMMYT Wheat Program requests, receives, and specifically develops genetically diverse germplasm with resistance to FHB. Various reports documenting these sources are available (Gilchrist et al. 1997a, 1997b; 1999). Also, genetic studies aimed at determining modes of inheritance have been carried out and published (Singh et al. 1995; van Ginkel et al. 1996). In recent years efforts by the pathology group have concentrated on differentiating germplasm in regard to the four types of resistance commonly applied in FHB (I, II, III, and IV). Our breeding strategy has focused on combining different resistances in adapted backgrounds (Singh and van Ginkel 1997).

A group of relatively new CIMMYT bread wheat lines have recently been found to have high levels of resistance to FHB; until now they have not been commonly used in breeding programs targeting FHB. These entries are listed in Table 1.

Abiotic Stress Tolerance

Breeding for tolerance to drought, heat, and aluminum toxicity began in the early 1980s at CIMMYT. Our strategy has been to incorporate stress tolerance into germplasm that is already high yielding and has adequate disease resistance. We have found that high yield potential and adaptation to drought, heat, and aluminum toxicity are not negatively correlated and hence can be combined easily. Our strategy has led to the development of, among others, drought tolerant wheat variety Baviacora and heat tolerant variety Seri 82, excellent examples of how well these genetic combinations work.

Table 1. CIMMYT bread wheat lines carrying Type II resistance to fusarium head blight with infection values under 6%. The first five entries are comparative checks.

Cross	Selection history	Type II resistance (%)
MAYOOR	Check: Moderately resistant	7.91
SUMAI#3	Check: Moderately resistant	9.20
SERI/CEP80120	Check: Moderately susceptible	14.84
FLYCATCHER	Check: Moderately susceptible	21.04
BCN//DOY1/AE.SQUARROSA (447)	Check: Susceptible	32.93
SHA3/CBRD	CMSS92Y00595S-1SCM-0CHN-015Y-3SCM	2.50
NG8675/CBRD	CMSS92Y00639S-1-5SCM-2M-6Y-010SCM-0Y-0SCM	2.52
HXL8088/DUCULA	CMSS93Y02492S-2Y-010M-010Y-010M-10Y-1M-0Y-3SJ-0Y	2.59
CROC_1/AE.SQUARROSA (205)//BORL95	CIGM90.250-4Y-3B-4Y-0B-2M-24M-0Y-010SCM-0Y-0Y-0Y	3.41
GUAM92//PSN/BOW	CMSS92M01860S-015M-0Y-050M-0Y-11M-0Y	3.64
TNMU/3/JUP/BJY//SARA	CMBW91M02016S-0M-040Y-1AL-2AL-7Y-0M-3SJ-0Y	3.70
R37/GHL121//KAL/BB/3/JUP/MUS/4/2*YMI #6/5/CBRD	CMBW91Y01575S-4Y-010M-010Y-015M-2Y-0M-1SCM-010Y-010SCM-1PZ-0Y	4.31
MILAN/DUCULA	CMSS93B01075S-74Y-010M-010Y-010M-8Y-0M-2SJ-0Y	4.72
THB//MAYA/NAC/3/RABE/4/MILAN	CMSS92Y02157T-50Y-015M-010Y-010Y-9M-0Y	4.84
NG8319//SHA4/LIRA	CMBW90M2302-6M-010M-010Y-015M-6Y-0M-0ECU-0Y	4.84
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-9Y-0M-0URY	4.85
R37/GHL121//KAL/BB/3/JUP/MUS/4/2*YMI #6/5/CBRD	CMBW91Y01575S-4Y-010M-010Y-015M-5Y-0M	4.92
NG8319//SHA4/LIRA	CMBW90M2302-6M-010M-010Y-015M-8Y-0M-5SJ-0Y	4.92
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-6Y-0M-3SJ-0Y	5.00
KAUZ/TNMU	CMSS93B01069S-54Y-010M-010Y-010M-8Y-0M-3PZ-0Y	5.00
MAYOOR//TK SN1081/AE.SQUARROSA (222)	CASS94Y00009S-18PR-2M-0M-1Y-0M	5.00
SHA3/SERI//G.C.W 1/SERI	CMBW91Y01596S-2Y-010M-010Y-015M-6Y-0M-1SJ-0Y-010SCM-2PZ-0Y	5.26
HXL8088/DUCULA	CMSS93Y02492S-2Y-010M-010Y-010M-10Y-1M-0Y-2PZ-0Y	5.26
SHA3/CBRD	CMSS92Y00595S-4GH-0M-0SCM-0Y	5.26
TNMU/TUI	CMBW89M3847-64M-0AL-5AL-2B-0Y	5.30
ALUCAN/DUCULA	CMBW89M3764-36M-0AL-2AL-2B-0Y-5PZ-0Y	5.36
IAS64/ALDAN//URES/3/TNMU/4/TNMU	CMBW90M4487-0TOPY-14M-11AL-0AL-07Y-1M-0Y-1SJ-0Y	5.36
SABUF/5/BCN/4/RABI//GS/CRA/3/AE.SQUARROSA (190)	CASS94Y00042S-9PR-1M-0M-1Y-0M	5.51
793.3402//BUC/PVN/3/KAUZ/4/NJ8611	CMSS92Y02234T-7Y-015M-015Y-010M-2Y-0M-1SCM-010Y-010SCM-0Y	5.56
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-9Y-0M-2SCM-010Y-010SCM-0Y-0SCM	5.61
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-10Y-0M	5.65
TNMU/MUNIA	CMSS93B01052S-18Y-010M-010Y-010M-6Y-1M-0Y	5.66
NING8745/3/2*CHUM18//JUP/BJY	CMBW91Y02939M-030TOPM-9Y-010Y-015M-1Y-0M-0E-0ECU	5.74
R37/GHL121//KAL/BB/3/JUP/MUS/4/2*YMI #6/5/CBRD	CMBW91Y01575S-4Y-010M-010Y-015M-2Y-0M-1SCM-010Y-010SCM-3SJ-0Y	5.74
NG8675/CBRD	CMSS92Y00639S-1-5SCM-2M-6Y-010SCM-0Y	5.74
THB/CEP7780//SHA4/LIRA	CMBW90M2456-9M-010M-010Y-015M-10Y-0M	5.77
SHA3/CBRD	CMSS92Y00595S-5GH-0M-0Y-0SCM-0Y	5.85
NL456/VEE#5//PASA/3/BOW/GEN//KAUZ	CMSS93Y03376T-44Y-010Y-010M-010Y-8M-0Y	5.88
TUI/MILAN	CMSS92Y00540S-030Y-015M-0Y-0Y-18M-0Y	5.88
ISD-75-3-1/MO88//PRL/VEE#6	CMBW90M4731-0TOPY-42M-3Y-010M-3Y-9M-2KBY-05KBY-0B-0KEN	5.93

Data source: L. Gilchrist, CIMMYT Wheat Program.

Raising Wheat's Yield Potential

A new wheat plant type

CIMMYT bread wheat breeders are working on a new wheat plant type that, if it becomes a reality, will have higher yielding capacity than current wheats. The new plants have bigger spikes and produce twice as many grains as current wheats (Figure 4). These plants are a blend of genetic resources from all over the world—Yugoslavia, Canada, Mexico, Morocco, and Israel. If successful, the new plants could boost wheat yields by as much as 30%.

The new plant type has been dubbed "agropolitetra" wheat based on the Latin names of the contributing species. In addition to the outstanding traits described above, these new wheats will have intermediate tillering capacity, broad leaves, and thick stems. Most of these traits have already been incorporated into the agropolitetra wheats, but the grain they produce is shriveled, and most plants are susceptible to diseases such as leaf and stripe rusts. Thus scientists are still working to help the plant fill its grains. The aim is to achieve a balance, with a slightly reduced head size, but with spike fertility completely restored. The ideotype is also being exploited by the hybrid breeding program.

Figure 4. The new wheat plant type (right) has bigger spikes and produces twice as many grains as "normal" wheat (left).

Hybrid wheat

Work on hybrid wheat production was renewed at CIMMYT in the 1990s in response to the expressed interest of the national agricultural research systems of client countries such as India and China. The main advantage of hybrids is that they allow the exploitation of heterosis (hybrid vigor) to increase wheat grain yields.

CIMMYT was able to take up hybrid research because new, more effective chemical hybridizing agents (CHAs) for creating male sterility have made hybrid development less difficult. Effective CHAs such as Genesis®,[1] approved by the US Environmental Protection Agency in 1997, permit the production of large numbers of hybrids from very diverse germplasm in a short period of time. At CIMMYT Genesis® is being used to develop bread wheat hybrids from high yielding, widely adapted advanced lines. Results indicate that positive heterosis for grain yield exists in CIMMYT bread wheat lines under irrigated conditions. Also promising is that the highest yielding hybrid (10.6 t / ha at 12% moisture content) in recent two-year tests had a 17% yield advantage over the check cultivar. If successful, these efforts will ultimately lead to materials that could increase yields by 10-15% above those of currently planted commercial varieties.

Getting developing world farmers to adopt hybrid wheat will depend largely on the cost of hybrid seed, which is higher than that of conventional wheat because of the extra costs associated with male sterilization and cross-fertilization. To solve this problem, CIMMYT is working on improving seed set of female lines in the field. Hybrid production is also strongly affected by climatic conditions such as temperature, rain, relative humidity, and wind. CIMMYT is therefore studying different locations to determine their suitability for hybrid seed production.

Agropolitetra and hybrid wheats should enter yield trials in 2001. We are confident that trial results will confirm the promise of these new wheats.

Wheats bred from wild grass species

Species that grow in the wild and are closely related to wheat are a novel source of new genetic diversity for many traits associated with high yield, including disease resistance. By crossing durum wheat with some of these wild relatives, researchers have created "synthetic" bread wheats that allow them to tap into the desirable genes present in wild species. (They are called "synthetics" because they synthesize, or bring together, the diversity in wild species in a form that breeders can use.)

---

[1] Genesis is a registered trademark of the Monsanto Company.

Synthetic wheats possess resistance to many diseases (e.g., Karnal bunt, fusarium head scab, helminthosporium spot blotch) as well as tolerance to environmental stresses such as heat, drought, and lodging. Though not adequate for farm production, synthetics can be crossed readily with high yielding wheats, thereby acting as a “genetic bridge” that allows useful traits to be transferred to improved wheat. Disease resistance can be extremely valuable for preserving yields; for example, scab alone has been reported to cause losses of billions of dollars and millions of tons of grain in the US and China. To date, the CIMMYT Wheat Wide Crosses Unit has formed about 830 synthetics and, of these, several lines have shown very high levels of resistance to scab (e.g., infection rates of only 5–10%, compared to 45–60% in susceptible checks).

Durum Wheat

In the 1998/99 crop cycle durum wheat yields under optimum conditions in northwestern Mexico reached 11.7 t/ha, 17% higher than Altar, the previous highest yielding durum (10 t/ha). Besides being good yielders, these durums are tolerant to drought and heat. They are also very input efficient, which allows them to take advantage of the nutrients in the soil to produce higher yields in marginal environments. These increases in durum wheat’s yield potential were achieved by successfully raising both spikes per square meter and the number of grains per spike. This suggests that a nearly optimum balance in yield components has been achieved, and that future progress has to be based on increasing biomass production, most likely with the aid of physiological selection criteria and molecular markers to accelerate the breeding process.

Table 2. Performance of synthetically derived lines compared to that of Baviacora 92 under irrigated conditions, 2001 cycle, Yaqui Valley, Sonora, Mexico.

Cross	Grain yield (% of Bav92)	Days to flowering	Days to physiol. maturity	Plant height (cm)
Altar84/*Ae.sq.*219//2*Seri	106	94	145	109
Cndo/R143//Ente//Mexi75/3/ *Ae. sq.*/4/2*Fct/5/Parus	105	84	132	105
Altar84/*Ae. sq.*219//2*Seri	105	89	139	122
Croc1/*Ae. sq.*224//2*Opata	105	84	134	108
Cndo/R143//Ente//Mexi75 3/*Ae. sq.*/4/2*Fct/5/Kauz*2/ Yaco//Kauz	104	97	145	111
Duerd2/*Ae. sq.*214//2*SKauz	104	79	130	109
Duerd2/*Ae. sq.*214//2*Bcn	104	88	136	106
Cndo/R143//Ente//Mexi75/3/ *Ae. sq.*/4/Weaver/5/Oasis/ SKauz//4*Bcn	103	91	135	109
Croc1/*Ae. sq.*205//Borl.95	103	93	145	96
Cndo/R143//Ente//Mexi75/3/ *Ae. sq.*/4/2*Fct/5/Parus	102	84	132	103

Data source: R. Villareal, CIMMYT Wheat Program.

A special effort is being made to develop durum wheat for marginal environments in regions such as West Asia and North Africa (WANA), where it is used to make bread, couscous, and other local foods that make up the basic diet of a large portion of the population. Farmers in WANA usually grow durum in low moisture conditions, and the crop must be capable of tolerating drought. To provide them with durums that do well despite water scarcity, CIMMYT researchers have started simulating different levels of drought stress through the use of drip irrigation, which makes it possible to apply the exact amount of water to the soil surface without flooding the subsoil. The end result will allow CIMMYT breeders to tailor wheats to specific drought-stressed regions and provide farmers with varieties they can rely on to produce well year after year.

Triticale

Triticale is now grown on more than 3 million ha worldwide. Its popularity is due to its vastly improved yield potential and grain quality and the great advantage it has over other crops for use as food or feed. Different types of triticale are now available for making cookies, flatbread, pasta, and yeast bread (mixed with wheat flour). Other triticales have been developed specifically for use as a dual-purpose (feed and forage) source for livestock. Preliminaries studies have shown that from a nutritional standpoint these dual-purpose triticales are significantly better for animal consumption than conventionally used crops.

Triticale has the added advantage of doing well in drylands, acid soils, sandy and saline soils, and insect- and disease-infested areas. These traits suggest that triticale could be appropriate for stressed farm environments in South America, North Africa, Kenya, and South Africa.

Raising Yields in Marginal Areas

In the last two decades, wheat yield potential has been rising at a more rapid rate in marginal areas than in favorable environments. Data generated from CIMMYT’s International Spring Wheat Yield Nursery (ISWYN) and the Elite Spring Wheat Yield Trial

(ESWYT) indicate that growth in wheat yield potential in drought-prone environments has been rising at an annual rate of about 3.1% from 1979-99. In contrast, wheat yield potential in favorable environments has been rising at a rate of 1% a year.

What has caused wheat yield potential to grow so fast in marginal areas? In some cases, newer, higher yielding wheat varieties developed for favored areas finally became available to farmers in more marginal areas. CIMMYT's Veery wheats, for example, were originally developed for favorable environments about two decades ago, but have adapted well to most marginal environments. Their descendants have yielded better than other cultivars in both high yielding and stress environments. Since 1979, wheat yields in dry environments have grown at a rate of 3.48% per year, compared to 0.82% per year under irrigated conditions (Table 3).

Table 3. Trends in developing country wheat yield potential by environment, Elite Spring Wheat Trial, 1979-99.

	Environments			
	Irrigated ME1	High rainfall ME2	Dry ME4	Hot ME5
Growth rate (%/year)	0.82	1.16	3.48	2.10
Yield gain (kg/year)	53.50	62.50	87.70	46.10

Source: Lantican et al. (2001).

Application of Biotechnology in Wheat Breeding

The CIMMYT Wheat Program makes use of different biotechnological methods to accelerate and facilitate its research. A prime example is our wide crosses unit, which was established 30 years ago and has produced a treasure trove of synthetic wheats whose utility we are just starting to explore. In addition, the Program, in collaboration with CIMMYT's Applied Biotechnology Center, is applying methodologies such as molecular markers and genetic transformation as aids in, for example, improving resistance to barley yellow dwarf (BYD) and determining the genetic diversity in CIMMYT wheats.

Farmer Participatory Research

For the past four years the CIMMYT Wheat Program has made special efforts to strengthen wheat research targeting the less productive areas of South Asia through farmer participatory research. Farmer participatory variety selection (PVS) is being conducted in the Eastern Subcontinent of South Asia (northern Pakistan, eastern India, and Nepal), which trails other areas in the region in the adoption of improved wheat varieties and resource conserving technologies. Though wheat production is an economic mainstay in the region, it lags far behind its potential, as evidenced, for example, by the fact that the average wheat yield is only 50% of that in the Indian Punjab. As a result, grain production increases in the region are not keeping up with the high population growth rate (2.2% a year).

Farmer PVS activities are concentrating on two important factors that are keeping wheat yields low in the area: farmers' cultivation of old, low-yielding, disease-prone varieties and the lack of an effective system for placing new technologies in their hands. Researchers are trying PVS as an alternative technology-delivery system for getting farmers to try new technologies and accept them.

An example of such activities is the PVS exercise that was conducted in Kotounge Village, Bahtapur District, Kathmandu Valley (located at approximately 1500 masl, the mid-hills) in Nepal during the 1999/2000 season. The main wheat variety in the mid-hills is the old, low yielding, and disease susceptible variety RR-21 (=Sonalika).

A participatory field day was organized to allow farmers to quantitatively assess 10 improved wheat lines and/or varieties grown in a farmer-managed trial. Thirty farmers (men and women) preferred wheat variety BL-1473 due to its early maturity, bold seed, good straw yield, high fertility, and lodging tolerance. BL-1473 yielded 30% more grain than RR-21.

A survey conducted a few days before the PVS exercise began showed that the ratio of new, improved vs old varieties (mainly disease susceptible RR-21) in the area was 10% to 90%. We are optimistic that this ratio will be reversed in 2001/02 and that the new variety will be adopted by farmers in the mid-hills, since 95% of seed dissemination occurs from farmer to farmer.

Preparing for the Future

The only way to face the future with a certain degree of confidence is to prepare for it to the best of our ability. The challenges confronting the international agricultural research centers are enormous, but not impossible. The key to successfully dealing with them, particularly in the area of plant breeding, where products take 10 years or more to emerge, is to plan ahead. If we constantly size up the needs of our clients, the national agricultural research systems of the developing world, we will be able to modify our breeding strategies accordingly. We have to maintain enough flexibility and openness to identify and assay new methods that could accelerate our work or make it more efficient.

The different approaches I have described in this paper give an idea of the spectrum of "frontier" technologies that the CIMMYT Wheat Program is working on, but we are constantly evaluating the potential and relevance of new technologies. Our first priority is to choose the most appropriate methods available, and then balance the mix of new and proven approaches we apply, to ensure that we continue to achieve the productivity gains needed to fulfill the ever-increasing demand for wheat in the developing world.

References

Gilchrist, L., S. Rajaram, A. Mujeeb-Kazi, M. van Ginkel, H. Vivar, and W. Pfeiffer. 1997a. Fusarium scab screening program at CIMMYT. In: H.J. Dubin, L. Gilchrist, J. Reeves, and A. McNab (eds.), *Fusarium Head Scab: Global Status and Future Prospects,* pp. 7-12. Mexico, D.F.: CIMMYT.

Gilchrist, L., S. Rajaram, M. van Ginkel, A. Mujeeb-Kazi, and J. Franco. 1997b. Characterizing *Fusarium graminearum* resistance of CIMMYT bread wheat germplasm. *Cereal Research Communications* 25 (3-2):655-657.

Gilchrist, L., S. Rajaram, M. van Ginkel, C. Velázquez, and J. Crossa. 1999. Transferring fusarium head blight resistance from bread wheat sources to high yielding advanced lines. In: National Fusarium Head Blight Forum; South Dakota, pp. 162-163.

Lantican, M.A., P.L. Pingali, and S. Rajaram. 2001. Growth in wheat yield potential in marginal environments, pp. 75, these proceedings.

Pinstrup-Andersen, P., R. Pandya-Lorch, and M.W. Rosegrant. 1999. *World Food Prospects: Critical Issues for the Early Twenty-first Century.* Washington, DC: International Food Policy Research Institute (IFPRI).

Singh, R.P., Hong Ma, and S. Rajaram. 1995. Genetic analysis of resistance to scab in spring wheat cultivar Frontana. *Plant Diseases* 79:238-240.

Singh, R.P., and M. van Ginkel. 1997. Breeding strategies for introgressing diverse scab resistances into adapted wheats. In: H.J. Dubin, L. Gilchrist, J. Reeves, and A. McNab (eds.), *Fusarium Head Scab: Global Status and Future Prospects,* pp. 86-92. Mexico, D.F.: CIMMYT.

van Ginkel, M., W. van der Schaar, Y. Zhuping, and S. Rajaram. 1996. Inheritance of resistance to scab in two wheat cultivars from Brazil and China. *Plant Diseases* 80:863-867.

Warren E. Kronstad Memorial Symposium

N.E. Borlaug

As a scientist and a human being, Warren Kronstad was a giant of a man, not only for me personally, but for many others. He was the pride of Oregon State University (OSU), and a dear friend and colleague for nearly 40 years.

Warren was an outstanding agricultural research leader and distinguished professor, who contributed greatly to wheat research and production in the USA and also internationally. I dare say that he was a mentor to more foreign graduate students in wheat improvement and production than anyone of his generation. He has touched many lives around the world.

Domestic Small Grains Research and Selected Achievements

Warren's research contributions to wheat production in the Pacific Northwest are legendary. Beyond a series of important methodological contributions to plant breeding and genetics, Kronstad and his OSU research team have developed many genetically superior cultivars including the soft white winter wheats Yamhill, Hyslop, McDermid, Stephens, Hill, Malcolm, Gene, and Hoff; two winter barleys, Casbon and Adair; and two winter oats, Lane and Amity.

Through identifying and pyramiding durable resistance genes, Kronstad-developed cultivars have had extended lives. Stephens, which at one time covered 75% of the winter wheat area in the Pacific Northwest, has been a major wheat cultivar for more than two decades.

Although repeatedly recognized by the wheat producers of Oregon, perhaps the highest tribute to Warren's achievements was the establishment of the OSU Wheat Research Endowed Chair: a US$ 1,000,000 endowment funded by the Oregon wheat producers and matched by Oregon State legislature.

Turkish Wheat Research and Production Program

Warren's contributions to international research were also substantial. Together with his OSU colleague, the late Tom Jackson, Warren developed a highly successful research and technology transfer program in the late 1960s to introduce semidwarf wheats into coastal areas of Turkey, with funding from the United States Agency for International Development (USAID) and the Turkish government. Some 23,000 tons of six wheat cultivars from the CIMMYT Wheat Program were imported into Turkey in 1968. These varieties were integrated into a successful package of management practices. Twelve OSU county extension agents were sent to Turkey to work with Turkish counterparts to disseminate the high-yield wheat package. Subsequently, Warren led a team of OSU specialists in weed control, dryland management, extension, and preparation of educational materials to work with Turkish scientists to develop improved wheat management practices on the Anatolian plateau, where most wheat is grown in Turkey. The package practices, built around improved summer fallow rotation, had a significant impact on yields. The introduction of new cultivars into the coastal areas, combined with the improved crop management practices on the Anatolian plateau, led to an almost three-fold increase in Turkish wheat production between 1967 and 1977.

In addition to the work in Turkey, a graduate training program was established at OSU under Warren's direction, where 15 young Turkish scientists were trained to MSc and PhD levels in various aspects of wheat research and production. Over the years, the OSU international graduate training program has expanded beyond Turkey. Through the program, more than 100 students from over two-dozen countries, including a number of outstanding Mexican scientists, have been awarded MSc and PhD degrees.

Winter Wheat Germplasm Enhancement

Under Warren Kronstad's leadership, a highly effective international network for exchanging genetic material and information on winter and facultative wheat was developed, involving the International Maize and Wheat Improvement Center (CIMMYT), the International Centre for Research in the Dry Areas (ICARDA), and, eventually, 45 countries. The countries of the former Soviet Union and the People's Republic of China, which historically had been highly protective of their plant genetic resources, became participants in this network.

The International Winter x Spring Screening Nursery (IWSWSN) is sent annually to all major research centers where winter and facultative wheats are important. A shuttle breeding approach is employed: select F_3 lines are identified in Pendleton, Oregon, and are shuttled to CIMMYT / ICARDA-Turkey and CIMMYT-Mexico for subsequent selection. Following several cycles of selection, the most promising lines are included in IWSWSN. This system of shuttle breeding and multilocational international screening, in which segregating populations are exposed to diverse selection pressures, has led to the development of cultivars with both broad and specific adaptation and high and stable yields.

Importance of International Germplasm Exchange and Testing

Many in this roomplant scientists may not know that organized international germplasm testing only began about 50 years ago in response to a disease epidemic of enormous proportions. In 1950, a devastating stem rust epidemic (race 15b) threatened all commercial wheat varieties in the USA and Canada. In response, the United States Department of Agriculture (USDA) appealed to eight countries—Mexico, Colombia, Ecuador, Peru, China, Brazil, Argentina, and Canada—to join in testing 1,000 wheat lines selected from the US World Wheat Collection, as well as advanced generation lines from several of the breeding programs in these countries, especially Mexico.

The results of the USDA's First International Stem Rust Nursery exceeded expectations in identifying stem rust resistant parents, and, today, much of the stem rust resistance in commercial wheat can be traced to the breeding materials identified from those early nurseries.

There were other benefits from this international cooperative effort of even greater importance than the identification of germplasm with resistance to race 15b of stem rust. A new mechanism for widespread international testing of germplasm—first in wheat and later in many other food crops—was in the process of formation.

CIMMYT's predecessor organization, the Office of Special Studies, an agricultural program of the Mexican Government and the Rockefeller Foundation, was a major contributor of advanced lines to the USDA's First International Stem Rust Nursery and to subsequent versions of this nursery. In addition, by 1962 a Rockefeller-FAO program for the Near East was sponsoring a regional wheat yield trial, and Rockefeller-Mexico also assembled a spring wheat yield trial for the Americas. In 1964, these were merged to become the International Spring Wheat Yield Trial (ISWYN), which CIMMYT prepared and distributed annually to hundreds of locations worldwide over the next 30 years. This nursery permitted breeders from around the world to test their best varieties over a broad range of geographic locations. The resulting data was invaluable in the development of the broadly adapted, high-yielding semidwarf wheat varieties with resistance to stem rust and other diseases, first in Mexico and later in many countries around the world.

International testing helped to break down psychological barriers that had separated the efforts of plant breeders in different organizations. Before the USDA's First International Stem Rust Nursery, many breeders were reluctant to release advanced lines from their breeding programs to fellow scientists for fear that the new varieties would be named and released without proper recognition of the breeder or organization. Early-generation segregating materials were rarely distributed to other scientists, largely for the same reason.

It became accepted policy that any line tested internationally could be used by collaborating scientists for breeding purposes or for distribution as a commercial variety, provided the source of the material was acknowledged. Not only did international testing introduce new genetic variability into national breeding efforts, it also provided individual breeders with the opportunity to simultaneously evaluate the adaptation and disease stability of their promising new materials in many different environments worldwide.

I believe it is fair to say that the advent of international testing marked the beginning of the modern era of plant breeding. It also gave rise to the Green Revolution, which saved untold millions from starvation in the 1960s and 1970s.

Through multilocational testing over a range of elevations and latitudes, we have been able to develop wheat germplasm with broad adaptation and general (race-nonspecific) disease resistance. Stable resistance to stem rust (*Puccinia graminis tritici*) has existed for more than 40 years. Moderate resistance to leaf rust *(P. recondita tritici)* exists, but the stability is still inadequate. Prior to 1960, devastating epidemics of these diseases, particularly stem rust, commonly occurred at least once every decade in many parts of both the developing and developed world.

Intellectual property rights (IPR), so important for mobilizing private capital for agricultural research, is a complicated issue and goes beyond the scope of this paper. However, I have concerns—along the same lines as obsolete plant quarantine regulations—about the potential of IPRs to disrupt the international flow of germplasm among scientific institutions. While it is not clear whether public sector institutions will generate significant revenue from biological patents, the potential for this to happen can affect the willingness of breeders to share germplasm for fear of jeopardizing future royalty income. Genetic conservation efforts may also be seriously hampered by the fear that the collecting agencies stand to gain from patenting economically useful genes.

Somehow we must find a way to keep international germplasm exchange and testing networks relatively free, open, and unfettered. A publicly funded germplasm system can and should complement proprietary research programs. However, the public program should also remain as an alternative provider of improved germplasm, both to maintain a "counterweight" to proprietary research and to serve nations where private research interest and activity is lacking.

These were matters of great concern to Warren Kronstad, and this symposium is an excellent opportunity for us to reflect on how best we can keep international cooperation and international germplasm exchange and testing alive and prospering.

Yield Potential of Bread Wheat Hybrids Produced by Genesis®

B. Cukadar and M. van Ginkel

Experts predict that the demand for wheat will increase by 40% in the next 20 years. Meeting this increased demand constitutes an enormous challenge, especially because yield levels of wheat may have reached a plateau in recent years. To increase wheat yield levels and meet the growing world demand for wheat, breeders need to exploit new technologies such as those now used to facilitate the development of hybrid wheat.

Although wheat hybrid production has been attempted in the past, it was for the most part abandoned due to the difficulties inherent to its development. However, interest in hybrid wheat was renewed in the 1990s, due to the availability of new, more effective chemical hybridizing agents (CHAs).

Compared to cytoplasmic male sterility systems, effective CHAs permit the production of large numbers of hybrids from very diverse germplasm in a very short period of time. Genesis®, a CHA produced by the Monsanto Company, induces male sterility in female lines when applied at the appropriate growth stage. It was approved by the US Environmental Protection Agency in 1997. That same year, the International Maize and Wheat Improvement Center (CIMMYT) re-started its hybrid wheat program in collaboration with Monsanto.

Heterosis may give hybrids a yield advantage over "normal" wheats. Yield advantages as high as 10-17% over the leading check cultivars have been reported for hybrid wheat in Italy and the UK. In China, a yield advantage of up to 30% has been reported for hybrids produced using CHAs. Other advantages have also been reported, such as hybrids' higher yield stability compared to pure lines.

The objectives of this study were to identify spring bread wheat hybrids with high yield potential under the irrigated conditions of the Yaqui Valley in northwestern Mexico.

Materials and Methods

During the 1996/97 growing season, advanced CIMMYT bread wheat lines were crossed as females to five high yielding male lines through the use of Genesis®. Hybrids were produced by crossing the same set of female lines to different male lines in a factorial mating design that allows calculating the lines' combining abilities for different traits. Female and male variation provides information about the general combining ability of female and male lines, respectively, whereas female by male interaction provides information about specific combining ability for hybrid combination.

A total of 148 hybrids were included in two separate yield trials during the 1997/98 growing season. One trial included hybrids that adhered to a complete factorial design (11 female lines with 5 male lines). Some combinations did not yield enough seed to meet the requirements of a factorial design. Therefore, all those hybrids were included in the second experiment. The first year hybrids were evaluated for yield potential, height, bread-making quality, and leaf rust reaction, and the best 42 hybrids were promoted to the second year of evaluation in the 1998/99 growing season.

All yield trials were conducted under fully irrigated conditions in Ciudad Obregon, Sonora, Mexico. The experimental design was a latinized alpha lattice. Plot size was 4.8 m^2, including two beds, 0.8 m wide and 3 m long. Three and two replications were evaluated during the 1997/98 and

1998/99 growing seasons, respectively. Two commercial varieties (Bacanora and Rayon) were included as checks in the trials. All female and male parental lines were also included in the trials to calculate heterosis. Seeding density for hybrids and parental lines was calculated based on 200 viable seeds per m^2. Each check was planted at two different densities: the farmer's density (100 kg/ha) and the hybrid density.

Table 1. Comparison of highest hybrid yields with those of check cultivar Rayon at 12 % grain moisture content for data combined over two years, Cd. Obregon, Mexico.

Entry	Yield (t/ha)	% Rayon
61	10.62	117
51	10.43	115
3	10.34	114
2	10.23	113
LSD (0.05)	0.93	
CV (%)	5.27	

Table 2. Analysis of variance for yield of hybrids grown during the 1997/98 growing season at Cd. Obregon, Mexico.

Source of variation	Degrees of freedom	Mean square
Replication	2	17.95
Female (F)	10	8.20**
Male (M)	4	46.08**
F x M	40	1.87**
Error	108	0.21

** Significant at the 0.01 probability level.

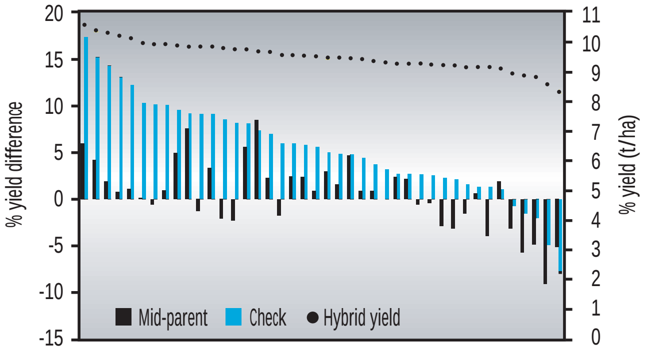


Figure 1. Comparison of hybrid with mid-parent and check cultivar Rayon for yield, sorted by hybrid yield.

Grain yield was adjusted to 12% moisture content. Adjusted entry means for yield were calculated for each experiment, and then the data were combined over two years as a randomized complete block design.

Results and Discussion

Hybrids that yielded significantly more than the commercial cultivar Rayon are presented in Table 1. The yield advantage of these hybrids over Rayon ranged from 13 to 17% when data were combined over two years. However, the difference between these hybrids and their mid-parent yield values was not significant. Mid-parent heterosis for the highest yielding hybrid was 6% (Figure 1).

Overall general combining ability (GCA) effects were more important than specific combining ability (SCA) effects for yield (Table 2). These results indicated that additive gene effects were more important than non-additive gene effects in the variation expressed among these hybrid combinations. It is possible to obtain hybrids with high mid-parent heterosis for yield. For example, hybrids that included line 3 as a male parent had the highest mid-parent heterosis when compared to hybrids with male parent 1 and/or 4 (Figure 2). However, absolute yield levels of these hybrids were not always as high as those of the check cultivar and the other hybrids. The yield of male parent 3 was the lowest (6.3 t/ha) of all entries in the trial, resulting in lower mid-parent values. These findings indicated that low yielding lines should not be selected as parents, since additive gene effects are more important than non-additive gene effects for yield.

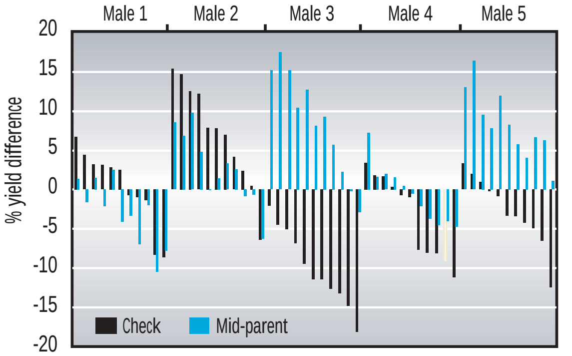


Figure 2. Yield difference between hybrid and mid-parent, and between hybrid and check cultivar Rayon, based on 1997/98 data sorted by male parent.

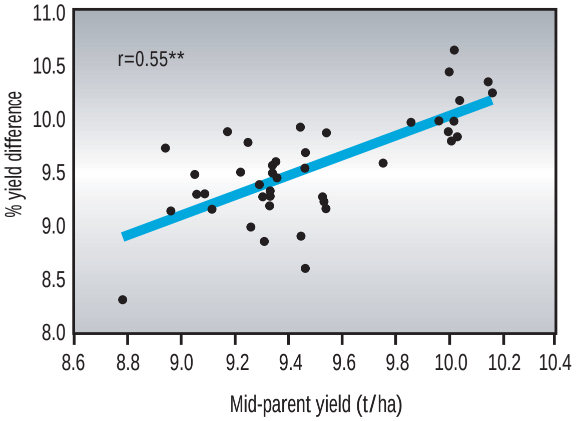


Figure 3. Relationship between hybrid and mid-parent value for yield.

** Significant at the 0.01 probability level.

When yield levels of hybrids were compared to those of their high-, low-, and mid-parents, a significant positive correlation was found; the highest correlation coefficient was observed with mid-parent yield (Figure 3). In other words, the higher the mid-parent value, the higher the hybrid yield.

The difference between the yield levels of the highest yielding hybrid and its high-parent was not significant; however, the yield advantage over the leading cultivar was high in both years. This high yielding parental line also gave the highest GCA effects when used either as female or male parent in hybrid combinations. Because of its high susceptibility to leaf rust, this line cannot be grown commercially. However, leaf rust susceptibility can be overcome by using the major genes present in the complementary parent. For this reason, we continue to use this line in our hybrid program.

Conclusions

These preliminary results indicate that there is heterosis for grain yield in CIMMYT wheat lines under irrigated conditions. Hybrids that yielded better than leading cultivars were obtained.

Based on the positive correlation between yields of hybrids and their mid-parent values and relatively large, significant additive GCA effects, it can be concluded that among the germplasm used in this study the highest yielding advanced lines will produce the highest yielding hybrids.

Acknowledgment

We would like to acknowledge the full technical support and partial financial support of the Monsanto Company for this work.

Inheritance of Associated Adult Plant Stripe and Leaf Rust Resistance in Spring Wheats Developed in CIMMYT

A. Navabi, R.P. Singh, J.P. Tewari, and K.G. Briggs

Abstract

A one-way diallel cross was made among 5 adult plant resistant (APR) spring wheat genotypes from the International Maize and Wheat Improvement Center (CIMMYT) and a susceptible variety, Avocet-*YrA*. Resistant genotypes have shown low levels of stripe and leaf rust severity at several locations globally, despite their seedling susceptibility to most common races of stripe and leaf rusts in Mexico. F_1 crosses, F_2 populations, and F_2-derived F_3 lines were developed in the greenhouse at the University of Alberta, and field-evaluated at two CIMMYT research stations in Mexico, Toluca and El-Batan, under artificial inoculation with the stripe and leaf rusts, respectively. APR was partially dominant-intermediate in crosses with the susceptible parent. APR to stripe rust appeared to be based on the interaction of *Yr18* and at least 3 additional genes having an additive effect, while APR to leaf rust was controlled by *Lr34* and two additive genes. General combining ability (GCA) was found to be the major component of variation among the crosses. This indicated that additive gene effects are more important than non-additive gene effects in the inheritance of APR to both diseases. There was an associated resistance response to both diseases, as suggested by the highly significant correlation between stripe rust and leaf rust severities across the generations.

Introduction

Stripe rust (caused by *Puccinia striiformis*) and leaf rust (caused by *P. triticina*) are two major diseases of wheat. Genetic resistance is the most widely used, and environment-friendly means of disease control. The resistance, however, is subject to change as new virulent races develop in the pathogen population. Adult plant resistance (APR), characterized as a type of interaction between host and pathogen in which adult plant is, partially or completely, resistant despite susceptibility in the seedling stage, is generally known as being more durable. The *Yr18* and *Lr34* genes are closely linked and are present in many high-yielding wheat varieties. Although, according to Ma and Singh (1996), and Singh and Gupta (1992) when alone, *Lr34-Yr18* does not provide enough resistance under high stripe or leaf rust pressure. Resistant genotypes that are being studied in this project were developed at the International Maize and Wheat Improvement Center (CIMMYT), in order to incorporate additive factors in the *Lr34-Yr18* background.

Objectives

The objectives of this study were to 1) study the inheritance of APR to stripe and leaf rust in five spring wheat CIMMYT lines, 2) to estimate the number and type of APR genes, and 3) to study the gene effect, and combining abilities for APR.

Plant Material

Five CIMMYT spring wheat genotypes that showed adult plant resistance to stripe and leaf rusts in several locations globally, and Avocet-*YrA*, susceptible to both diseases were chosen for genetic study.

Crossing and Population Development

One-way diallel crosses were made, and F_1, F_2, and F_2-derived F_3 were developed in greenhouse, at the University of Alberta, Canada.

Field Evaluation

Parental genotypes, and F_1 crosses, F_2 populations and F_2-derived F_3 families were field-evaluated at two CIMMYT stations, El-Batan and Toluca, in the highlands of Central Mexico, separately inoculated with leaf and stripe rusts. YR pathotype MEX96-11, virulent on *Yr 2, 3, 6, 7, 9, 27,* and *A;* and LR pathotype MCJ/SP, avirulent/virulent on *Lr2a, 2b, 2c, 3ka, 9, 16, 19, 21, 22a, 24, 25, 28, 29, 30, 32, 33, 34, 35, 36/1, (3), (3bg), 10, 11, 12, 13, 14a, 14b, 15, 17, 18, 20, 22b, 23, 26, 27+31,* and *37* were sprayed on the spreader rows.

Experimental Design

F_1 and F_2 diallel trials were planted in RCBD with three replications, and F_2-derived F_3 families were planted in an augmented design with repeating parents as the check, after every 10 plots.

Qualitative Analysis

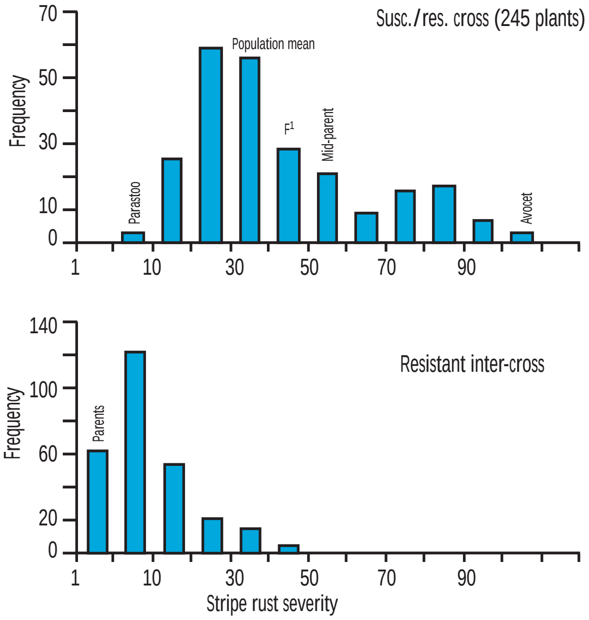
Distribution of F_2 plants and F_3 families for rust reaction in susceptible/resistant crosses.

Cross	PTR	F_2 PTS	Others	χ^2 4 gene	P
Puccinia striiformis					
Avocet/Saar	0	2	217	2.38	> 0.25
Avocet/Simorgh	3	2	272	4.20	> 0.05
Avocet/Homa	1	3	258	3.83	> 0.10
Avocet/Parastoo	0	3	242	5.32	> 0.05
Avocet/Cocnoos	0	3	225	5.89	> 0.05

Tested ratio: 1:1:254

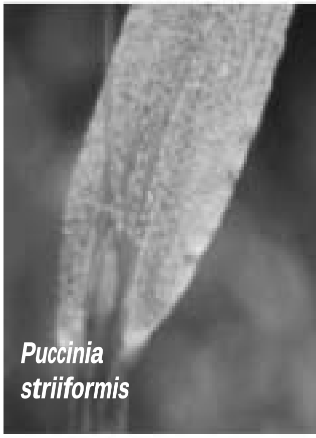
	F_1 severity	F_2-derived F_3*				χ^2	
	(0-100)	HPTR	HPTS	SegI	SegS	4 gene	P
Puccinia striiformis							
Avocet/Saar	50	0	0	92	38	2.15	>0.25
Avocet/Simorgh	15	0	0	102	28	1.95	>0.50
Avocet/Homa	40	1	1	95	33	0.98	>0.75
Avocet/Parastoo	50	1	1	86	30	1.29	>0.50
Avocet/Cocnoos	50	0	0	88	32	1.08	>0.75
P. triticina							
Avocet/Saar	20	1	1	39	37	1.51	>0.50
Avocet/Simorgh	30	1	2	33	34	2.87	>0.10
Avocet/Homa	40	3	1	51	25	5.03	>0.05
Avocet/Parastoo	10	3	1	44	20	6.50	Low
Avocet/Cocnoos	40	0	0	26	26	3.11	>0.25

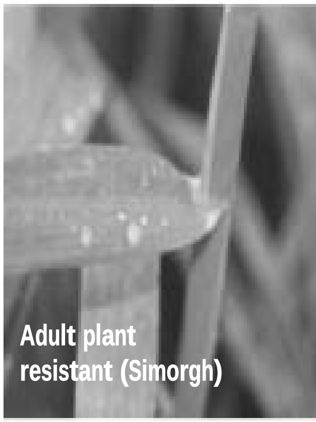
PTR: Parental type resistant
PTS: parental type susceptible
HPTR: Homozygous parental type resistance
HPTS: Homozygous parental type susceptible
SegI: Segregating intermediate
SegS: Segregating susceptible
Tested ratios: 4 gene: 1:1:190:64
3 gene: 1:1:36:26

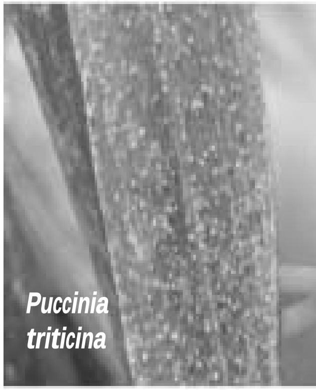


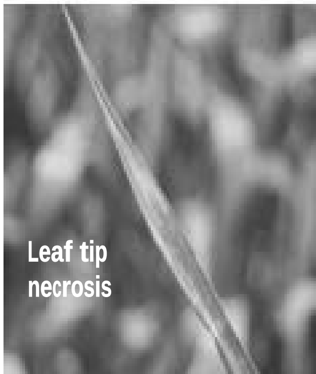
Frequency distribution of *Puccinia striiformis* severity of F_2 plants.


Puccinia striiformis


Puccinia striiformis


Adult plant resistant (Simorgh)


Puccinia triticina


Leaf tip necrosis

Quantitative Analysis

Mean squares for final disease severity of parents, F_1 and F_2 generations derived from a one-way diallel cross of spring wheat infected with *Puccinia striiformis* and *P. triticina.*

		P. striiformis		*P. triticina*	
SV	**df**	**F_1**	**F_2**	**F_1**	**F_2**
Replication	2	0.20**	0.009^{ns}	0.024^{ns}	0.008^{ns}
Entries	20	1.09**	0.81**	0.82**	0.72**
GCA	5	3.98**	3.28**	2.59**	2.66**
SCA	15	0.12**	0.07**	0.24**	0.08**
Error	40	0.08	0.007	0.025	0.006
$[2\sigma^2_g/(2\sigma^2_g + \sigma^2_s)]$⍓		0.91	0.92	0.73	0.90

Coefficients of correlation

	F_1YR	F_2YR	F_1LR
F_2YR	0.95**		
F_1LR	0.64**	0.73**	
F_2LR	0.77**	0.86**	0.85**

Duncan's multiple ranges of six spring wheat lines and their progenies for the final stripe rust and leaf rust severities.

	P. striiformis		*P. triticina*	
Genotype	**F_1**	**F_2**	**F_1**	**F_2**
Avocet-*YrA*	100.0 a$^{\Psi}$	100.0 a	100.0 a	100.0 a
Avocet/Saar	46.6 b	41.1 b	20.0 cd	30.9 b
Avocet/Simorgh	13.3 c	25.7 c	26.6 bc	28.5 b
Avocet/Homa	36.6 b	34.7 b	38.3 b	18.6 c
Avocet/Parastoo	53.3 ab	37.3 b	6.6 ef	12.2 d
Avocet/Cocnoos	53.3 ab	40.4 b	38.3 b	33.4 b
Saar	5.0 de	4.3 f	5.0 fg	2.0 j
Saar/Simorgh	2.0 fg	3.0 gh	10.0 de	6.5 e
Saar/Homa	2.3 fg	7.5 e	3.6 g	2.7 hij
Saar/Parastoo	10.0 cd	16.5 d	6.6 ef	3.8 gh
Saar/Cocnoos	3.6 ef	6.6 e	6.67 ef	5.9 ef
Simorgh	0.3 h	1.0 i	10.0 de	4.5 fg
Simorgh/Homa	1.0 hg	2.3 h	10.0 de	6.7 e
Simorgh/Parastoo	2.3 fg	7.5 e	5.0 fg	2.5 ij
Simorgh/Cocnoos	1.0 gh	3.9 fg	6.6 ef	6.0 ef
Homa	5.0 de	3.9 fg	1.0 h	3.1 hi
Homa/parastoo	6.6 cde	8.2 e	1.0 h	1.1 k
Homa/Cocnoos	5.0 de	7.1 e	13.3 d	4.8 efg
Parastoo	2.3 fg	4.5 f	1.0 h	1.0 k
Parastoo/Cocnoos	8.3 cd	7.4 e	5.0 fg	3.5 ghi
Cocnoos	5.0 de	3.7 fg	3.6 g	1.0 k

**, ^{ns} Significant at P<0.01 and not significant, respectively.

⍓ Components of variance ratio (Baker 1978).

Ψ Means in a column followed by the same letter are not significantly different (P<0.05).

Conclusion

- APR to stripe rust appeared to be based on the interaction of *Yr18* and 3 additional genes having an **additive** effect.
- APR to leaf rust was controlled by *Lr34* and two **additive** genes.
- Segregation for disease severity levels higher than the parents were observed in inter-crosses of resistant parents, indicating that some additive genes are polymorphic.
- Although SCA (which is composed of dominance plus inter-allelic interaction or epistasis) was also significant in all cases, the ratio proposed by Baker (1978) was often close to unity. This suggests that additive gene effects were more important than non-additive effects for APR to stripe and leaf rusts.
- There was an associated APR response to both diseases as suggested by the highly significant coefficient of correlation across the generations.
- The resistance is expected to be **durable**, since sources of *Lr34-Yr18* linkage, in addition to additive factors, have shown long-lasting resistance to both diseases in widely-grown cultivars throughout the world.

Acknowledgment

This work was supported by funds provided by the Ministry of Agriculture, I.R. Iran to CIMMYT, and the Alberta Agricultural Research Institute (AARI) Matching Grants Program.

References:

Baker, R.J. 1978. Issues in diallel analysis (a method for studying the genetics of complex traits in plant breeding). *Crop Science* 18(4):533-536.

Burow, M.D., and J.G. Coors. 1994. DIALLEL: a microcomputer program for the simulation and analysis of diallel crosses. *Agronomy Journal* 86(1):154-158.

Ma, H., and R.P. Singh. 1996. Contribution of adult plant resistance gene *Yr18* in protecting wheat from yellow rust. *Plant Disease* 80(1):66-69.

Singh, R.P., and A.K. Gupta. 1992. Expression of wheat leaf rust resistance gene *Lr34* in seedlings and adult plants. *Plant Disease* 76(5):489-491.

Warren E. Kronstad Crop Science Memorial Conference Room

N. Scott

Dr. Warren E. Kronstad, Oregon State University Wheat Breeder and Geneticist, died on 21 May 2000, leaving us with a tremendous legacy of contributions to wheat improvement. With a research career spanning nearly 40 years, there are few individuals in the world who have had a greater impact on world agriculture.

Dr. Kronstad and his collaborators developed high-yielding, disease resistant wheat varieties grown throughout the Pacific Northwest, increasing grain yields, production stability, and contributing to the economic development of the entire wheat industry. Releases include the soft wheat Stephens, which has been in commercial production for over 20 years, and varieties such as Yamhill, Hyslop, McDermid, Hill, Malcolm, Gene, Temple, Weatherford, Winsome, Connie, and Foote.

Dr. Kronstad was active in international wheat improvement since the 1960s when he was part of a team that lead Turkey from deficit to surplus wheat production. For over 20 years, in collaboration with the International Center for Maize and Wheat Improvement (CIMMYT), Dr. Kronstad directed a major international program to systematically cross winter and spring wheat germplasm pools and develop widely adapted, high-yield germplasm using a unique shuttle breeding strategy. Cooperating with researchers in more than 125 countries to facilitate germplasm exchange and genetic improvement, the program resulted in new high-yield varieties released in over 20 developing countries.

Dr. Kronstad was a skilled teacher in plant breeding, cytogenetics, genetics, and cereal production and was the major professor for more than 100 graduate students from 27 countries. His students have made significant contributions to agricultural improvement throughout the world in the areas of variety development, agronomy and basic sciences, and will continue to do so for decades to come.

Dr. Kronstad's achievements in variety development, germplasm development, genetics, international agriculture, teaching, and graduate training were recognized in prestigious awards from major scientific organizations, government agencies, foundations, and industry, both nationally and internationally. These include Fellow of ASA, CSSA, and AAAS; Dekalb Genetics, Crop Science Distinguished Career Award; Crop Science Award, Alexander von Humboldt Foundation Award; four Distinguished Professor Awards at Oregon State University; Presidential End World Hunger Award; Paul Harris Fellow Award of the International Rotary Foundation; USDA Distinguished Service Award; Distinguished and Meritorious Service Awards of the American Farm Bureau; Washington State University Alumni Achievement Award; recognition from the governments of Turkey, Mexico and many more. He held the Oregon State University Wheat Research Endowed Chair, which in 1998 was renamed the Kronstad Endowed Chair for Wheat Research.

The Warren E. Kronstad Memorial Conference Room

As a lasting memorial to Dr. Kronstad, the Oregon Wheat Foundation is leading a project that will refurbish and dedicate a conference room in the OSU Crop Science Building in his honor. The Warren E. Kronstad Memorial Conference Room will serve to highlight Warren's career and accomplishments and permanently display his many professional awards. The room will serve to remind our students, faculty, visiting scientists, and guests of the dynamic history and impact that Dr. Warren E. Kronstad and Oregon State University have had on international wheat improvement.

The conference room will include bookshelves, cabinets, and display shelves for Dr. Kronstad's awards and memorabilia. A display wall will enclose white boards and a projection screen under sliding panels decorated with a wheat theme. The room is to have multi-function capability, for use in small conference gatherings, planning sessions, classes, and as resource library. Equipped with computer and projector, access to phone and internet lines, and audio and video conferencing capability, the conference room will benefit OSU efforts in graduate training and Cereal Research programs for years to come.

The Oregon Wheat Foundation

The Oregon Wheat Foundation was established in 1980 to serve Oregon wheat producers through a variety of programs, including scholarships, fellowships, research support, agriculture leadership programs, and food donations to the less fortunate.

Join us now in creating this lasting tribute to Dr. Warren E. Kronstad. Donors of US$ 100 or more will be recognized in a memorial plaque displayed prominently in the conference room. Your gifts and donations are fully tax deductable under 501C3.

From a Single Grain

As said in the Bible (John 12:24) "Very truly, I tell you, unless a grain of wheat falls into the earth and dies, it remains just a single grain; but if it dies, it bears much fruit."

We often think of sacrifice in reductionist terms of what must be given up or denied, but the paradox of the gospel lies in a simple grain of what. From a single seed, laid open to the possibilities of growth, springs the bounty of overflowing bushels. The energy released from selflessness can feed the world.

For more than twenty years I worked from the cereal project at OSU beside a dedicated scientist, Warren Kronstad, who always deflected praise and deferred to the accomplishments of the "team". He patiently worked with those of us who knew nothing of plant breeding or genetics and built a team who together produced new varieties of wheat with record-breaking yields. He seldom played the part of the elevated project leader, but sat with the rest of us in a cold Corvallis drizzle, pulling anthers from wheat flowers to make the start of a new variety. Or you might find him sickling rows of wheat, shoulder to shoulder with graduate students and summer workers, under the penetrating Pendleton sun. His "vacations" were often spent in developing countries lending support to former students who were struggling to build programs with meager tools among abundant roadblocks.

Though I now work in a different field, each August when I drink the beauty of the vast golden sea of wheat stretching endlessly to the blue horizon, I am reminded that all of that abundance may claim its heritage from a single grain that lost its singularity in the quantity of the whole. And if I look closely, waving back at me and encircling the globe, I see Norm, Raj, Glenn, Willie, Fred, Randy, Mary, Krisda, Abderrazak, José Luis, Max, Chen, Luz, Heng-Li, Sonnia, Debbie, Miguel, Federico, Mengu, Guillermo, Peggy, Connie, Susan, Pat, Memo, María, Alicia, Karim, Ali, Mohammad, Polat, Andrés, Amor, Becky, Steve, Ming, Antonio, Ariel, Jim, Mike, Cevdet, Pedro, Marina, Moustafa, Nick, Mark, César, Dato, Colleen, Abdennadher, Michel, Selman, Larry, David, Baltazar, Sonja, Getachew, Carlos, Julio, Choi, Leonardo, Michael, José, Modan, Ahmed, Ertug, Cindy, Moncef, Necati, Erdogan, Claudio, Mesut, Don, Khan, Darío, Hal, Maatougui, Masood, Luis, Min, Mou, Benacef, Ricardo, Vichien, Rahman, Salah, Ottoni, Chrystal, Helle, Juan, Karen, Ira, Jaime, Somvong, Apichart, Rubén, Kamil, Nusret, Shi-Ping, Chris, John, Bob, Frank, …and Warren.

Influence of Earliness *per se* Genes on Flowering Time in CIMMYT Wheats

J. van Beem, A.J. Worland, and M. van Ginkel

Introduction

The main environmental factors affecting phasic development in wheat are vernalization, photoperiod, and temperature (Pirasteh and Welsh 1980). The adaptability of semidwarf wheats developed at the International Maize and Wheat Improvement Center (CIMMYT) to diverse environments depends to a large extent on variation in these factors. Numerous studies have indicated that a factor (or factors) besides vernalization and photoperiod influences the rate of development of wheat. Syme (1968) found that the basic development period for wheat was influenced by mean daily temperature. Ford et al. (1981) coined the term "earliness genes" and proposed that they were different from the genes controlling photoperiod sensitivity.

More recently, Miura and Worland (1994) found that genes on all three chromosomes of Group 3 could have striking effects on ear-emergence time. Slafer (1996) re-examined the assumptions that earliness genes are independent from photoperiod and vernalization and that differences in earliness genes apply only to the vegetative period up to floral initiation.

The objectives of the present study were to 1) examine the differences in rate of development and earliness *per se* effects in CIMMYT wheats under two temperature regimes, and 2) test the assumption that earliness *per se* is a genotypic character unaffected by temperature.

Methods

Seeds of 52 CIMMYT (or CIMMYT-derived) lines and 12 testers were imbibed for 48 hours at room temperature and vernalized for 8 weeks at 4ºC. After removal from vernalization, the seedlings were standardized for length (Figure 1). Ten plantlets per entry were sown in pots and placed in a 24 h photoperiod regime at two day/night temperatures: 23/12ºC and 16/4ºC (Figure 2). The number of days from transplanting to flowering was recorded for 8 plants per entry. *Eps* was calculated as the difference between days to flowering of the variety and days to flowering of the earliest variety in the set.

Results and Discussion

From previous studies (Flood and Holloran 1984) it is known that eight weeks of cold treatment and 24 hours of light will satisfy the vernalization and photoperiod requirements of wheat. Differences in days to flowering among the lines were considered to be due to the earliness *per se* genes. Figure 3 shows the mean days to flowering of CIMMYT wheats and testers after removing the response to photoperiod and vernalization. In

Figure 1. *Eps* characterization at CIMMYT. Seedlings were vernalized for 8 weeks at 4ºC. Seedling length was standardized before transplanting to growth chambers.

Figure 2. Growth chambers at CIMMYT. Vernalized cultivars were grown at day/night temperatures of 23/12ºC or 16/4ºC under 24 h photoperiod.

general, all lines flowered later under the cold regime (top line). The range in the delay of flowering due to cold temperatures was 0 to 27 days. The number of days to flowering for CNO79/PRL was the same under both temperature regimes, indicating insensitivity to temperature. The varieties Nesser, Gen3*/PVN, and Chilero exhibited the strongest sensitivity to cold temperature by delaying flowering by 26-27 days.

To determine whether earliness genes act independently of temperature, the change in ranking between *Eps* at 23/12ºC and *Eps* at 16/4ºC was plotted in Figure 4. A positive change in ranking indicates an acceleration in flowering under warm temperatures due to *Eps* genes. This would suggest that, relative to the other varieties in the set, the *Eps* genes in a given variety are sensitive to warmth and cause faster development. A negative change in *Eps* ranking indicates that *Eps* gene sensitivity is expressed as a delay in development under warm conditions, relative to the other varieties in the set. The magnitude of the sensitivity varied widely. In varieties to the right of the plot (Figure 4), flowering was delayed by cold temperature, and the *Eps* ranking of these varieties was greatly affected by changes in temperature. This would suggest that the *Eps* genes in these varieties are, in all likelihood, temperature genes. The varieties whose *Eps* ranking changed due to temperature were: Pastor, Enkoy, PBW343, Chinese Spring, Rayon, Weaver, Irena, Turaco/Chil, PGO/Seri//BAU, Pitta, GOGATSUKOMUGI, Inquilab91, Kauz, VEE #5/Sara, CHUGOKU 114, TEMU 1032.94, Embrapa 16, Chum18//JUP/BJY, Stephens, ROQUE F 73, SONORA 64, Don Ernesto, Chilero, Gen*3/PVN, Nesser, CNO79/PRL, and TEMU1024.95.

In varieties to the left of the plot (Figure 4), flowering was delayed by cold temperatures, but *Eps* ranking remained consistent regardless of temperature. For this group, the data suggest that *Eps* genes are not temperature genes but "static" genetic characters for early flowering. The varieties that ranked consistently for *Eps* effects were: Scan, Star, Pavon, Chil/PRL, Hubei, Ciano F67, Chilero/BUC, Nourin 61, Bacanora, HE/2*CNO79, Seri, Weaver/Roblin, and Temuco1024.95. For the variety CNO79/PRL flowering was not affected by temperature but the *Eps* ranking changed drastically. It is likely that the change in rank was not due to sensitivity to temperature but rather to the change in ranking of varieties within the set.

From these data it is clear that the rate of development in most CIMMYT genotypes is responsive to temperature. These results are in agreement with numerous studies (Angus 1981; Slafer and Rawson 1994) that found that not only were all genotypes responsive to temperature but there was genotypic variation in sensitivity to temperature. While all CIMMYT genotypes flowered earlier in warm temperatures, the degree of sensitivity to temperature also varied widely and resulted in interactions between temperature and genotype. Lastly, *Eps* appeared to be related to temperature genes in most CIMMYT varieties, but may also be associated with a "static" or constant character for early flowering. This is in sharp contrast with results reported by Slafer et al. (1995) who found that in four genotypes the intrinsic earliness factor is a complex interaction between temperature and development. This study

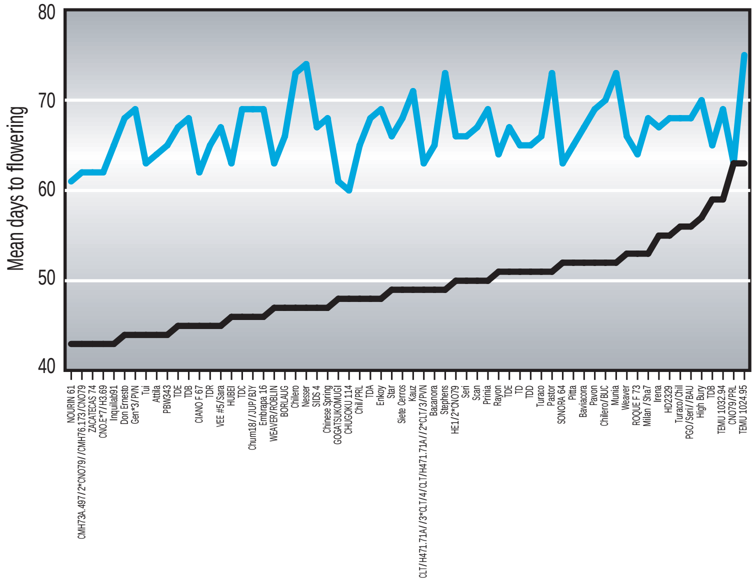


Figure 3. Mean days to flowering of CIMMYT wheats and testers after removing the response to photoperiod and vernalization. The top line corresponds to the 16/4ºC regime, and the bottom line corresponds to the 23/12ºC regime.

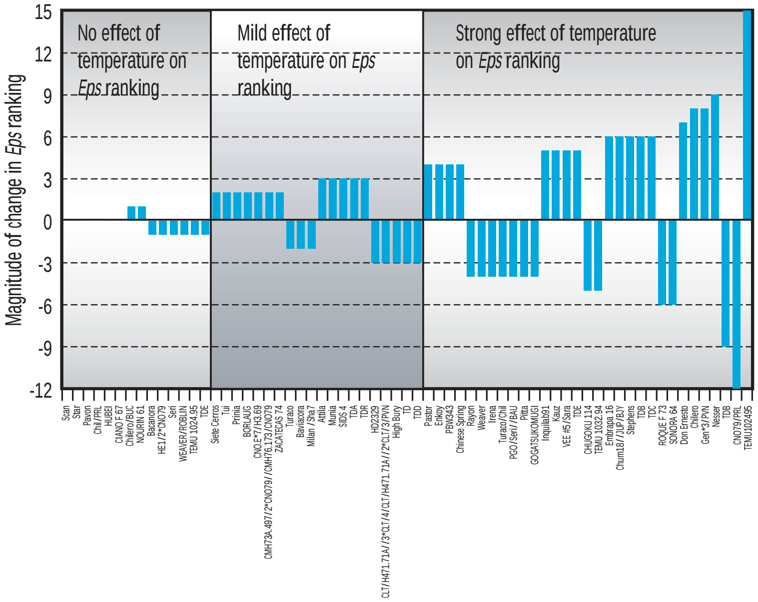


Figure 4. Change in the *Eps* ranking of genotypes grown under two temperature regimes.

examined 52 CIMMYT (or CIMMYT-derived) lines and 12 testers and found that *Eps* was related to temperature in 27 lines. However, there were 13 lines in which *Eps* appeared to be a factor related to "intrinsic" earliness in flowering and independent of temperature.

References

Angus, J.F., D.H. MacKenzie, R. Morton, and C.A. Schafer. 1981a. Phasic development in field crops. II. Thermal and photoperiodic responses of spring wheat. *Field Crop Research* 4:269-282.

Angus, J.F., R.B. Cunningham, M.W. Moncur, and D.H. MacKenzie. 1981b. Phasic development in field crops. I. Thermal response in seedlings phase. *Field Crop Research* 3:365-378.

Flood, R.G., and G.M. Holloran. 1984. Basic development rate in spring wheat. *Agronomy Journal* 76:260-264.

Ford, M.A., R.B. Austin, W.J. Angus, and G.C.M. Sage. 1981. Relationships between responses of spring wheat genotypes to temperatures and photoperiodic treatments and their performance in the field. *Agricultural Science Cambridge* 96:623-634.

Miura, H., and A.J. Worland. 1994. Genetic control of vernalization, day-length response, and earliness *per se* by homoeologous Group–3 chromosomes in wheat. *Plant Breeding* 113:160-169.

Pirasteh, B., and J.R. Welsh. 1980. Effect of temperature on the heading date of wheat cultivars under a lengthening photoperiod. *Crop Science* 20:453-456.

Slafer, G.A., and H.M. Rawson. 1994. Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. *Australian Journal of Plant Physiology* 21:393-426.

Slafer, G.A. 1996. Differences in phasic development rate amongst wheat cultivars independent of responses to photoperiod and vernalization. A viewpoint of the intrinsic earliness hypothesis. *Journal of Agricultural Science* 126:403-419.

Slafer, G.A., and H.M. Rawson.1995. Intrinsic earliness and basic developmental rate assessed for their response to temperature in wheat. *Euphytica* 83:175-183.

Syme, J.R. 1968. Ear emergence of Australian, Mexican, and European wheats in relation to time of sowing and their response to vernalization and daylength. *Australian Journal of Experimental Agriculture and Animal Husbandry* 8:578-581.

Building Up Multiple Disease Resistance in Barley

F. Capettini, H. Vivar, L. Gilchrist, and M. Henry

Breeding to incorporate multiple disease resistance has been one of the main goals of the ICARDA/CIMMYT[1] Barley Breeding Program. Among other things, participants developed an enhanced gene pool and varieties possessing resistance to the main barley diseases in an agronomically improved genetic background. Selection in environments that ensured higher heritability of resistance was a major reason for success. Results for the most prevalent diseases in the Americas are presented here.

The Diseases

Stripe rust (*Puccinia striiformis*)

Selection for stripe rust resistance has been carried out since its appearance in the region in 1984. Sources of resistance were obtained after screening approximately 20,000 samples in Colombia and Mexico. Inoculation is conducted at the Toluca Experiment Station through the creation of infection borders and hills planted with susceptible genotypes. Partial stripe rust resistance was found, and cultivars with contrasting differences in the latent period of infection were characterized, obtaining a more durable type of resistance.

Leaf rust (*Puccinia hordei*)

Results of leaf rust research in Montana and Holland helped to identify parents for use in breeding. Every year 10-12 ha of segregating populations and yield experiments in the Yaqui Valley are artificially inoculated through infection borders using fresh pathogen spores. Epidemics are almost always present and selection is efficient.

Scald (*Rhyncosporium secalis*)

In the 1980s, a sample of entries from the world collection showing resistance after being screened in California was introduced to Mexico. Environmental conditions at Toluca are usually optimal for the development of this important barley disease. Every year 7-10 ha of experiments and segregating populations are artificially inoculated, creating relatively high epidemics that easily differentiate genotypes with different levels of resistance. Previous research found that disease development in resistant genotypes had small AUDPC values as compared to susceptible ones. This slow-scalding gene pool is frequently used in the program.

Fusarium head blight (*Fusarium graminearum*)

Selection for this devastating disease started in 1995 in response to its rapid rise in importance in North and South America. Twenty-three lines with different degrees of resistance after screening in Japan and Mexico were used as initial sources for the resistance program. Genotypes are screened under artificial epidemics at Toluca. The ICARDA/CIMMYT program was among the pioneers in screening and describing the independently inherited Type I (initial infection) and Type II (fungus spreading) types of resistance in barley (Figure 1), which had been previously described in wheat. Genotypes having both types of resistance were identified and confirmed through several years of testing and are widely used as resistance sources.

Barley yellow dwarf virus (BYDV)

Research on BYDV aims to characterize genotypes for their individual reaction to three biotypes: MAV, PAV, and RPV. BYDV symptoms are frequent under natural conditions at Toluca and selection against susceptible genotypes is usually carried out,

---

[1] ICARDA = International Centre for Agricultural Research in the Dry Areas.
CIMMYT = International Maize and Wheat Improvement Center.

but artificial inoculation with greenhouse-reared aphids is done in screening nurseries under field conditions to ensure uniform infection, differentiate biotype reaction, and reduce the risk of escapes. Four plots are planted with each genotype and three of them are inoculated with one biotype each. The fourth plot is a check kept free of aphids by insecticide applications.

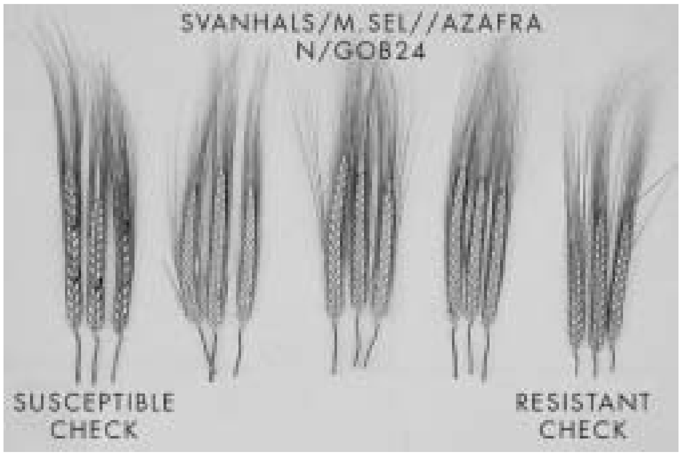


Figure 1. Fusarium head blight Type II resistance in two-row barleys.

Figure 2. Barley yellow dwarf virus screening under artificial inoculation, Toluca.

Assembling Resistant Genotypes

We created “templates” to incorporate resistance to all diseases into a high yielding genetic background. At the first stage, resistance to scald and leaf rust was incorporated, followed by templates where resistance to stripe rust and to other diseases was added. This process continued for 20 years, with two generations per year, to pyramid resistance to the diseases described above and to net blotch, spot blotch, and stem rust.

An example of success is the variety Shyri, released in Ecuador in 1989. The disease resistance present in Shyri was studied in detail at Oregon State University (OSU) using molecular markers. QTLs for resistance to scald, net blotch, BYDV, stripe rust, and leaf rust were found. Shyri was also found to be resistant to fusarium head blight and partially resistant to leaf rust.

Another success story is China, where an estimated 400,000 ha of the country’s 1 million ha barley area is sown to ICARDA/CIMMYT varieties, largely due to their high yield potential and resistance to both fusarium head blight and barley yellow mosaic virus. In several provinces the variety Zhenmai-1 (Gobernadora) yielded 20-25% more than the local varieties. In a genetic study carried out by OSU, a large effect QTL was found for FHB Type II resistance near the centromeric region of chromosome 2.

Besides the impact evidenced by the release of cultivars in different countries, the success of the program can be also measured by the large germplasm pool with resistance to different diseases in an improved agronomic background that is available to breeding programs worldwide.

Genotypes presenting higher levels of fusarium head scab resistance in more than three years of testing. Many genotypes combine two to three different sources of resistance.

Pedigree	Head type	Damage % type I	Damage % type II
TOCTE//GOB/HUMAI10/3/ATAH92/ALELI	2	5.60	7.07
PENCO/CHEVRON-BAR	6	1.51	17.32
ZHEDAR#1/SHYRI//OLMO	2	5.68	8.04
ATAH92/GOB	2	4.88	4.27
CANELA/ZHEDAR#2	2	5.28	5.33
MNS1	6	3.43	17.12
ZHEDAR#1/4/SHYRI//GLORIA-BAR/COPAL/3/ SHYRI/GRIT/5/ARUPO/K8755//MORA	2	3.21	4.03
SVANHALS-BAR/MSEL//AZAF/GOB24DH	2	3.29	8.76
Checks			
AZAFRAN (MR-R)	2	8.50	8.30
GOBDH83(R-R)	2	5.10	7.60
GOBDH89(S-S)	2	13.40	27.70
PENCO/CHEVRON-BAR (R-MR)	6	4.69	12.05

Selected six- and two-row genotypes resistant to at least five diseases and presenting high yield.

Variety or pedigree	PAV	BYDV[1] MAV	RPV	Stem rust	Leaf rust	Scald	Grain type	Stem rust	Yield (t/ha)
Six-row									
EGYPT4/TERAN78//P.STO/3/QUINA	R	R	R	R	40S	TR	C		9.0
BELLA UNION	R	R	R	30S	TR	TR	C		8.2
ALPHA/DURRA//CORACLE/3/ALELI/4/MPYT169.1Y/LAUREL//OLMO/5/GLORIA-BAR..	R	R	R	R	TR	R	C		8.0
DC-B/SEN/3/AGAVE/YANALA//TUMBO/4/CEN-B/2*CALI92	R	R	R	5S	TR	MS	C		7.3
PETUNIA 1	R	R	R	5MS	TR	R	D	R	7.1
BBSC/CONGONA	R	R	R	R	TR	TR	D		6.8
CARDO/VIRDEN//ALOE	R	R	R	-	TR	-	C		6.7
PALTON	R	R	R	TR	TR	TR	C		6.6
DC-B/SEN/3/AGAVE/YANALA//TUMBO/4/CEN-B/2*CALI92	R	R	R	5MS	TR	TR	C		6.5
QUINN/ALOE//CARDO	R	R	R	TR	TR	TR	C		6.4
SEN/SLLO/3/RHODES/CI14100//LIGNEE527	R	R	R	30S	TR	R	C		6.4
MONROE/4/ASE/3CM//RO-B/3/SMA1/5/MATICO	R	R	R	R	TR	R	C		6.3
Two-row									
MADRE SELVA	R	R	R	R	TR	R	C	TS	7.1
ABN-B/KC-B//RAISA/3/ALELI	R	R	R	TR	TR	R	C		6.9
CONDOR-BAR/3/PATTY.B/RUDA//ALELI/4/ALELI	R	R	R	TR	TR	R	C		6.7
ARUPO*2/KC-B//ALELI	R	R	R	R	TR	S	C		6.7
LIMON	R	R	R	TR	TR	R	C	TS	6.6
INCIENSO	R	R	R	5MS	TR	TR	C	TS	6.5
COMINO/3/MATICO/JET//SHYRI/4/ALELI	R	R	R	R	TR	R	C		6.5
POROTILLO	R	R	R	R	TR	TR	D		6.3
HLLA/GOB//HLLA/3/CANELA	R	R	R	-	10MS	-	C		5.8
CALENDULA	R	R	R	R	TR	R	D		5.7
GOBERNADORA/HUMAI10//CANELA/3/ALELI	R	R	R	-	TR	-	C		5.4
DUMARI	R	R	R	10S	TR	TR	D	VS	5.3

---

[1] PAV, MAV, and RPV are three biotypes of barley yellow dwarf virus (BYDV).

Grain Yield and Quality of CIMMYT Durum Wheat under Water and Nitrogen Stress

J.I. Ortiz-Monasterio R., R.J. Peña, and W.H. Pfeiffer

Introduction

Close to 95% of durum wheat cultivars released in developing countries are derived from germplasm developed by the International Maize and Wheat Improvement Center (CIMMYT). Insufficient water and low nitrogen levels are the two main abiotic stresses present in durum wheat production systems around the world. The objective of the study reported here was to evaluate grain yield and grain quality of durum wheat landraces and CIMMYT durum wheat genotypes under water and nitrogen stress.

Materials and Methods

A field experiment was established at CIMMYT's research station in Cd. Obregon, Sonora, Mexico, during the 1998/99 crop cycle. A two-factorial treatment design was used. Factor A consisted of four environments: 1) water stress and nitrogen stress (Figure 1), 2) water stress and no nitrogen stress (Figure 2), 3) no water stress and nitrogen stress (Figure 3), 4) no water stress and no nitrogen stress (Figure 4). Factor B had eight genotypes: one landrace (selected for good performance under low nitrogen), two released cultivars, and five advanced lines. The experiment was design as a randomized complete block design with eight treatments (genotypes) and three replications across the four environments. The four environments were within meters of each other.

Pasta-making quality was determined by measuring protein quantity (NIR analysis), protein quality (as indicated by SDS sedimentation, mixograph dough mixing time, and mixogram peak height), and flour yellowness (Minolta, b). Grain yield was measured in an area of 3.6 m^2 and expressed at 12% moisture.

Results

Grain yield

Averaged over all eight genotypes, the effect of nitrogen stress alone reduced grain yield by 57%, water stress alone by 65%, and water and nitrogen stress together by 71% with respect to the non-stressed plots (grain yield: 7,088 kg/ha) (Figure 5). In all four environments, the landrace was outyielded by released cultivars Altar 84 and Rascon 43 and/or by new advanced lines. In the non-stressed environment, two advanced lines (Kucuk and Sooty/Rascon) outyielded the released

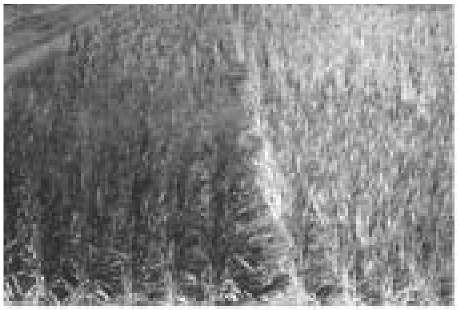


Figure 1. Water and nitrogen stress.

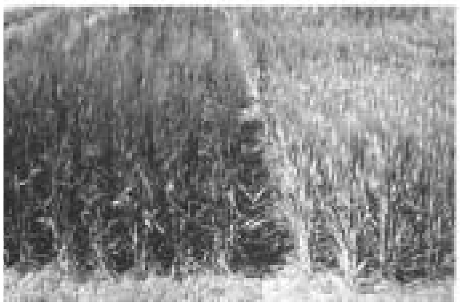


Figure 2. Water stress and no nitrogen stress.

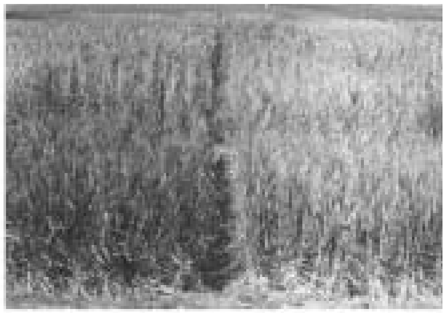


Figure 3. No water stress and nitrogen stress.

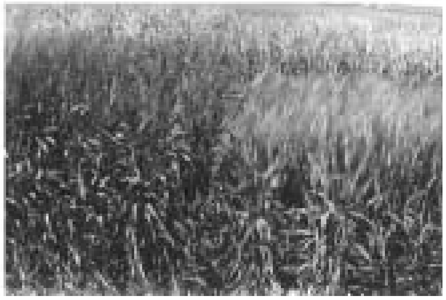


Figure 4. No water stress and no nitrogen stress.

cultivars (Table 1). Under nitrogen or water stress there was no difference between the released cultivars and the new advanced lines. However, when nitrogen and water stress were present together, the advanced line Sooty/Rascon and cultivar Rascon 43 had 38 and 23% higher yield, respectively, than Altar 84 (Table 1).

Grain quality

There were significant differences among cultivars for most quality parameters within each of the four environments. Rascon 43 was recently released under the name Nacori 97 in the Yaqui Valley of Mexico for its good quality. Sooty/Rascon had better quality based on sedimentation values than released cultivars in all four environments. The environment had a significant effect on flour protein. The highest protein concentration was obtained under + water stress and - nitrogen stress, while the lowest was obtained with the - water stress and + nitrogen stress treatment (Figure 5). The two environments with nitrogen stress were better for discriminating low vs. high protein cultivars; the best one had nitrogen and water stresses present together. Across environments there has been continuous progress in nitrogen use efficiency as measured by protein yield (Table 2). Under water stress, nitrogen application did not show an effect on gluten strength parameters (Figure 6). Just the opposite occurred under the no water stress conditions. In general the yellow color of the endosperm increased with the application of nitrogen (Figure 7).

Figure 5. Grain yield and percentage protein under four environments averaged across eight genotypes.

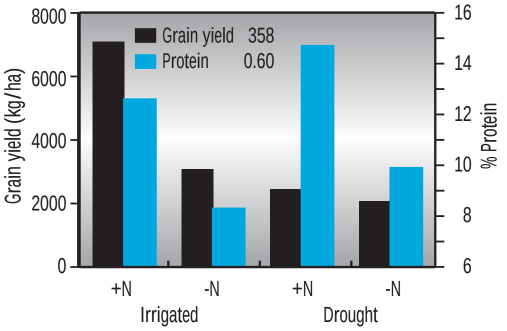


Table 1. Grain yield of eight durum genotypes in four contrasting environments of moisture and nitrogen during 1998/99.

Durum cultivar	Grain yield (12% moisture) (kg/ha) Irrigated 300 N	 Irrigated 0 N	 Drought 300 N	 Drought 0 N	Average across environments
Landrace					
Barrigon Yaqui	4751	2826	1958	2083	2905
Cultivars					
Altar 84					
CD22344-A-8M-1Y-1M-1Y-2Y-1M-0Y	6980	3125	2480	1711	3574
Rascon_43					
CD83484-B-2M-030YRC-040M-14YRC-4PAP-0Y	6659	2737	2566	2134	3524
AJAIA_12/F3LOCAL/SEL.ETHIO.135.85)//PLAT….					
CD98331-C-3Y-040M-040YRC-4M-1Y-0B	7446	3386	2735	1981	3887
Advanced lines					
PLATA_1/SNM//PLATA_9					
CD97899-H-2Y-040M040YCR-13M-1Y-0B	7381	3201	2196	2088	3717
SN TURK MI83-84 375/NIGRIS_5//TANTLO_1					
CD94483-A-3Y—040M-030Y-2PAP-1Y-0B	7381	2822	2633	1910	3686
KUCUK					
CD91B2620-G-8M-030Y-030M-2Y-0M-2Y-0B	8056	3352	2754	1928	4023
SOOTY_9/RASCON_37					
CD91B1938-6M-03Y-030M-4Y-0M-0B-1Y-0B	8054	3163	2261	2778	4064
Mean	7088	3076	2448	2077	3672
CV	6.24	10.18	11.81	13.91	9.24
LSD (0.05)	651	461	425	424	769

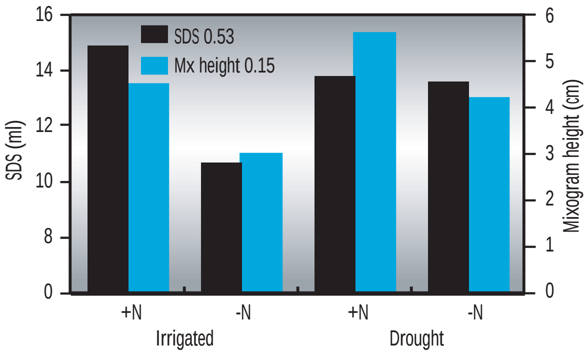


Figure 6. SDS sedimentation and mixograph values under four environments averaged across eight genotypes.

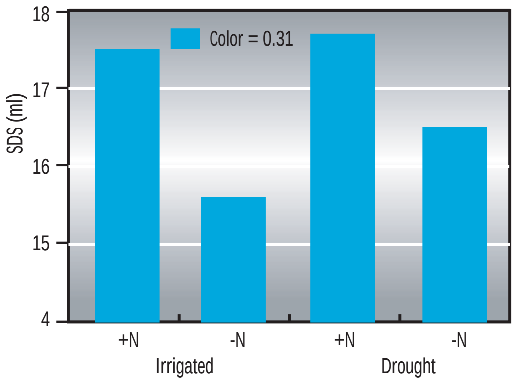


Figure 7. Grain color under four environments averaged across eight genotypes.

Conclusions

- Under nitrogen and/or water stress, at a yield level of 2 t/ha and above, the released CIMMYT cultivars and/or advanced lines showed higher yield, better protein quality, and more yellow pigment content than the landrace evaluated.
- Among the genotypes tested, there was more genetic diversity for protein quality than protein quantity.
- A new advanced line, Sooty/Rascon, showed better performance under water and nitrogen stress than the released cultivars.
- In the absence of water stress, nitrogen fertilization is necessary for quality attributes to be expressed, particularly gluten quality. In contrast, under water stress and low yielding conditions, nitrogen fertilization is not as important to realize the gluten quality of the crop.

Table 2. Grain protein concentration of eight durum genotypes in four contrasting environments of moisture and nitrogen during 1998/99.

	Grain protein (%)					
Durum cultivar	Irrigated 300 N	Irrigated 0 N	Drought 300 N	Drought 0 N	Average across environments	Protein yield (kg prot./ha) averaged across environments
Landrace						
Barrigon Yaqui	13.05	8.10	14.03	9.78	11.24	331
Cultivars						
Altar 84 CD22344-A-8M-1Y-1M-1Y-2Y-1M-0Y	12.43	7.63	14.78	9.25	11.02	408
Rascon_43 CD83484-B-2M-030YRC-040M-14YRC-4PAP-0Y	13.70	9.30	15.00	10.48	12.12	445
AJAIA_12/F3LOCAL/SEL.ETHIO.135.85)//PLAT.... CD98331-C-3Y-040M-040YRC-4M-1Y-0B	12.03	7.78	14.43	8.25	10.62	430
Advanced lines						
PLATA_1/SNM//PLATA_9 CD97899-H-2Y-040M040YCR-13M-1Y-0B	12.10	8.63	14.55	10.03	11.33	425
SN TURK MI83-84 375/NIGRIS_5//TANTLO_1 CD94483-A-3Y—040M-030Y-2PAP-1Y-0B	12.88	8.70	15.10	9.58	11.56	444
KUCUK CD91B2620-G-8M-030Y-030M-2Y-0M-2Y-0B	12.15	7.73	14.55	9.10	10.88	454
SOOTY_9/RASCON_37 CD91B1938-6M-03Y-030M-4Y-0M-0B-1Y-0B	12.70	8.13	14.80	10.98	11.65	480
Mean	12.63	8.25	14.65	9.68	11.30	427
CV	2.29	2.63	2.34	5.31	3.16	9.66
LSD (0.05)	0.42	0.32	0.5	0.76	0.6	59

Automated Interpretation and Storage of Fingerprinting Data

S. Dreisigacker, P. Zhang, M. Warburton, and C. Lopez

Introduction

Today, highly polymorphic molecular markers such as microsatellites or AFLPs are powerful tools for germplasm characterization and grouping, based on genetic relatedness. The high output of data production with the marker methodology gives a permanent task for automated handling of data interpretation and data storage. Agricultural scientists and information technicians in several centers of the Consultative Group for International Agriculture Research (CGIAR) are developing the International Crop Information System (ICIS), which is a database that includes germplasm and pedigree information of several crops. Here we show how to automatically categorize and input raw fingerprinting (molecular marker) data of wheat into ICIS (Figure 1).

GeneScan Analysis Software

For fingerprinting studies, CIMMYT uses, among other methodologies, an ABI PRISM sequencer (ABI377) to collect SSR marker data. The marker fragments are labeled with multiple fluorescent dyes and undergo electrophoretic separation in polyacrlamide gels, laser detection and computer analysis. The different fluorescent dyes allow and facilitate multiplex- reactions (Figure 2).

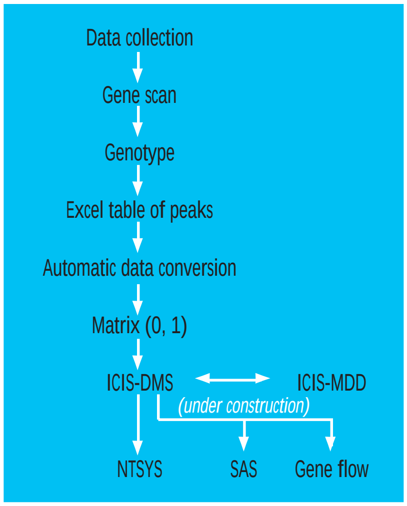


Figure 1. Steps of analysis for interpretation and storage of fingerprinting data.

The GeneScan Analysis software (Applied Biosystems) is designed for fragment analysis. Raw data (peaks) collected from ABI PRISM instruments, will automatically be identified, quantitated, and sized. The software utilizes an internal lane standard to plot a DNA standard curve. The relative size of each labeled DNA fragment is then determined based on this internal lane standard curve. This eliminates any lane-to-lane variability (Figure 3).

Genotyper Software

The Genotyper software (Applied Biosystems) utilizes the peak size and quantification data generated by Genescan Analysis software to create an allelic size table. After importing the data, you can view the electropherograms of each allele for each individual along with the allele identification as determined by Genotyper. Given a predefined range of base pairs, the computer will identify which peaks belong to each allele of the locus (Figure 4). Tools built into the software filter and remove PCR-related artifacts for each electropherogram (e.g., stutter bands and bands due to non-templated nucleotide addition of Taq Polymerase). Defined relevant alleles will be reported in a standard table, which can be exported in MS Exel. Therefore, the software facilitates fragment analysis and reduces time and subjective human scoring.

ICIS-DMS

The Excel file is converted via an automatic program to a matrix indicating the presence or absence of each allele (0, 1). Data of the same marker generated in different laboratories may be merged into one matrix. This type of matrix can be stored in the ICIS-DMS, or output for further analysis using NTSYS, SAS, GeneFlow, or other analysis packages. The pedigree and field data stored on each line in IWIS can be combined with the marker data for analysis.

ICIS-Molecular Data Display

the ICIS-MDD program is a tool for manipulation of molecular data in ICIS. The ICIS-MDD groups the individuals together in a histogram according to the alleles they contain (Figure 5). The histogram allows us to determine which peaks belongs to which allele for Genotyper automatic allele calling. The ICIS-MDD will also calculate frequencies of alleles in a population. Other tools are currently under construction.

(See a full color version of figures on the CIMMYT web page.)

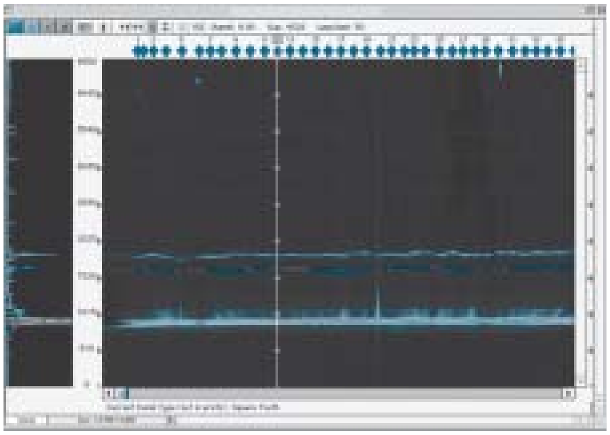


Figure 2. Gel image of an ABI Prism SSR marker run.

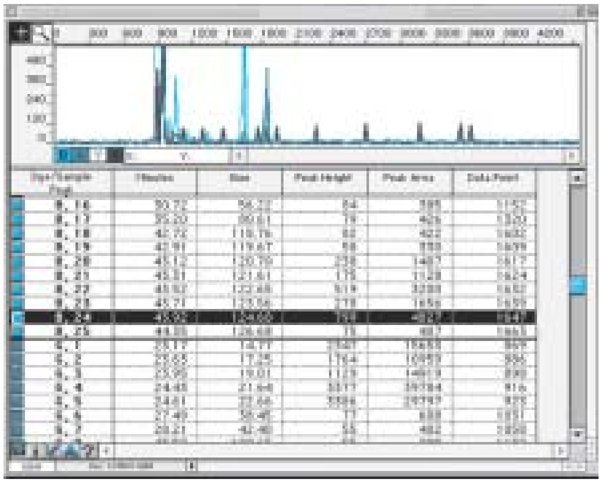


Figure 3. Results window of the fragment analysis program Genescan.

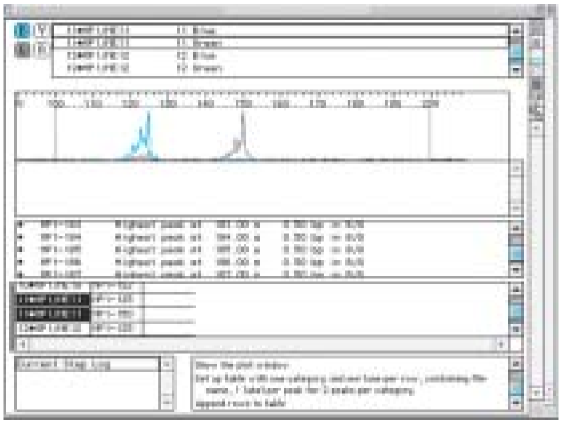


Figure 4. Main window of Genotyper, a software program for allele identification.

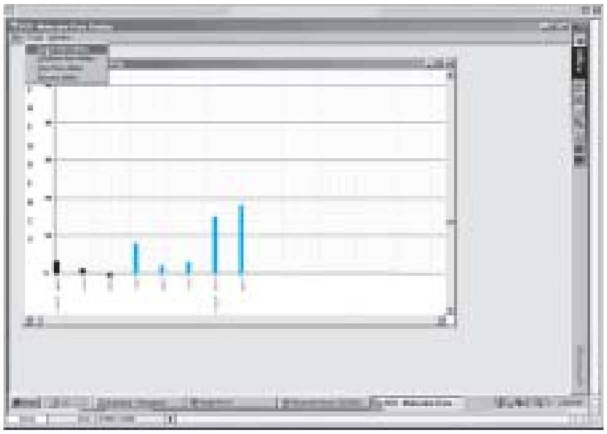


Figure 5. Final dentrogram of the ICIC-Molecular Data Display.

Pathogenicity and Virulence of Eight *Fusarium graminearum* Isolates Originating in Four Regions of Mexico

L. Gilchrist, C. Velazquez, and J. Crossa

Introduction

The expression of wheat host plant resistance to head blight caused by *Fusarium graminearum* Schw. varies widely, depending on environmental conditions (rainfall, temperature) and the inoculum used (age, concentration, incremental substrate, and isolates). It is important to have good control of these factors to avoid variation in the expression of resistance.

At present, a mixture of highly virulent pathogen isolates is commonly used as inoculum in screening wheat for fusarium head blight (FHB) resistance in the belief that there are no vertical races in *F. graminearum*, as noted in the literature. There are, nonetheless, significant differences in pathogenicity among isolates that can greatly influence the measurement of resistance levels (Mesterhazy 1997).

In our program, differences in pathogenicity observed during FHB resistance evaluation made us suspect there was significant cultivar x isolate interaction. This led us to initiate the study reported here, the main objective of which was to evaluate and confirm the presence of cultivar x isolate interaction.

Materials and Methods

During the 2000 crop cycle in Atizapan, Toluca, Mexico, a trial was carried out in which four resistant (Sumai #3, Frontana, Catbird, and Sha4/Chilero) and one susceptible (Flycatcher) wheat cultivars were inoculated with eight different *F. graminearum* isolates. The test isolates originated in Tepatitlan (isolates 3, 4, 5, 6), Jesus Maria (2), and El Tigre (1) in the state of Jalisco, and in Patzcuaro (7, 8), in the state of Michoacan (Figure 1).

The trial was planted with three replications; the cultivar was the main plot and the isolate, the sub-plot. The inoculum was increased in mungo bean medium, and its concentration adjusted to 50,000 spores/ml after five days. Twenty wheat spikes per plot were inoculated at flowering using the cotton method (Gilchrist et al. 1997).

Supplementary moisture in the form of mist irrigation was provided on the four rainless days. The different treatments were evaluated 30 days after inoculation by counting the number of affected spikelets per spike. Results were analyzed using categorical data analysis.

Figure 1. Geographical areas affected by fusarium head blight in Mexico from where the test isolates were collected.

Results and Discussion

Results of the analysis of variance (Table 1) showed highly significant differences at 0.001% between isolates, cultivars, and cultivar x isolate interactions. Isolate 1 from El Tigre was the most virulent, and 7 and 8 from Patzcuaro the least virulent (Table 2). The cultivar Frontana showed the best resistance to the eight isolates used (Table 3). Table 4 shows the absolute ratio of infected:healthy grains for each wheat cultivar with each isolate.

Conclusion

These results confirm the genotype x isolate interactions observed in Toluca in 1998. The data are unique because no other study has detected this interaction. These results help to understand the differential reaction (susceptible-resistant) observed in some varieties in different locations. The reason these results have not been replicated is that the appropriate genotypes and isolates have not been used, that is, it is necessary to choose those individuals within the host and pathogen populations that would allow detection of this event.

References

Gilchrist, L., S. Rajaram, M. van Ginkel, M. Kazi, and J. Franco. 1997. Characterizing *Fusarium graminearum* resistance of CIMMYT bread wheat germplasm. In: The 5th European Fusarium Seminar.

Mesterhazy, A. 1997. Breeding for resistance to Fusarium head blight of wheat. In: H.J. Dubin, L. Gilchrist, J. Reeves, and A. McNab (eds.), *Fusarium Head Blight: Global Status and Future Prospects.* Mexico, D.F.: CIMMYT.

Table 1. Analysis of variance of blighted spikelets of five wheat cultivars inoculated with eight individual *Fusarium graminearum* isolates, Atizapan, Toluca, Mexico, 2000.

Source	DF	Chi square	Prob
Cultivar	4	565.02	***
Isolate	7	178.10	***
Cultivar x isolate	28	106.38	***

*** Significant at P<0.001.

Table 2. Analysis of contrast among the five test wheat cultivars inoculated with eight individual *Fusarium graminearum* isolates, Atizapan, Toluca, Mexico, 2000.

Cultivars	2	3	4	5
1	***	***	***	NS
2		*	***	***
3			***	***
4				***

*, *** Significant at P<0.05 and P<0.001, respectively.
NS Not significant.

Table 3. Analysis of contrast among the eight *Fusarium graminearum* isolates used to inoculate five cultivars, Atizapan, Toluca, Mexico, 2000.

Isolates	2	3	4	5	6	7	8
1	***	***	***	***	***	***	***
2		**	NS	NS	NS	NS	NS
3			*	**	**	**	**
4				NS	NS	*	*
5					NS	NS	NS
6						NS	NS
7							NS

*,**, *** Significant at P<0.05, P<0.01, and P<0.001, respectively.
NS Not significant.

Table 4. Absolute ratios of infected:healthy grains on four resistant and one susceptible wheat cultivars inoculated with eight different *Fusarium graminearum* isolates from four regions of Mexico, Atizapan, Toluca, Mexico, 2000.

	Isolates							
Cultivars	1	2	3	4	5	6	7	8
Sha4/Chil	0.194	0.098	0.096	0.103	0.093	0.135	0.085	0.090
Catbird	0.111	0.060	0.880	0.880	0.054	0.046	0.053	0.062
Sumai#3	0.090	0.046	0.079	0.055	0.053	0.065	0.059	0.054
Frontana	0.055	0.051	0.058	0.035	0.039	0.051	0.039	0.043
Flycatcher	0.210	0.127	0.131	0.132	0.131	0.084	0.108	0.082

Increasing Durum Wheat Yield Potential and Yield Stability

W.H. Pfeiffer, K.D. Sayre , T.S. Payne, and M.P. Reynolds

To gauge historic progress in durum wheat yield potential due to breeding, the relative performance of five cultivars (Cocorit 71, Mexicali 75, Yavaros 79, Altar 84, and Aconchi 89) were assessed in Maximum Yield Potential Trials (MYPTs) conducted at Cd. Obregon, Mexico. Improvements in grain yield were associated with increased biomass yield (Figure 1), though harvest index decreased. Changes in grain yield were due to increased grains/m^2 via more grains/spike. Additionally, rate of grainfill increased, cultivars headed and matured later, and had improved test weights.

Genetic progress of contemporary CIMMYT durum germplasm was investigated by comparing the best performing durum genotypes from the MYPTs. The mean of the five hallmark checks was used for comparison to minimize the effect of individual genotype x environment interactions. These comparisons retrospectively chart changes that have occurred through genotypic improvement and suggest strategies to increase yield *per se* in the future.

For the past decade, elite germplasm exhibited genetic advances for nearly all the agronomic components (Figures 2 and 3) with the greatest changes observed in grain yield, biomass, and grains/m^2. Increases in biomass production rate from crop emergence to physiological maturity and from anthesis to physiological maturity were high. Most recently, increases in both spikes/m^2 (+8.9%) and grains/spike (+7.2%) resulted in a dramatic rise of +16.9% for grains/m^2. Grain biomass production rate (+16.6%), spike weight (+4.8%), and vegetative growth rate (+4.5%) all increased while the downward trend in 1000-grain weight (–2.8%) continued. More recent genotypes are later in heading and maturity, with a surprisingly shorter grainfill duration.

Contrasting the performance of top yielding durums with top yielding bread wheat genotypes may produce models for the identification of alternate avenues

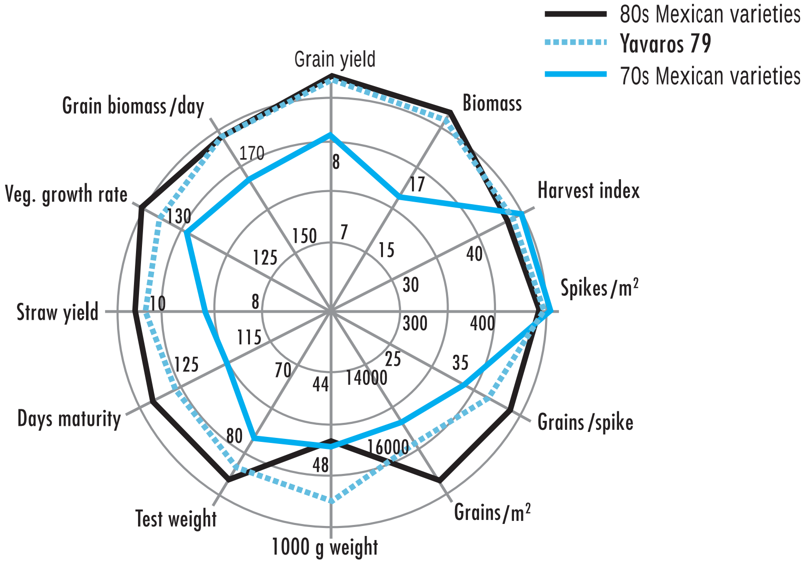


Figure 1. Comparison of agronomic traits of hallmark durum wheat cultivars released in the early 1970s (Cocorit 71, Mexicali 75, Yavaros 79), and 1980s (Altar 84, Aconchi 89), evaluated in Maximum Yield Potential Trials, Cd. Obregon, 1991-99.

to obtaining higher yield for either crop. Pfeiffer et al. (1996) suggested that lower numbers of spikes/m^2 and grains/m^2 in durums compared with bread wheat should receive special attention in durum improvement since past experience indicated superior bread wheat performance was associated with number of spikes/m^2. Figure 4 discloses a gradual correction of this delinquency in contemporary durum wheats, and reveals a converging of yield architecture in durum and bread wheat.

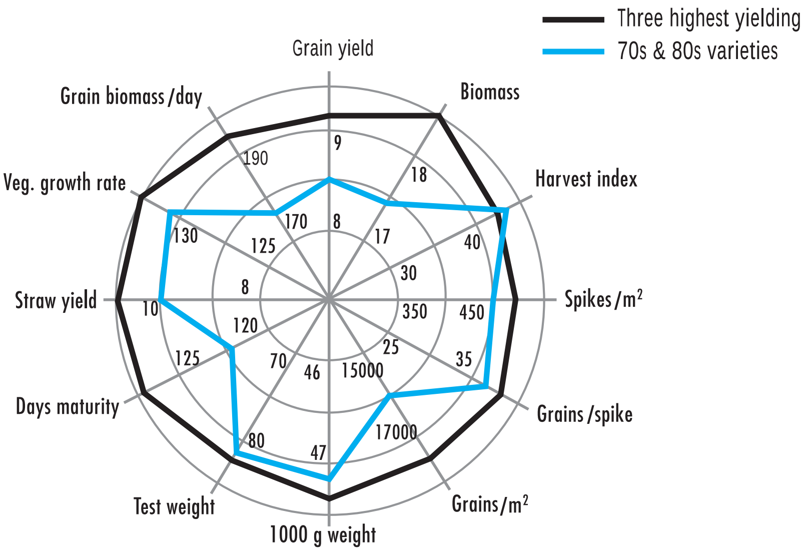


Figure 2. Comparison of agronomic traits of contemporary durum wheat advanced lines compared with the hallmark check cultivars (Cocoriti 71, Mexicali 75, Yavarons 79, Altar 84, Aconchi 89), evaluated in Maximum Yield Potential Trials, Cd. Obregon, 1991-99.

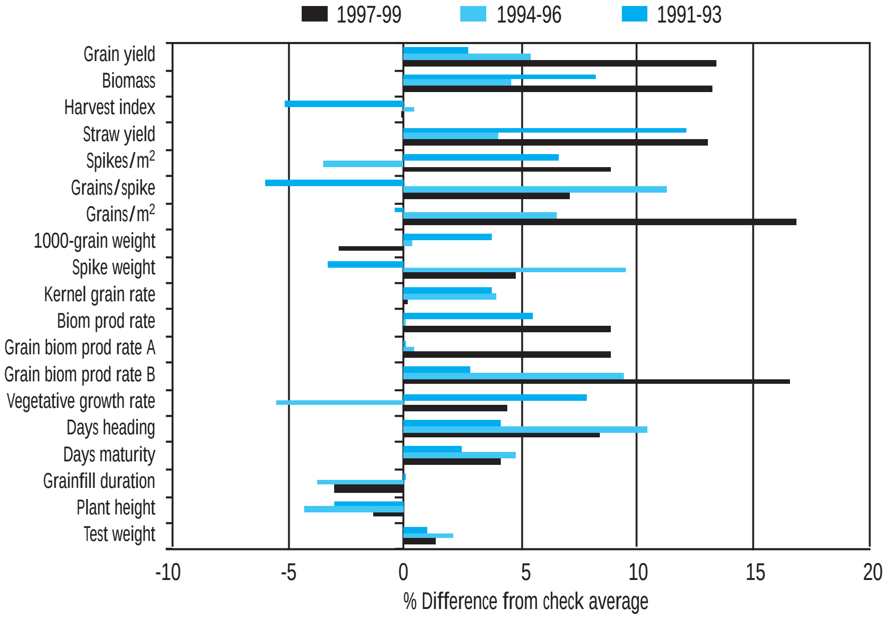


Figure 3. Comparison of agronomic traits of contemporary durum wheat advanced lines measured in three periods vs. the five hallmark cultivars, evaluated in Maximun Yield Potential Trials, Cd. Obregon, 1991-99.

Earlier efforts to increase biomass focused on manipulating grains/m^2 and, later, on augmenting the number of grains/spike, both of which are suitable traits in phenotypic selection. Selecting for grains/m^2 via a higher number of grains/spike proved superior in raising GYP. Negative effects on grains/m^2 were minor and 1000-grain weight was maintained. Over 1997-99, simultaneous increases in spikes/m^2 and grains/spike produced the highest increase in grains/m^2, GYP, and biomass. The balance in yield components may have approached a near optimal constellation, as results of crop comparison suggest. With limited scope for increasing the partitioning of assimilates to the grain, future progress has to be based on increased biomass.

Physiological strategies that can be applied empirically to accelerate the rate of breeding progress include improved radiation use efficiency (RUE) and therefore increased total plant biomass, increased grain number, and increased kernel weight. These strategies should be incorporated into analytical, marker-assisted selection approaches and advanced empirical breeding concepts (Pfeiffer et al. 2000).

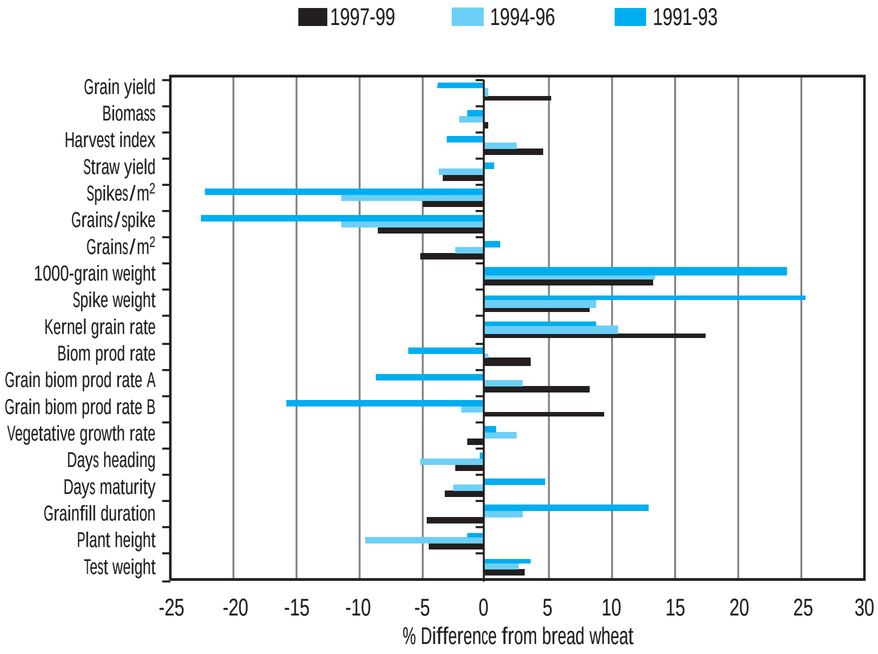


Figure 4. Comparison of agronomic traits of contemporary durum wheat advanced lines measured in three periods vs. the highest yielding bread wheats, evaluated in Maximun Yield Potential Trials, Cd. Obregon, 1991-99.

Parallel enhancement of yield components that determine grains/m^2 may be recommended to minimize competition among yield factors with overlapping developmental stages. Further expansion of the reproductive phase or higher growth rates during different phenological stages should result in higher biomass during this presumably source limited period.

Determination of individual grain weight is essentially independent of yield components associated with grains/m^2. Nevertheless, grains/m^2 and 1000-grain weight are negatively associated, as the decline in grain weight over time has been over-compensated by an increase in grain number. Given high trait heritability and immense genetic variation for 1000-grain weight, with maximum values above 75 mg/grain, from a breeding perspective improvement of grain size, *ceteris paribus*, is a promising strategy to raise yield *per se*. Heterosis for grain size in wheat and triticale hybrids, the primary trait affected, indicates enormous potential supporting a hypothesis that gains can be achieved without sacrificing grains/m^2.

Achievements in improving GYP can be traced to concomitant improvements in raising yield *per se* and increasing yield stability. MYPT data reveal that in years with an overall performance below the long-term average, more recently developed genotypes exhibit greater performance stability than the hallmark checks (Pfeiffer et al. 1996). Superior spatial, temporal,

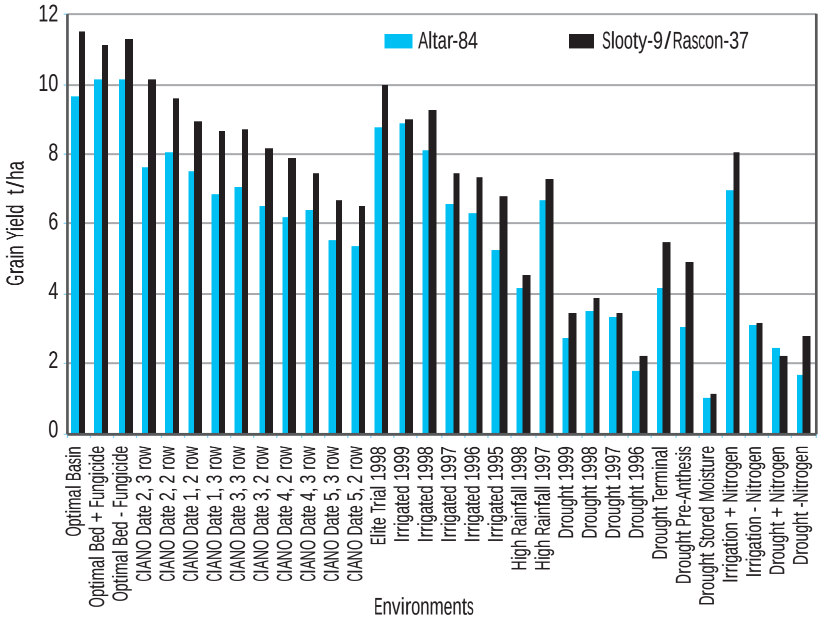


Figure 5. Grain yield performance of Sooty-9/Rascon-37 compared to Altar-84 in 32 different environments, 1995-99.

and systems stability can be combined with maximum yield *per se* (Figure 5). However, while current GYP stabilization efforts have emphasized individual buffering of homozygous genotypes, greater consideration to population buffering effects in heterozygous populations and different population structures should occur in future breeding efforts.

Progress in GYP and associated traits relies on existing genetic variation. The genetic diversity spectrum used in tactical and strategic durum improvement includes major tetraploid varieties, advanced lines, and unimproved/landrace germplasm from the spring and winter gene pools, interspecific and intergeneric sources, and AAB and ABB genome hexaploid synthetics. Alien chromosome substitutions and translocations are a promising option for increasing GYP and their effects in durum are currently under study.

References

Pfeiffer, W.H., K.D. Sayre, and M. Mergoum. 1996. Enhancing genetic grain yield potential in durum wheat and triticale. In: M.P. Reynolds, S. Rajaram, and A. McNab (eds.), *Increasing Yield Potential in Wheat: Breaking the Barriers*, pp. 208-213. Mexico, D.F.: CIMMYT.

Pfeiffer, W.H., K.D. Sayre, and M.P. Reynolds. 2000. Enhancing genetic grain yield potential and yield stability in durum wheat. In: *Durum wheat improvement in the Mediterranean region: New challenges.* Options Mediterranées, Serie A, No. 40, pp. 83-93. Zaragoza, Spain: CIHEAM-IRTA.

Characterization of Durable Rust Resistance Genes with Molecular Markers in Wheat

**M. William, R.P. Singh, J. Huerta, G. Palacios,
K. Suenaga, and D. Hoisington**

Background

Rust diseases, specifically leaf rust and yellow rust, are common foliar fungal diseases in many wheat growing regions of the world. Developing wheat cultivars with slow rusting genes has been part of a global wheat breeding strategy undertaken at the International Maize and Wheat Improvement Center (CIMMYT) that would enhance wide adaptability and yield stability of improved CIMMYT wheats. Although 10-12 slow rusting genes are known to be present in CIMMYT spring wheats, only *Lr34* and *Lr46* for leaf rust and *Yr18* for yellow rust have been characterized to date.

The objectives of this project are:

1. To identify genes that confer durable resistance to leaf and yellow rust in wheat.
2. Associate molecular markers with such genes, thereby enabling their manipulation by the breeders.

We report the results obtained so far.

Populations

1. Avocet x Pavon 76 - 146 F_5 lines
2. Avocet x Parula - 141 F_6 lines

Phenotyping

Leaf rust and yellow rust severity, measured as percentage of leaf area infected, were evaluated in field experiments conducted over three years. Spreader rows inoculated with one selected pathotype of each rust were used to infect both leaf rust and yellow rust in the populations. The distribution of yellow rust severity in Avocet x Pavon 76 population is shown in Figure 1.

Marker development

Bulked segregant analysis (BSA) with AFLPs and linkage mapping with a set of microsatellites and RFLPs were used. In each of the two populations, bulks were made by taking equal amounts of DNA from 7-12 entries that were most resistant to both leaf rust and yellow rust as well as most susceptible to the two diseases jointly. In addition to the bulks made that jointly accounted for the two diseases, bulks were also made individually for leaf rust and yellow rust. Forty-eight *Pst1*/*Mse1* primer combinations were used in BSA. Polymorphic AFLPs selected from BSA were screened across the full populations.

The MAPMAKER program was used for linkage analysis and *qGene 2.27* was used for QTL analysis.

Results

Avocet x Pavon 76 population

Bulked segregant analysis enabled the identification of markers linked to *Lr46* and it was also observed that there is another gene in close association with *Lr46* that confers resistance

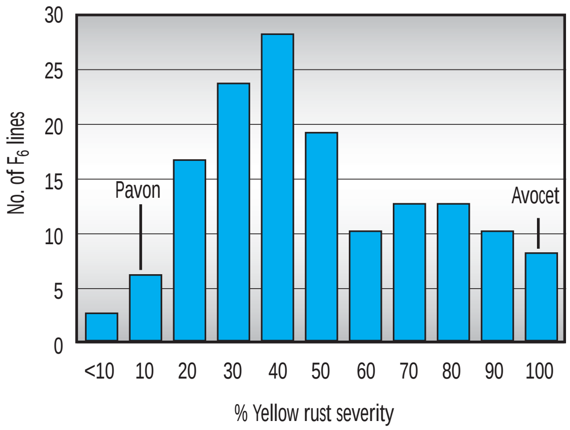


Figure 1. Distribution of 146 F_6 lines for yellow rust severity in Avocet-Pavon population.

to yellow rust (newly designated as *Yr29*). By mapping the AFLP markers in the ITMI population, the genomic location of *Lr46*/*Yr29* was established in the distal end of chromosome 1BL (Figures 2 and 3). Table 1 summarizes the loci identified in Avocet X Pavon 76 that condition resistance to leaf rust and yellow rust. In this population, we have been able to identify three loci located on chromosomes 1BL, 4B, and 6A that confer resistance to both leaf rust and yellow rust. There are two other loci, located on chromosomes 6B and 3BS that have significant effects only on yellow rust (Table 1).

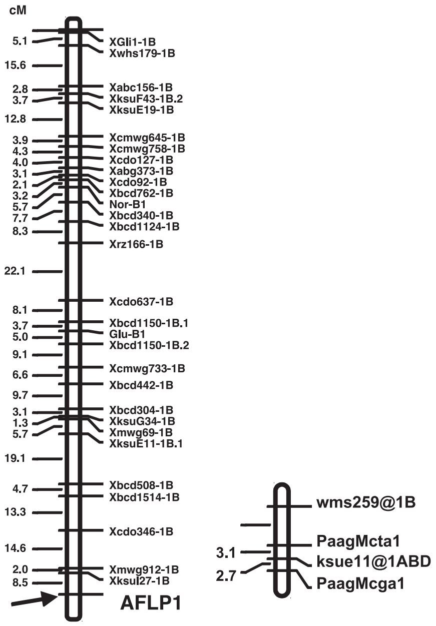


Figure 2. 1B linkage group - ITMI genetic map.

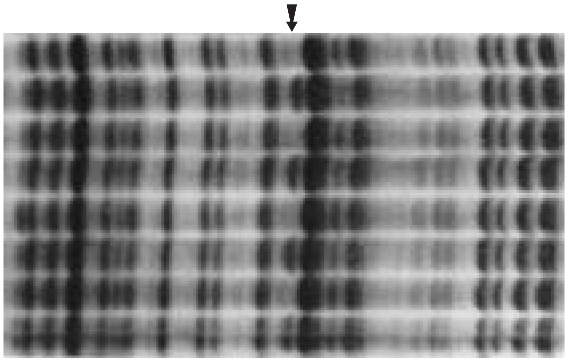


Figure 3. AFLP segregation pattern of the population. Marker associated with resistance is indicated by the arrow.

Avocet x Parula population

Linkage mapping in this population enabled the identification of a microsatellite marker that is linked to leaf tip necrosis (*Ltn*) at 4.5cM, which is known to be tightly linked to *Lr34*/*Yr18* (Table 2). In addition, BSA enabled identification of three other loci that have significant effects on leaf rust. Three out of the four loci found to be associated with resistance to leaf rust also have some effect on yellow rust (Table 2).

Conclusions

- In the two populations studied, we identified a total of 7 and 9 QTLs for leaf rust and yellow rust resistance, respectively.
- Six of the above QTLs, including the *Lr34*/*Yr18* and *Lr46*/*Yr29* regions, conferred resistance to both leaf and yellow rusts.
- Two slow rusting resistance genes for yellow rust resistance have been designated as *Yr29* and *Yr30*.
- Gene *Yr30* is in the same 3BS chromosomal region where slow rusting stem rust resistance gene *Sr2* is located.

Table 1. Loci conditioning resistance to leaf rust and yellow rust in Pavon 76.

		Reduction (%) in mean disease severity		
Location	Marker	Leaf rust	Yellow rust	Named genes
1BL	Wms259	35	27	*Lr46*, *Yr29**
4B	Wms495	18	15	
6A	Wms356	14	18	
6B	PAggMCAA	-	18	
3BS	PACgMCgT	-	11	*Yr30*, *Sr2*

Table 2. Loci conditioning resistance to leaf rust and yellow rust in Parula.

		Reduction (%) in mean disease severity		
Location	Marker	Leaf rust	Yellow rust	Named genes
7DS	Wms130/Ltn	56	46	*Lr34*, *Yr18*
7B or 7D	Pcr156	29	-	
1BL	PAAgMCTA1	15	16	*Lr46*, *Yr29**
3BS	Glk 683	-	10	*Yr30*, *Sr2*
Unknown	PAAgMCTA3	22	14	

* New gene designations.

Genetic Diversity for Improving Scab Resistance in Wheat

A. Mujeeb-Kazi, A. Cortés, V. Rosas, S. Cano, J. Sánchez, L. Juárez, and R. Delgado

Introduction

The International Maize and Wheat Center (CIMMYT) Wheat Wide Crosses program at the has been exploiting accessions of the primary gene pool diploid (2n=2x=14, DD) wheat relative *Aegilops tauschii* (syn. *Aegilops squarrosa, Triticum tauschii*) for the past 10 years. Because of their wide diversity, global distribution, and genetic proximity to the D genome of bread wheat, the accessions provide a unique opportunity for bread wheat improvement.

Ae. tauschii accessions have been indiscriminately hybridized with *T. turgidum* to produce 800 synthetic hexaploids (SHs) so far. All SHs have a spring habit, which has accelerated screening without having to deal with vernalization and other constraints. Synthetics resistant to scab have been crossed to susceptible bread wheats in an attempt to transfer the *Ae. tauschii* resistance to superior bread wheat cultivars. To diversify the resistance available in *Ae. tauschii* and its accessions, perennial Triticeae species of the tertiary gene pool have also been hybridized to bread wheat, leading to amphiploids and backcross derivatives. The above two groups of materials form the present objective of alien germplasm screening for *Fusarium graminearum* using artificial inoculation in the field in Atizapan, Toluca, Mexico. Test germplasm is distributed over all three Triticeae gene pools.

Materials and Methods

Germplasm

- 800 SH wheats, derived from crosses of 34 *T. turgidum* and 460 of the 490 *Ae. tauschii* accessions.
- Advanced progenies from resistant synthetic/susceptible bread wheats.
- Amphiploids of *Thinopyrum bessarabicum* and *Th. elongatum* with bread wheat, and some BCI self-fertile intergeneric hybrid combinations.
- Disomic 44 chromosome addition derivatives from bread wheat/*Leymus racemosus*// bread wheat combinations.
- Disomic addition lines of *Th. bessarabicum.*
- 190 A genome hexaploids derived from durum x A genome diploid combinations (2n=6x=42, AAAABB) and 50 B genome hexaploids from durum/*Ae. speltoides* accessions (2n=6x=42, AABBBB).

Location and plot size

- CIMMYT station, Toluca, Mexico (19º17'N, 99º39'W, 2640 m above sea level).
- Plot size: a) Unreplicated hill plots of all genetic stocks comprised of SH wheats, amphiploids, BCI self-fertiles, and disomic addition lines; and b) two 2-m rows, 15 cm between rows in 90-cm beds.

Disease inoculation

- Fusarium head scab isolates were obtained from Toluca, Patzcuaro, and El Tigre, Mexico. A concentration of 50,000 spores/ ml of water was used for the inoculum. [1]
- Cotton inoculation method: A tiny tuft of cotton permeated with inoculum suspension is placed in a floret by opening the glumes of a spikelet in the middle part of the spike with a pair of tweezers. The spike is then covered with a glassine bag to prevent damage. Five to ten random spikes were inoculated per entry.

Disease evaluation

Disease was scored 30-35 days after inoculation. Inoculated spikes were harvested, percent fusarium-infected spikelets evaluated, and scab scores of inoculated spikes averaged.

---

[1] Inoculum was provided by CIMMYT's Wheat Pathology Laboratory (Dr. L.I. Gilchrist and staff).

Cytology

- Mitosis and Giemsa C-banding: Standard protocols based on aceto-orcein staining for mitosis and 4% Giemsa staining used in CIMMYT's wide crosses laboratory were followed.
- The meiotic procedure utilized alcoholic carmine and aceto-carmine combination of staining (Mujeeb-Kazi et al. 1994). The fluorescent in situ hybridization (FISH) meiotic protocol was adapted from Islam-Faridi and Mujeeb-Kazi (1995).

Results and Discussion

Resistance in synthetic hexaploid wheats

The SH wheats (*T. turgidum* x *Ae. tauschii*) most resistant to *F. graminearum* during field screening at Toluca, Mexico, are presented in Table 1. Only those entries with less than 15.0% infection scores (Type II) are shown. Resistant bread wheat (BW) check Sumai scored less than 15%, while the susceptible BW check cultivar Flycatcher ranged between 24.6 and 45.5% with a cross year mean of 33.8%. The susceptible durum wheat Altar 84 had a mean score of 40.8%. Figure 1 shows a susceptible durum wheat, and a *F. graminearum*-resistant SH using artificial inoculation in the field.

Resistance in bread wheat/synthetic hexaploid advanced derivatives

The most advanced and promising entries from the BW/SH combinations were further tested for the other three scab resistance categories (Types I, III, IV). Four were found to possess combined resistance to all four types of scab (Table 2). These are currently being used in bread wheat breeding at CIMMYT and in collaborative activities with the US Scab Initiative (Figures 2a and b) (Mujeeb-Kazi et al. 1998).

The combination Mayoor//TK SN 1081/*Ae. tauschii* (222) and several of its sister lines exhibit superior scab resistance across its four categories and also possess resistance to *S. tritici*, *Tilletia indica,* and *H. sativum*. One line was crossed with Flycatcher (susceptible to all the above stresses), and the F_1 seed was used to produce 160 doubled haploids (DH) for molecular mapping/phenotyping.

Table 1. Promising D genome synthetic hexaploids screened for head scab (Type II) at Toluca, Mexico.

Germplasm pedigree	1999	2000
YUK/*Ae. tauschii* (217)[1]	11.4	11.8[2]
68.111/RGB-U//WARD/3/FGO/4/RABI/5/*Ae. tauschii* (629)	11.9	10.0
68.111/RGB-U//WARD/3/FGO/4/RABI/5/*Ae. tauschii* (878)	12.4	13.1
68.111/RGB-U//WARD/3/FGO/4/RABI/5/*Ae. tauschii* (882)	11.1	13.6
SORA/*Ae. tauschii* (884)	12.9	13.5
68.111/RGB-U//WARD/3/FGO/4/RABI/5/*Ae. tauschii* (890)	11.4	14.1
CETA/*Ae. tauschii* (895)	10.8	13.2
GAN/*Ae. tauschii* (180)	10.7	10.9
LCK59.61/*Ae. tauschii* (313)	11.5	12.2
SCOOP 1/*Ae. tauschii* (358)	12.0	13.9
YUK/*Ae. tauschii* (217)	11.4	11.8
TRN/*Ae. tauschii* (700)	13.4	13.7
DOY1/*Ae. tauschii* (333)	11.1	13.9
DVERD_2/*Ae. tauschii* (1027)	14.6	11.7
MAYOOR//TK SN1081/*Ae. tauschii* (222)	11.7	5.7
FLYCATCHER (Mean across years)		33.8
SUMAI-3 (Mean across years)		12.0
ALTAR 84		40.8

[1] *Ae. tauschii* accession in wide crosses working collection.

[2] Percentage score means from 10 spikes tested.

Figure 1. Fusarium Type II testing showing in a) durum wheat susceptibility, and b) resistance in the synthetic hexaploid.

Table 2. Some promising bread wheat/synthetic hexaploid derivatives tested in Toluca for the various scab resistance categories (Type I to IV) and grain finish.

Lines	Type I[1] 1998-99	Type II[1] 1998-99	DON (ppm)	Test weight losses (%)	Grain (0-5)[2]
TURACO/5/CHIR3/4/SIREN//ALTAR 84/*Ae. tauschii* (205)/3/3*BUC CASS94Y00034S-24PR-2B-0M-0FGR-0FGR-0FGR	8.0	9.9	0.6	5.3	2
BCN//DOY1/*Ae. tauschii* (447) CASS94Y00006S-53PR-2B-0M-0FRG-0FRG-0FRG-0FRG	9.6	10.1	1	2.6	1
MAYOOR//TK SN1081/*Ae. tauschii* (222) CASS94Y00009S-18PR-3M-0M-0FRG-0FRG-0FRG	7.3	9.9	1.2	6.1	1
MAYOOR//TK SN1081/*Ae. tauschii* (222) CASS94Y00009S-50PR-2B-0M-0FRG-0FRG-0FRG	4.1	11.7	1.2	6.5	1
SUMAI # 3 (resistant check)	3.0	12.9	0.3	38.6	3
FRONTANA (moderately resistant check)	11.6	22.4	2	7.7	2

[1] Percent damage.
[2] 0 = Excellent (no differences in appearance with fungicide protected grain).
Source: Mujeeb-Kazi et al. (1998).

The tertiary gene pool for bread wheat improvement

New genetic diversity. Tertiary pool species hold promise for providing additional genetic diversity for scab resistance. Of high priority at this stage are crosses of wheat x *Th. bessarabicum* and their backcross derivatives, where the *ph* locus is involved to promote the introgression of alien genes. Several disomic additions of *Th. bessarabicum* in wheat have been identified as low scoring Type II infection stocks. These are being exploited for achieving genetic introgressions in addition to the priority use of the amphiploid (*T. aestivum*/*Th. bessarabicum*) (Mujeeb-Kazi 1998).

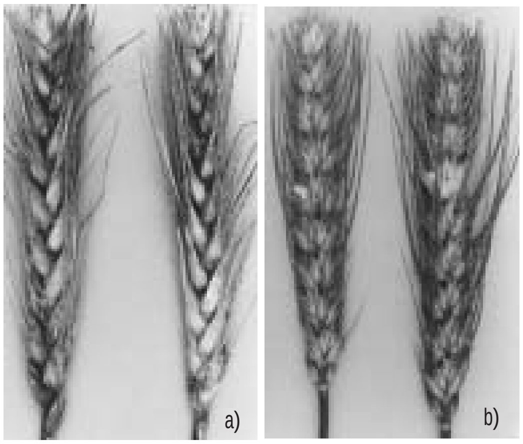


Figure 2. Fusarium Type II testing showing in a) bread wheat (BW) susceptibility, and b) resistance of a derivative from the susceptible BW/resistant SH with the Mayoor//TK SN 1081/*Ae. tauschii* (222) pedigree.

The functioning of the cytogenetic manipulation process, where *ph ph* plants are first detected by the PCR technique, exhibits high meiotic pairing (Figures 3a and b) and demonstrates wheat/*Th. bessarabicum* chromosome associations identified by FISH. The *ph* based manipulation protocol is anticipated to permit multiple exchanges and may short-cut the transfer process where several chromosomes control resistance.

***Scab resistance from* Leymus racemosus.** A wheat x *L. racemosus* F_1 hybrid was first produced in CIMMYT in 1981. Its C-banded profile was reported later (Mujeeb-Kazi et al. 1983) as was its potential for scab resistance. More recently Chen et al. (1997) reported that three of the *L. racemosus* addition lines developed by them demonstrated scab resistance. We thus re-examined our earlier uncategorized 44 chromosome stocks (Chinese Spring/*L. racemosus*//CS/3/Pvn (n)) in the MV-2000 Toluca cycle. Currently six disomic addition lines have been identified with low scab scores based upon C- banding. Three ditelocentric lines with low Type II scores have also been identified. Each entry is targeted for subsequent *ph* based manipulation.

Durum wheat improvement

- Several diploid (2n=2x=14, AA) accessions combined with elite durum cultivars yielded AAAABB hexaploids, after their AAB F_1 hybrids were colchicine doubled. In the initial screening only five of the 174 hexaploids exhibited Type II promise with mean infection scores between 13.5% to 15.0%. These will be evaluated further. Novel B genome hexaploids (2n=6x=42, AABBBB) have been produced that may have potential for scab resistance.
- Another strategy in place is attempting to incorporate resistant D genome diversity into the A genome via homoeologous exchange facilitated by the *ph1c* genetic durum stock Capelli. Cytological evidence from F_1 hybrids validate A and D genome chromosome pairing.

Conclusions

- Synthetic hexaploid wheats derived from *T. turgidum x Ae. tauschii* crosses express moderate but satisfactory levels of scab resistance.
- Resistance from SH wheats has been transferred to elite-but-susceptible bread wheat cultivars.
- One promising line—the multiple disease resistant Mayoor//TK SN1081/*Ae. tauschii* (222)—has been crossed with Flycatcher (susceptible) and a DH population developed for molecular mapping.
- Tertiary pool diversity for scab identified in some *Thinopyrum* and *Leymus* species is being introgressed into bread wheat.
- Durum improvement for scab is being addressed via AAAABB, AABBBB hexaploid genetic stocks and by the scab resistant D genome to A genome homoeologous transfers.

References

Chen, P., D. Liu, and W. Sun. 1997. New countermeasures of breeding wheat for scab resistance. In: H.J. Dubin, L. Gilchrist, J. Reeves, and A. McNab (eds.), *Fusarium Head Scab: Global Status and Future Prospects*, pp. 59-65. Mexico, D.F.: CIMMYT.

Islam-Faridi, N.I., and A. Mujeeb-Kazi. 1995. Visualization of Secale cereale DNA in wheat germ plasm by fluorescent *in situ* hybridization. *Theoretical and Applied Genetics* 90:595-600.

Mujeeb-Kazi, A. 1998. An analysis of the use of haploidy in wheat improvement. In: M.M Kohli and M. Francis (eds.), *Application of Biotechnologies to Wheat Breeding*, pp. 33-48. La Estanzuela, Uruguay: CIMMYT-INIA.

Mujeeb-Kazi, A., L.I. Gilchrist, and R. Delgado. 1998. Potential of alien genetic diversity for improving resistance in wheat. *Agronomy Abstracts*, pp. 78.

Mujeeb-Kazi, A., Q. Jahan, and A.A. Vahidy. 1994. Application of a somatic and meiotic cytological technique to diverse plant genera and species in the Triticeae. *Pakistan Journal of Botany* 26:353-366.

Mujeeb-Kazi, A., M. Bernard, G.T. Bekele, and J.L. Miranda. 1983. Incorporation of alien genetic information from *Elymus giganteus* into *Triticum aestivum.* In: Proceedings of the 6th International Wheat Genetics Symposium, pp. 223-231.

Figure 3. Two meiocytes from the cytogenetically manipulated derivatives showing a) low chromosomal pairing and b) high chromosome pairing involving wheat and alien chromosomes as a consequence of the *Ph* and *ph* genes.

Simulation of the CIMMYT Wheat Breeding Program

J. Wang, M. van Ginkel, R. Trethowan,
D. Podlich, I. DeLacy, and M. Cooper

Introduction

The major objective of plant breeding programs is to develop new genotypes that are genetically superior to those currently available for a specific target mega-environment (ME) or a target population of environments (TPE). To achieve this objective, plant breeders employ a range of crossing and selection methods. For example, at the International Maize and Wheat Center (CIMMYT), the most frequently used method from the 1940s till the early 1980s was pedigree selection; modified pedigree/bulk selection started being used in the early 1980s. Today the selected bulk method is being used on certain populations in CIMMYT's bread wheat breeding program.

Generally speaking, quantitative genetics provides much of the framework for designing and analyzing selection methods used within breeding programs. However, assumptions in quantitative genetics are usually made to render some theories mathematically or statistically tractable. Some assumptions can be easily tested or satisfied by experimental designs. Others could never be true; for example, assumptions of no linkage and no genotype by environment interaction (GEI). Still other assumptions are difficult to test; for example, the existence of epistasis. Therefore, many predictions made in plant breeding programs are based on a relatively simple genotype by environment system.

Computer simulation provides us with a tool to investigate the implications of relaxing some of these assumptions and the effect this would have on the conduct of a breeding program.

The CIMMYT Wheat Breeding Simulation Project is jointly supported by the Grains Research and Development Council (GRDC) and the University of Queensland, Australia, and CIMMYT. The aims of this project are to:

- Design a simulation module based on QU-GENE software that will identify opportunities to further improve the efficiency of the CIMMYT wheat breeding and dissemination programs.
- Characterize the target population of environments (TPE) in client countries, including those in Australia, that are relevant to CIMMYT wheat breeding objectives and procedures, and store them in ICIS.
- Develop a QU-GENE/ICIS software and data exchange interface to enable the use of the genotype and environment characterization information held in ICIS for modeling CIMMYT and Australian wheat breeding strategies using QU-GENE.

Steps of a Simulation Project

1. Documentation of the CIMMYT wheat breeding program

The initial step toward breeding simulation is to document CIMMYT's wheat breeding programs and expound their operations and activities in a quantitative and breeding/genetic fashion. This detailed description is used for designing simulation software and should include:

- Constitution of entries in the crossing block: elite CIMMYT germplasm, major released cultivars, advanced lines from wide crosses, pathology, etc.
- Parental selection process for crossing and type of crosses (e.g., simple cross, top cross, and backcross).

- Germplasm flow from crossing blocks to yield trials and from there to International Screening Nurseries and Yield Trials (Figures 1 and 2).
- Breeding traits, among cross or family selection intensity, within cross or family selection intensity, sown-grain weight and population size, and harvest method in each generation.

2. Definition of a genotype by environment system

The underlying basis for simulation must be a genotype by environment system. The genes, their locations on the chromosomes, and their frequencies in breeding populations constitute the genetic component of the system. For simulation we only consider those loci with two or more alternative alleles. Some genes have been located on the chromosomes; however, most genes have not, especially for most agronomic and economic traits. For this purpose, we will make educated guesses on the number of genes and temporarily assign these genes on the linkage map. Then we will use historical data such as genetic gains and the magnitude of genotype by environment variation to test the assumption of gene number. The number of environments in the target ME and their frequencies constitute the environmental component of the system; gene effects under different environments are the interaction part of the system. For simulation, the following information should be specified:

- Genes for traits and gene linkage map, gene frequencies in crossing blocks, and genetic effects (additive, dominance, and epistasis).
- Constitution of the MEs.
- Adaptation landscape model for genotype by environment interaction: E(N:K), landscape representation of genetic adaptation (Figure 3).
- E: number of environments.
- N: number of genes.
- K: level of epistasis.

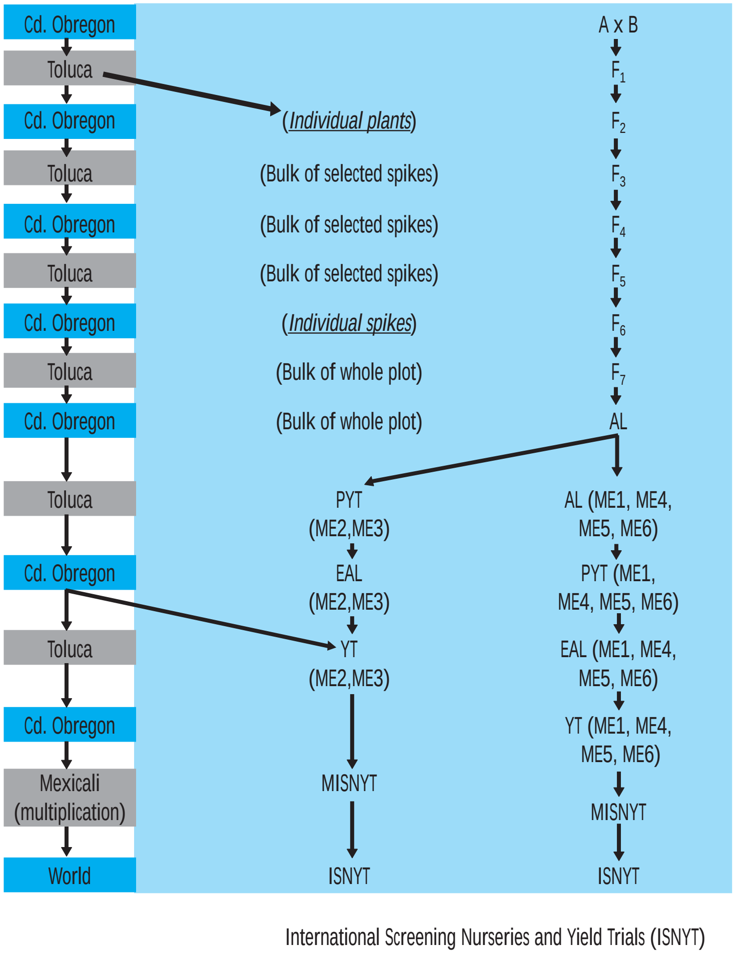
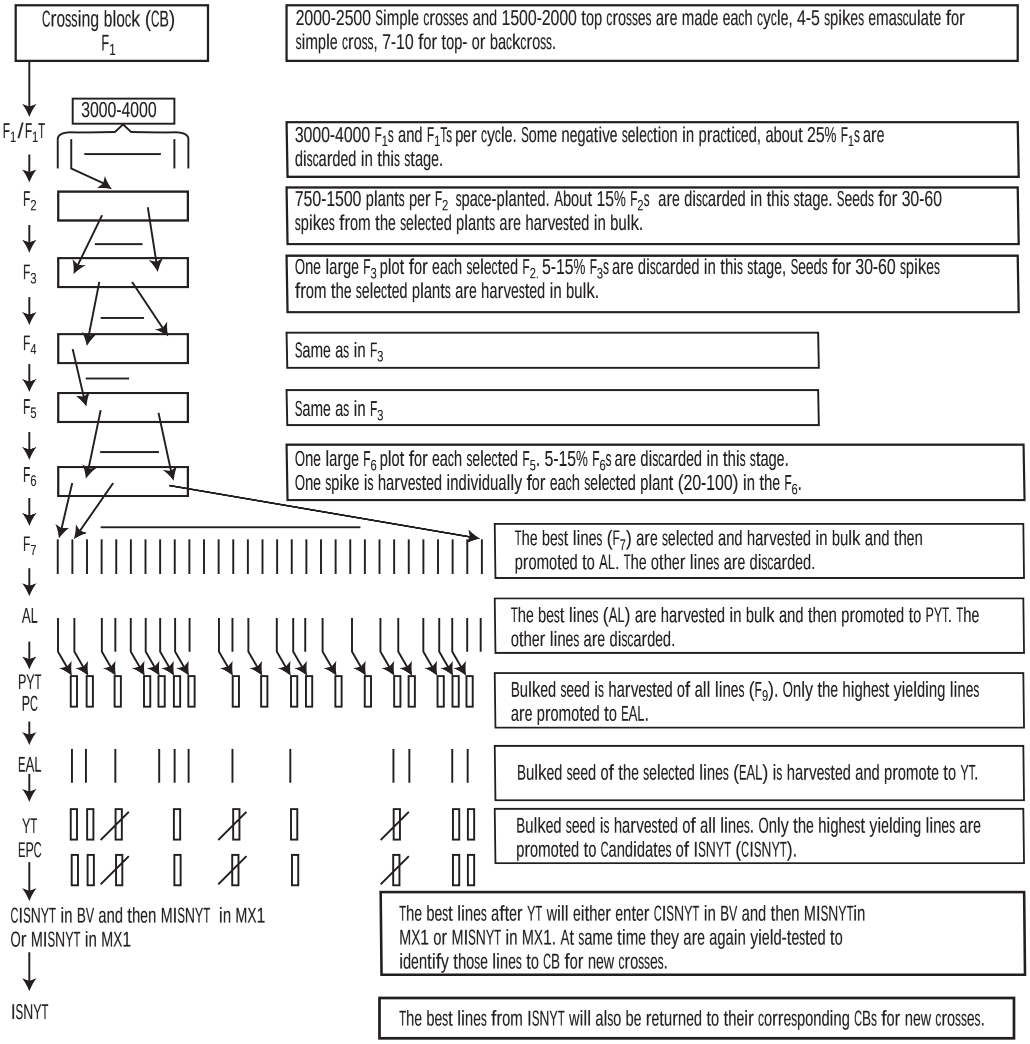


Figure 1. Germplasm flow in CIMMYT's bread wheat breeding program at the International Maize and Wheat Improvement Center.
Note: AL = advanced lines; PYT = preliminary yield trial; EAL = elite advanced line; YT = yield trial.

Plant Breeding Issues to be Determined by Simulation

Many issues in plant breeding can be studied by simulation



2000-2500 Simple crosses and 1500-2000 top crosses are made each cycle, 4-5 spikes emasculate for simple cross, 7-10 for top- or backcross.

3000-4000 F_1s and F_1Ts per cycle. Some negative selection in practiced, about 25% F_1s are discarded in this stage.

750-1500 plants per F_2 space-planted. About 15% F_2s are discarded in this stage. Seeds for 30-60 spikes from the selected plants are harvested in bulk.

One large F_3 plot for each selected F_2. 5-15% F_3s are discarded in this stage, Seeds for 30-60 spikes from the selected plants are harvested in bulk.

Same as in F_3

Same as in F_3

One large F_6 plot for each selected F_5. 5-15% F_6s are discarded in this stage.
One spike is harvested individually for each selected plant (20-100) in the F_6.

The best lines (F_7) are selected and harvested in bulk and then promoted to AL. The other lines are discarded.

The best lines (AL) are harvested in bulk and then promoted to PYT. The other lines are discarded.

Bulked seed is harvested of all lines (F_9). Only the highest yielding lines are promoted to EAL.

Bulked seed of the selected lines (EAL) is harvested and promote to YT.

Bulked seed is harvested of all lines. Only the highest yielding lines are promoted to Candidates of ISNYT (CISNYT).

The best lines after YT will either enter CISNYT in BV and then MISNYTin MX1 or MISNYT in MX1. At same time they are again yield-tested to identify those lines to CB for new crosses.

The best lines from ISNYT will also be returned to their corresponding CBs for new crosses.

Figure 2. Germplams flow of the selected bulk method.
Note: AL = advanced line; PYT = preliminary yield trial; EAL = elite advanced line; YT = yield trial; ISNYT = International Screening Nurseries and Yield Trials.

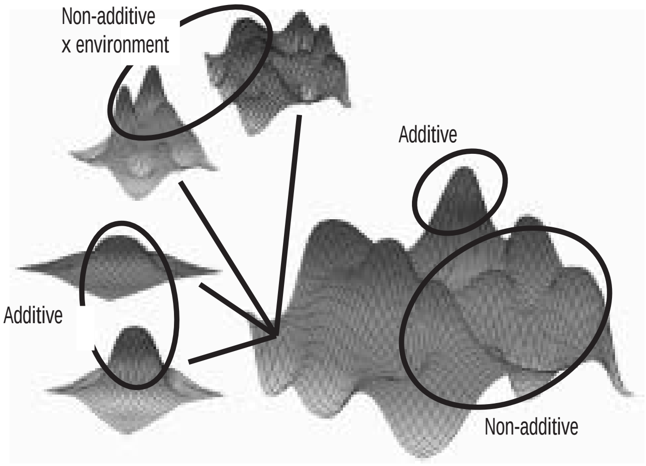


Figure 3. **Landscape representation of genotypic adaptation in environments: E(N:K).**

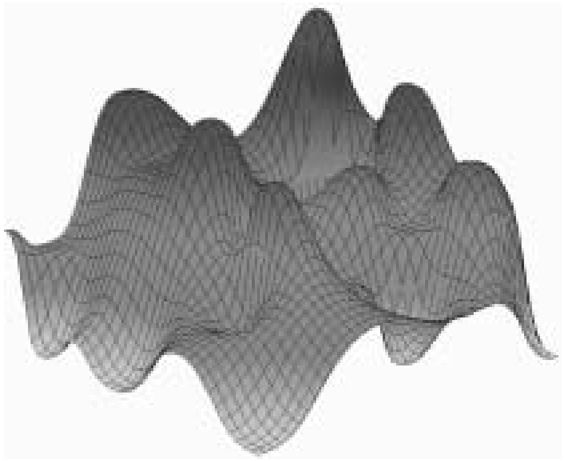


Figure 4. **A searching process of a selection strategy on the adaptation landscape.**

and field experiments. A few examples are:

- Comparison of pedigree selection, modified pedigree/bulk, and selected bulk methodologies that have been used in CIMMYT's wheat breeding programs (Table 1).
- Balance the number of crosses and the size of segregating populations (Table 1).
- Suitable selection intensity for each generation: high selection intensity in early generations or in late generations for a specific trait (Table 1).
- Effectiveness of different selection sites and their order/sequence in shuttle breeding (Table 1).
- Comparison of simple, top, back, and double crosses in regard to 1) introducing genes from the donor parent and 2) retaining genes from the adapted parent.
- Correlation between parents and their offspring: Can F_1 hybrids predict the performance of their advanced lines?
- Ways to better accommodate genotype by environment interaction and epistasis in plant breeding.
- Effective distance between markers and linked genes, and in which generation to apply marker assisted selection (MAS).
- Comparison of breeding/selection/evaluation methodologies to develop germplasm with wide and/or specific adaptation expressing stable yields.

Table 1. A hypothetical simulation experiment to compare modified pedigree/bulk and selected bulk.

		Modified pedigree/bulk					Selected bulk				
Growing mega-environment (ME)	Generation	No. of crosses or families	No. of plants in a plot	Among cross or family selection	Within family selection	Total no. of plants	No. of crosses or families	No. of plants in a plot	Among cross or family selection	Within family selection	Total no. of plants
ME1	F_1	100	20	0.70	1.00	2,000	100	20	0.70	1.00	2,000
ME2	F_2	70	1,000	0.85	0.08	70,000	70	1,000	0.85	0.04	70,000
ME1	F_3	4,760	70	0.30	0.15	333,200	60	500	0.90	0.05	29,750
ME2	F_4	1,428	70	0.35	0.15	99,960	54	625	0.90	0.05	33,469
ME1	F_5	500	70	0.40	0.15	34,986	48	625	0.90	0.05	30,122
ME2	F_6	200	140	0.70	0.20	27,989	43	750	0.90	0.14	32,532
ME1	F_7	3,918	70	0.30	1.00	274,290	4,099	70	0.30	1.00	286,929
ME2	AL	1,176	70	0.60	1.00	82,287	1,230	70	0.60	1.00	86,079
ME1	PYT	705	1,200	0.40	1.00	846,381	738	1,200	0.40	1.00	885,381
					Total	1,771,093				Total	1,456,261

Photosynthetic Traits Related to Yield Potential in Wheat: A Brief Review

P. Monneveux and M.P. Reynolds

Why Focus on Photosynthesis-Related Traits

- Progress in yield has shown to be strongly associated with harvest index (HI) (Calderini et al. 1995; Sayre et al. 1997), but HI is reaching its theoretical limit estimated at 60% (Austin et al. 1980).
- Yield increase may be strongly related to progress in biomass production (Waddington et al. 1987).
- Photosynthesis is the first process involved in biomass production.

Methodologies to Identify and Study Photosynthesis-Related Traits

- Comparison of modern wheat to its wild progenitors.
- Evolution of photosynthesis-related traits in a historic set of varieties.

Main Photosynthesis-Related Traits Associated with Yield Potential

- Stomatal aperture traits (SATs)
  - ◆ Maximal photosynthetic rate (A_m) and stomatal conductance (g_S) (Fischer et al. 1998).
  - ◆ Canopy temperature depression (CTD), which is easier to measure than photosynthetic rate or stomatal conductance (Reynolds et al. 1994).
  - ◆ Carbon isotope discrimination of the grain (DG) (Fischer et al. 1998).
  - ◆ Oxygen isotope ratio of flag leaves ($d^{18}O_l$) (Barbour et al. 2000).

- Electron transfer efficiency
  - ◆ Electron transport rate per unit chlorophyll in isolated thylakoids is greater in diploid than in hexaploid wheats (Austin et al. 1987).
  - ◆ Quantum yield efficiency (FPSII) is generally higher in modern wheats (Figure 1); comparison of net photosynthesis and FPSII values permits the evaluation of photorespiration.

- Leaf geometry and structure
  - ◆ Yield advantage of genotypes with erect leaves has been noted (Innes and Blackwell 1983), probably because light is more evenly distributed in the canopy and senescence of lower leaves is slower (Austin 1976).
  - ◆ Specific leaf dry weight (SLDW) negatively correlates with photosynthetic capacity (Dornhoff and Shibles 1976), DG (Araus et al. 1997) and yield potential (Figure 2).

- Photosynthetic pigment composition
  - ◆ Diploid species have greater total chlorophyll and Chla/b ratio than hexaploids (Austin et al. 1987). Siddique et al. (1989) observed that total chlorophyll has been enhanced and Chla/b ratio gradually fallen in a series of Australian wheats. Similar trends are noted for CIMMYT germplasm (Figure 3)
  - ◆ Decrease of Chla/b ratio in modern varieties indicates a decrease in the PSII reaction center complex relative to light-harvesting Chla/b protein complexes and suggests a loss of adaptation to high irradiance.

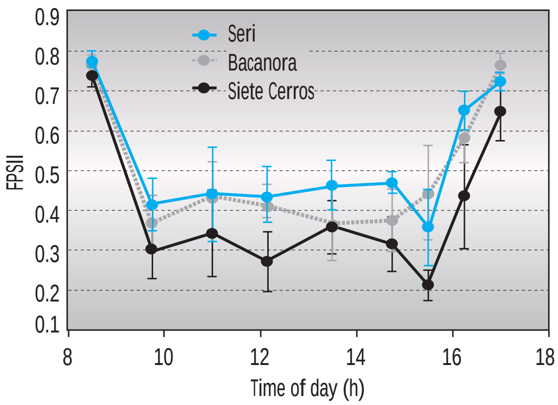


Figure 1. Day-course of quantum yield efficiency (FPSII) in the modern varieties Bacanora (1988) and Seri (1982) and the old variety Siete Cerros (1966), Tlaltizapan, Mexico, 2001.

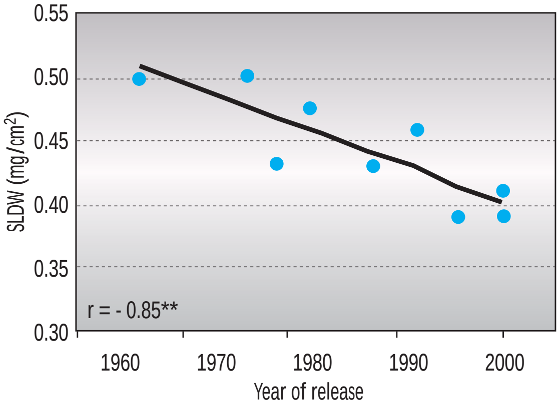


Figure 2. Relationship between specific leaf dry weight (SLDW) and year of release in a set of CIMMYT varieties, Tlaltizapan, Mexico, 2001.

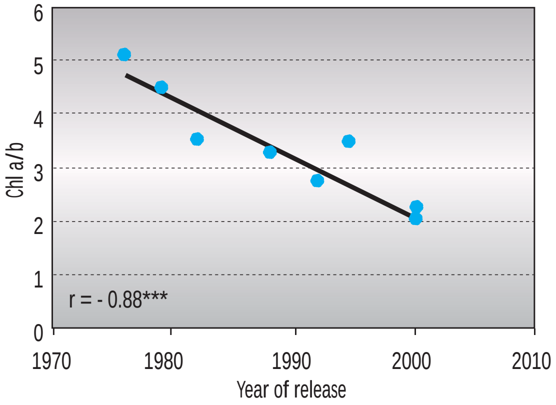


Figure 3. Relationship between Chla / b and year of release in a set of CIMMYT varieties, Tlaltizapan, Mexico, 2001.

References

Araus, J.-L., T. Amaro, Y. Zuhair, and M.M. Nachit. 1997. Effect of leaf structure and water status on carbon isotope discrimination in field-grown durum wheat. *Plant, Cell and Environment* 20:1484-1494.

Austin, R.B., J. Bingham, R.D. Blackwell, L.T. Evans, M.A. Ford, C.L. Morgan, and M. Taylor. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *Journal of Agricultural Science Cambridge* 94: 675-689.

Austin, R.B., M.A. Ford, J.A. Edrich, and B.E. Hooper. 1976. Some effects of leaf posture on photosynthesis and yield in wheat. *Annals of Applied Biology* 83:425-446.

Austin, R.B., M.A. Ford, T.E. Miller, and M.A.J. Parry. 1987. Progress in photosynthesis research. Vol. IV, pp. 361-368. Dordrecht, The Netherlands: Marinius Niijhoff Publishers.

Barbour, M.M., R.A. Fischer, K.D. Sayre, and G.D. Farquhar. 2000. Oxygen isotope ratio of leaf and grain material correlates with stomatal conductance and grain yield in irrigated wheat. *Australian Journal of Plant Physiology* 27:625-637.

Calderini, D.F., M.P. Reynolds, and G.A.Slafer. 1999. Genetic gains in wheat yield and main physiological changes associated with them during the 20th century. In: E.H. Satorre and G.A. Slafer (eds.), *Wheat: Ecology and Physiology of Yield Determination*. New York, NY: Food Products Press.

Dornhoff, G.M., and R.M. Shibles. 1976. Leaf morphology and anatomy in relation to CO_2 exchange rate of soybean leaves. *Crop Science* 16:377-381.

Fischer, R.A., D. Rees, K.D. Sayre, Z.-M. Lu, A.G. Condon, and A. Larque Saavedra. 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rates, and cooler canopies. *Crop Science* 38:1467-1475.

Innes, P., and R.D. Blackwell, 1983. Some effects of leaf posture on the yield and water economy of winter wheat. *Journal of Agricultural Science* 101:367-376.

Reynolds, M.P., M. Balota, M.I.B. Delgado, I. Amani, and R.A. Fischer. 1994. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Australian Journal of Plant Physiology* 21:717-730.

Sayre, K.D., S. Rajaram, and R.A. Fischer. 1997. Yield potential progress in short bread wheat in Northwest Mexico. *Crop Science* 37:36-42.

Siddique, K.H.M., R.K. Belford, M.W. Perry, and D. Tennant. 1989. Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Australian Journal of Agricultural Research* 40:473-487.

Waddington, S.R., M. Osmanzai, M. Yoshida, and J.K. Ransom. 1987. The yield of durum wheats released in Mexico between 1960 and 1984. *Journal of Agricultural Science Cambridge* 108:469-477.

Breeding for Grain Quality: Manipulating Gene Frequency

R.M. Trethowan, R.J. Peña, and M. van Ginkel

Introduction

Wheat breeders use grain or flour protein (FP%), sedimentation (SDS), and high molecular weight (HMW) glutenin subunit information to truncate their breeding populations early in the breeding process. This allows them to better utilize resources by testing genotypes in the later generations that have release potential. However, it is not clear what intensity of selection for FP%, SDS, and/or the HMW glutenin subunits will provide breeders with a reasonable probability of selecting genotypes in advanced generations with the required grain quality and high yield potential. This paper examines the optimal balance between selecting for grain quality using easy-to-measure characters and maintaining germplasm with high yield potential.

Materials and Methods

A total of 1,267 bread wheat genotypes were grown in replicated trials at CIMMYT's research station in northwestern Mexico (27ºN 109ºW, 40 masl) during 1994/95 and 1995/96. Grain yield was measured per plot and analyzed using SAS to produce means for each genotype. A 1-kg sample of seed of each genotype was taken from the first replicate of each trial for grain quality analysis. The following grain quality parameters were measured for each genotype: grain protein (GP%), flour protein (FP%), SDS-sedimentation (SDS), alveogram strength (ALW), alveogram tenacity/extensibility ratio (ALP/L), bread loaf volume (LV), and mixing time (MIX). High molecular weight (HMW) glutenin subunit composition, which is controlled by the *Glu-1* complex loci in chromosomes 1A, 1B, and 1D, was determined by SDS-PAGE.

The effect of truncating populations for FP% and SDS, and the ramifications for grain quality and yield were examined by calculating their impact, at various selection intensities, on the top 10% of individuals for ALW, P/L, LV, and grain yield.

Results

Flour protein as a predictor of grain quality and yield

If an arbitrary selection intensity of 50% is utilized for FP%, then the likelihood of selecting lines among the top 10% for LV is high (90%) (Figure 1). This likelihood drops to 75% for ALW and 52% for ALP/L at the same selection intensity as for FP%. However, the most dramatic consequence is the small number of lines among the top 10% for grain yield selected. Less than 20% of the highest yielding group are retained at the 50% selection intensity.

Sedimentation as a predictor of grain quality and yield

When SDS is used to examine the outcomes on grain quality and grain yield at the same selection intensity of 50%, a much stronger association with ALW was noted (Figure 2). The likelihood of obtaining lines in the top 10% for this character is 90%. This relationship does not change significantly as the selection intensity is further relaxed. The probability of obtaining lines ranking in the highest group for ALP/L and LV at the 50% selection intensity are 72% and 50%, respectively. Unlike FP%, there appeared to be no association between SDS and yield as the selection intensity of 50% identified slightly less than 50% of the highest yielding genotypes.

Sedimentation/flour protein as a predictor of grain quality and yield

In order to correct for possible associations between SDS and FP% among some genotypes, SDS was divided by FP% and the ratio was used to examine changes in selection intensity (Figure 3). At the 50% selection intensity for SDS/FP%, the probability of obtaining the best lines for ALW, ALP/L, grain yield, and LV were 75%, 72%, 60% and 56%, respectively. Interestingly, this ratio better predicted the high yielding genotypes as 60% of the best were identified at the 50% selection intensity.

Change in the frequency of some HMW glutenin sub-unit combinations with selection for improved ALW, ALP/L, and LV

When *Glu-A1* allelic variations were compared, the frequency of lines containing sub-unit 1 increased with increasing ALW (indicated by the higher frequency classes) (Figure 4). In contrast the 2* subunit was relatively evenly distributed across frequency classes. A similar pattern appeared when the subunit combinations 2*, 7+9, 5+10 and 2*, 17+18, 5+10 were compared for ALW (Figure 5). The frequency of genotypes containing 17+18 increased significantly with increasing ALW. At the *Glu-D1* locus there was a significant decrease in the frequency of lines carrying subunit 2+12 with increasing ALW (Figure 6). The 5+10 subunit was evenly distributed across the frequency classes.

The effects of varying HMW-glutenin subunit composition in this way upon ALP/L were considerably smaller (data not shown). The *Glu-A1* subunit 1 was more frequent with lower ALP/L (more extensible doughs) as was *Glu-B1* subunit 17+18. There was no significant change in the frequency of *Glu-D1* subunits with lower ALP/L. Similarly, subunits 1, 17+18, and 5+10 were the primary influences on LV differences.

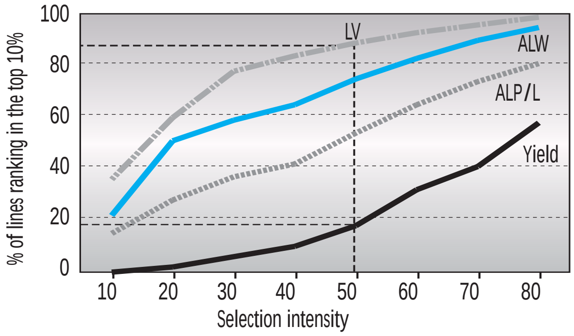


Figure 1. Change in the percentage of lines ranking in the top 10% for alveogram strength (ALW), alveogram tenacity/extensibility ratio (ALP/L), bread loaf volume (LV), and yield with decreasing selection intensity for flour protein.

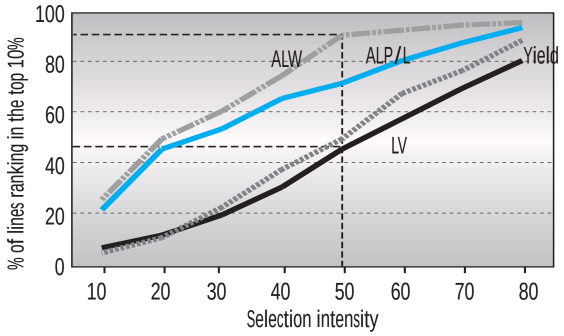


Figure 2. Change in the percentage of lines ranking in the top 10% for alveogram strength (ALW), alveogram tenacity/extensibility ratio (ALP/L), bread loaf volume (LV), and yield with decreasing selection intensity for sedimentation.

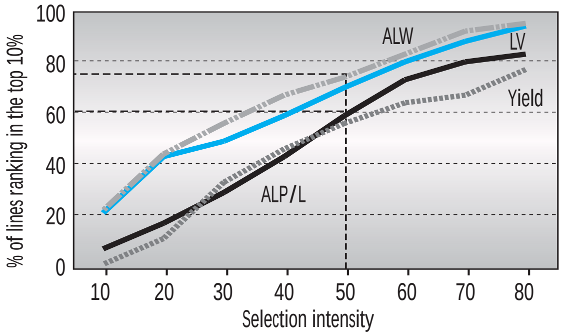


Figure 3. Change in the percentage of lines ranking in the top 10% for alveogram strength (ALW), alveogram tenacity/extensibility ratio (ALP/L), bread loaf volume (LV), and yield with decreasing intensity of selection for the sedimentation/flour protein ratio.

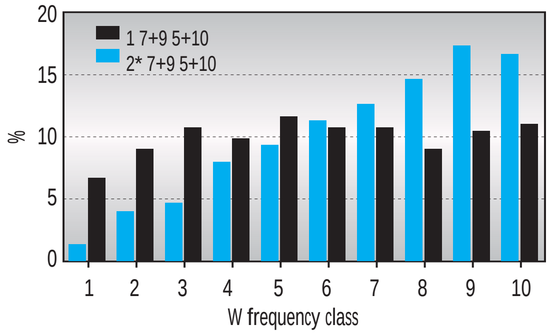


Figure 4. Change in the percentage of lines differing for their 1A HMW sub-units with increasing W.

Effects on grain quality and yield of removing sub-optimal HMW glutenins from populations already truncated for sedimentation/flour protein

Grain quality improved when genotypes containing either *Glu-A1* subunits 2*or 0, *Glu-B1* subunit 7+9, and *Glu-D1* subunit 2+12 were removed. As the ratio SDS/FP% gave the best resolution for the selection of grain quality and grain yield, it was decided to study the removal of genotypes carrying these sub-optimal HMW-glutenin subunits prior to truncating the populations on the basis of SDS/FP%. The results indicated that the probability of selecting genotypes with high ALW and ALP/L remained high (Figure 7). However, removing genotypes containing the 2*/0, 7+9, 2+12 combination lowered the capture of lines yielding among the top 10% from 60% (Figure 3) to 40%.

Discussion

The best resolution of selection for grain quality and yield was obtained from the ratio SDS/FP%. This ratio is weighted against genotypes producing high SDSs primarily on the basis of their high FP%. As FP% is influenced more by environmental factors than SDS, this ratio improved the heritability of selection. If the top 50% of lines are retained on the basis of this ratio, then estimates of the percentage of genotypes maintained with strong dough, good dough extensibility, and high grain yield are better than those estimated for SDS alone.

When lines carrying the sub-optimal band combinations 2*, 7+9, and 2+12 are removed prior to selection using SDS/FP%, there is a significant reduction in the number of high yielding genotypes maintained in the top 10% of lines for grain yield. This reflects the high yielding nature of many lines containing the 1B/1R translocation. Although generally poorer in grain quality, a significant proportion of 1B/1R carrying lines have good dough properties, as witnessed by the 20% reduction in yield once the 2*, 7+9, and 2+12 combinations were removed (Figures 3 and 7).

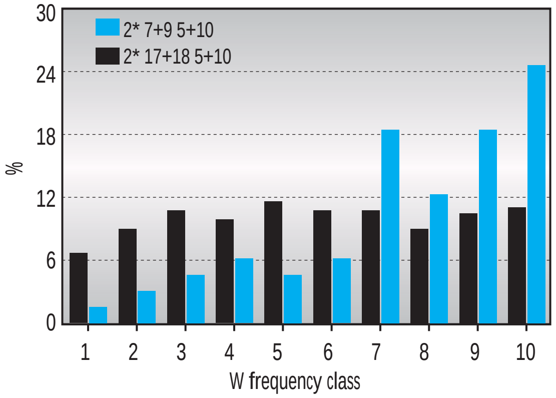


Figure 5. Change in the percentage of lines differing for 1B HMW subunits with increasing W.

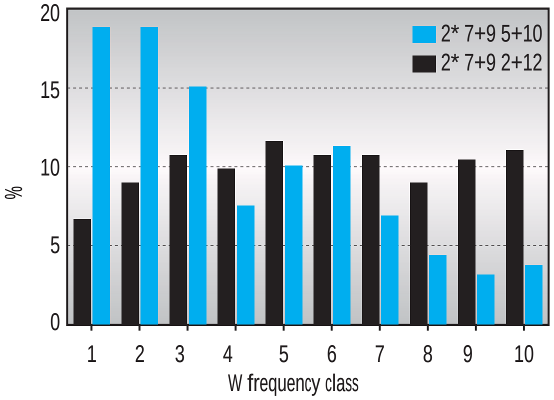


Figure 6. Change in the percentage of lines with differing 1D HMW subunit combinations with increasing W.

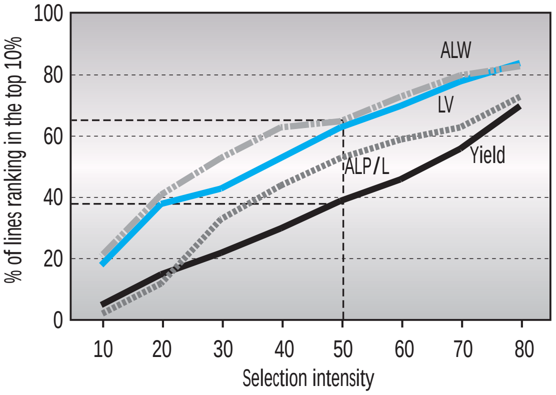


Figure 7. Change in the percentage of lines ranking in the top 10% for alveogram strength (ALW), alveogram tenacity/extensibility ratio (ALP/L), bread loaf volume (LV), and yield with decreasing sedimentation/flour protein ratio: 0/2* 7+9 2+12 HMW sub units removed.

Applications of Physiology to Wheat Breeding

M. Reynolds, B. Skovmand, R. Trethowan, R. Singh, and M. van Ginkel

Physiological Basis of Improved Yield and Biomass

Increases in both yield and biomass have been associated with the introgression of a chromosome segment containing *Lr19* (*Agropyron* 7DL.7Ag). Theoretically higher biomass may be achieved by:

- Increased interception of radiation (e.g., improved ground cover and "stay-green").
- Greater intrinsic radiation use efficiency (e.g., improve net photosynthesis and canopy architecture).
- Improved source-sink balance (e.g., increase potential grain number and weight) (Figure 1).

Experiments were conducted to determine which of these mechanisms were associated with greater yield and biomass (Table 1) in near-isogenic lines for the *Lr19* gene complex.

Radiation interception

- No differences in early biomass or "stay-green" in response to *Lr19*.
- Therefore, differences in final biomass not related to differences in ability to intercept light.

Radiation use efficiency

- Biomass accumulation and photosynthesis were greater after flowering in *Lr19* lines.
- No differences were observed before flowering (Table 2).

Source-sink balance: partitioning to spike, duration of spike growth

- *Lr19* increased partitioning of assimilates to developing spike.
- *Lr19* did not effect duration of juvenile spike growth (Table 2).
- This led to higher demand-driven photosynthetic rates during grainfilling.
- *Lr19* had no effect on light interception, photosynthesis pre-flowering, or phenological pattern.

Conclusions

- Increased biomass of *Lr19* lines resulted from and improved source-sink balance at flowering.

Table 1. Main effects on biomass, yield, and yield components for *Lr19* isolines in six spring wheat backgrounds, Obregon, NW Mexico, 1998-2000.

	Biomass (g/m^2)	Yield (g/m^2)	No. grains (per m^2)	Grains/ spike	Kernel wt. (mg)
Main effect					
Lr19	1,560	670	17,700	44.4	38.3
Control	1,440	610	15,600	39.9	39.4
P level	0.001	0.001	0.001	0.001	0.05
P level (interaction)	0.05	0.05	ns	ns	0.1

Exploiting Genetic Resources

Traits have been identified in CIMMYT's germplasm bank with potential to improve "source"

Table 2. Main effects of trait related to partitioning(source-sink), and photosynthesis in near-isogenic lines for the Lr19 translocation.

Trait	+Lr19	Check	P level
Partitioning (source-sink)			
Spike weight at anthesis (g)	0.775	0.732	0.14
Anthesis harvest index[1]	0.260	0.243	0.05
Photosynthesis (umol/m^2)			
Booting	23.9	22.8	ns
Grainfill	20.9	18.0	0.01

[1] Anthesis harvest index = dry weight of spike 7 d after anthesis/total culm dry weight.

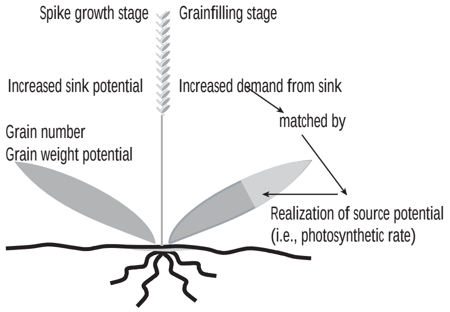


Figure 1. Improved source sink balance can increase plant biomass.

and "sinks" to raise yield potential, and to improve stress tolerance.

- Traits are introgressed into good backgrounds to establish potential genetic gains.
- "Source" and "sink" type traits are crossed together to obtain synergy.

Traits to improve spike fertility ("sink")

- Large spikes. Good sources available but seed often shrivelled (Figure 2).
- Multi-ovary florets. Trait expressed in high yield backgrounds.
- Branched spikelets. Introgressed with good results in Yugoslavia.
- Higher grain weight potential. Expressed when extra assimilates available in boot stage.
- Phenology. Genetic variation exists for duration of juvenile spike growth.

Traits to improve assimilate availability ("source")

- Green area duration. Rapid full light interception and stay-green sources identified.

Figure 2. Big spike wheat may improve "sink" potential.

- Stem reserves. Significant variation in accumulation and utilization exists.
- Erect leaf. Being introgressed into high biomass Baviacora (Figure 3).

Traits to improve stress tolerance

Many traits have been postulated to confer stress tolerance in wheat, depending on specific environments (Figure 4). Germplasm is being screened for sources of these characters.

Physiological Screening Tools

Canopy temperature depression

- Leaves are cooled when water evaporates from their surface, part of the process photosynthesis.
- Canopy temperature depression (CTD) affected by many physiological processes, indicates a genotype's fitness to its environment (Figure 5).

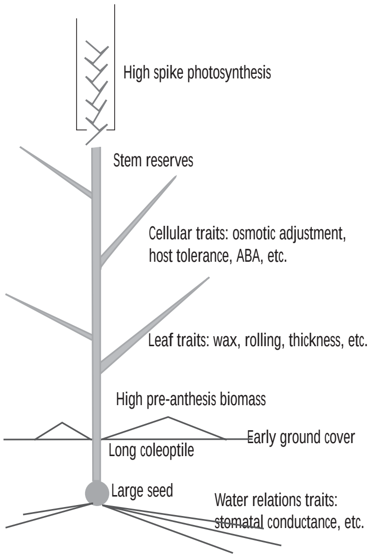


Figure 3. Traits associated with stress tolerance.

- CTD predicts yield best in irrigated situations when measured on sunny days in grainfilling.
- Under drought, morning measurements are recommended (Table 3).

Figure 4. Erect leaves and high chlorophyll content may improve "source" potential.

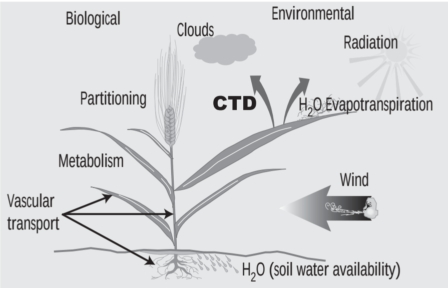


Figure 5. Factors associated with canopy temperature depression (CTD) in plants.

Table 3. Correlation between yield under terminal moisture stress and canopy temperature depression (CTD) measured pre-heading and during grainfilling on 25 sister lines of Seri82/Baviacora92, morning and afternoon, in two environments in Mexico, 1999/2000.

	Correlation with yield	
Trait	Obregon	Tlaltizapan
CTD AM prehead	0.82**	0.79**
CTD AM grainfill	0.79**	0.68**
CTD PM prehead	0.85**	0.72**
CTD PM grainfill	0.37	0.06

** Statistical significance at P>0.01.

Potential genetic gains by selecting for canopy temperature depression

- CTD measured on $F_{5:8}$ sister lines explained over 40% of the variation in yield (Figure 6).
- CTD of advanced lines predicted yield in heat stressed target countries (Reynolds et al. 1998).
- Stomatal conductance measured on single $F_{2:5}$ plants predicted yield of $F_{5:7}$ lines.

Aerial infrared imagery

- CTD was estimated remotely using aerial infrared (IR) imagery on relatively small yield plots (Table 4).
- Results validated the potential of aerial IR imagery to screen thousands of breeding plots in a day.

Spectral reflectance

- Sunlight reflected from a plot can be measured with a radiometer (Araus et al. 2000).
- Spectral reflectance (SR) estimates a range of physiological traits: chlorophyll, biomass, water status.

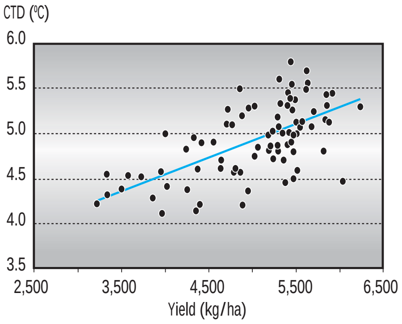


Figure 6. Relationship between canopy temperature depression (CTD) and yield of random derived $F_{5:8}$ sister lines from Seri-82/7Cerros-66, Obregon, 1997.

- The SR index NDVI was significantly correlated with biomass and yield of advanced lines.
- NDVI is being evaluating as a fast screening tool for yield, NUE, and triticale forage production.

Incorporating physiological selection traits into a breeding scheme

- Breeding strategies must take into account multiple factors in addition to physiological traits.
- Table 5 shows where physiological criteria might fit into a breeding scheme.

References

Araus, J.L., J. Casadesus, and J. Bort, 2000. A review of some rapid screening tools for physiological traits determining yield. In: M.P. Reynolds, I. Ortiz-Monasterio, and A. McNab (eds.), *Application of Physiology in Wheat Breeding.* Mexico, D.F.: CIMMYT.

Reynolds, M.P., R.P. Singh, A. Ibrahim, O.A. Ageeb, A. Larqué-Saavedra, and J.S. Quick. 1998. Evaluating physiological traits to complement empirical selection for wheat in warm environments. *Euphytica* 100:85-94.

Table 4. Comparison of canopy temperature depression (CTD) from infrared (IR) imagery with hand-held IR thermometers, Obregon, 1997.

		Correlation of CTD with yield			
		Aerial		Hand-held	
Trial		Phenotypic	Genetic	Phenotypic	Genetic
Seri-82/7Cerros-66 (random derived sisters)	81	0.40**	0.63**	0.50**	0.78**
Advanced lines (various pedigrees)	58	0.34**	nc	0.44**	nc

** Statistical significance at 0.01 level of probability.
nc Genetic correlations not calculated due to design restrictions.

Table 5. Theoretical scheme for incorporating physiological selection criteria into a conventional breeding program showing different alternatives for measuring traits, depending on available resources.

	Breeding generation when selection to be conducted			
Trait	All generations	F_3	F_4-F_6	PYTs/advanced lines
Simple traits				
Disease	Visual			
Height	Visual			
Maturity	Visual			
Canopy type			Visual	
Complex traits				
Yield			Visual	Yield plots
CTD			Small plots	Yield plots
Porometry		Plants	Small plots	Yield plots
Chlorophyll		Plants	Small plots	Yield plots
Spectral reflectance			Small plots	

Recombined *Thinopyrum* Chromosome Segments in Wheat Carrying Genes *Lr19* and *Bdv2*

R.P. Singh, M. Henry, J. Huerta-Espino,
A. Mujeeb-Kazi, R.J. Peña, and M. Khairallah

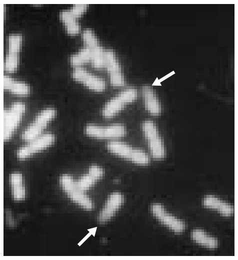
Introduction

Leaf rust (caused by *Puccinia triticina*) and barley yellow dwarf (BYD) (caused by barley yellow dwarf virus, BYDV) are important diseases of wheat in several wheat growing regions. Genetic resistance offers the most economical and environmentally safe control measure.

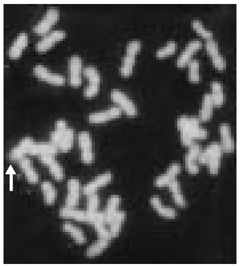
Sharma and Knott (1966) transferred a chromosome segment from *Thinopyrum elongatum* to chromosome 7DL of wheat (Figure 1a). This segment carries leaf rust resistance gene *Lr19*, which has had limited use in wheat improvement due to its linkage with a gene that causes yellowness of wheat flour. In a recent study Singh et al. (1998) found that the presence of this alien segment increases wheat grain yield by about 10%.

Using tissue culture, Banks et al. (1995) transferred a chromosome segment carrying BYDV resistance from *Th. intermedium* to wheat and obtained eight lines, commonly referred to as TC lines. The *Th. intermedium* fragment carried the only known BYDV resistance gene named *Bdv2*. Among TC lines, TC14 carries the smallest translocation that replaces the terminal part of wheat chromosome 7DL (Figure 1b).

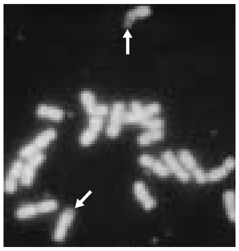
Figure 1. Fluorescent *in situ* hybridization (FISH) detail in partial mitotic:



a) *Triticum aestivum* cv. Oasis 86 with *Lr19*;



b) *Triticum aestivum* (TC14) with *Bdv2*;



c) Oasis 86//TC14/2*Spear with *Lr19* and *Bdv2*. Wheat DNA was biotin labeled and *Thinopyrum bessarabicum* DNA was used for blocking.

The objective of our work was to recombine the two alien chromosome segments in a wheat background to identify recombinants that combine genes *Lr19* and *Bdv2*, and lack the gene for yellowness of flour.

Materials and Methods

Two wheat varieties, 'Oasis 86' and 'Super Seri #2', carrying gene *Lr19*, were crossed with two other varieties, 'TC14/2*Spear' and 'TC14/2*Hartog' carrying *Bdv2*. Chromosome pairing was studied in meiosis of the F_1 plants. By testing with an *Lr19*-avirulent race of *P. triticina*, 118 individual F_2 plants derived F_3 lines from each of the four crosses were evaluated for homozygosity for *Lr19*.

The *Lr19* homozygous lines were evaluated for endosperm or flour yellowness by two methods: 1) visual evaluation of endosperm yellowness by cutting the seed in half, and 2) flour color determination using Minolta Color Meter, where "b" values were recorded. Acceptable "b" values are 8-12, while unacceptable light yellow to yellow "b" values are 15-20. Lines showing non-yellow endosperm and flour were advanced to the F_5 generation by harvesting individual plants in the F_4 generation that showed good agronomic features.

The F_1 plants from the two crosses involving Oasis 86 described above were top-crossed with 'Yecora+*Lr34*', whereas the remaining two F_1s were top-crossed with 'Seri.1B'. Yecora+*Lr34* and Seri.1B are very similar to Oasis 86 and Super Seri#2 but do not carry any alien chromosome translocation. The top-crossed seedlings were first tested for resistance to PAV-Mex isolate of

BYDV; plants with low virus titers in ELISA were retained, and then tested for the presence of *Lr19*-based resistance to leaf rust. Only those plants considered resistant to both diseases were grown and harvested. The leaf rust resistant F_2 progenies of these plants were advanced to F_3 and lines homozygous for gene *Lr19* were identified for further work as described above for the F_3 lines from simple crosses.

Cytological procedures for meiosis and fluorescent *in situ* hybridization (FISH) were similar to those of Mujeeb-Kazi et al. (1994) and Islam-Faridi and Mujeeb-Kazi (1995), respectively. From 21 F_4 lines (representing at least 21 recombination events), 235 individual F_5 plants were selected that were homozygous for *Lr19* and had white endosperm. An SSR marker, *gwm37*, mapping to 7DL and identified to be diagnostic for the *Th. intermedium* translocation (Ayala et al. 2001) was used to assess the presence or absence of the translocation. Because of its co-dominant nature, the marker allowed us to differentiate if the alien fragment was present in homozygous (1) or heterozygous (10) state, or whether it was absent (0) (Figure 2**)**. DNA extraction, PCR amplification, and separation of the amplified products on agarose gels were done as described by Ayala et al. (2001).

Five 7-day old seedlings of a total of 41 selected F_5 lines were inoculated with 10 BYDV-PAV viruliferous aphids (*Rhopalosiphum padi)* for a 48-h inoculation period. After spraying with the insecticide Pirimor, plants were grown in the greenhouse for 30 days. Virus titers were assessed by double antibody sandwich ELISA (DAS ELISA) on the flag-1 leaf, 10, 20, and 30 days after inoculation. The test was repeated once. For each repetition a non-infected seedling was tested for each line as a control for ELISA.

Results and Discussion

Meiotic chromosome pairing in F_1 plants

The presence of 21 chromosome ring bivalents in at least some cells (Table 1) indicated that the two chromosomes with alien translocations paired at metaphase I, suggesting that recombinants could be expected.

Flour yellowness

The two crosses involving Super Seri#2 did not give any *Lr19* homozygous line with white flour. Of the 21 recombinants identified (Table 2), 16 were from the simple cross Oasis 86//TC14/2*Spear, plus 3 more when the above cross was top crossed with Yecora+*Lr34*. The remaining 2 white-floured recombinants were derived from the cross Oasis 86//TC14/2*Hartog/3/Yecora+*Lr34*.

Status of molecular marker *gwm37* and barley yellow dwarf virus resistance

Of the 235 F_5 lines (homozygous for *Lr19* and white floured) tested, 121 did not carry *gwm37*, 28 were heterozygous for this marker, and 85 were homozygous. In total, 41 F_5 lines were tested, 19 homozygous for the marker *gwm37* and the remaining 22 lines, not carrying it. All lines that did not carry *gwm37* were susceptible to BYDV (high virus titers in ELISA) (Table 3). Most lines where *gwm37* was present were highly or moderately resistant to BYDV indicating the presence of the *Bdv2* gene. However, in four cases, lines homozygous for *gwm37* were susceptible (high titers). These results suggest that probably recombination also occurred between the molecular marker and the *Bdv2* gene.

FISH preparations

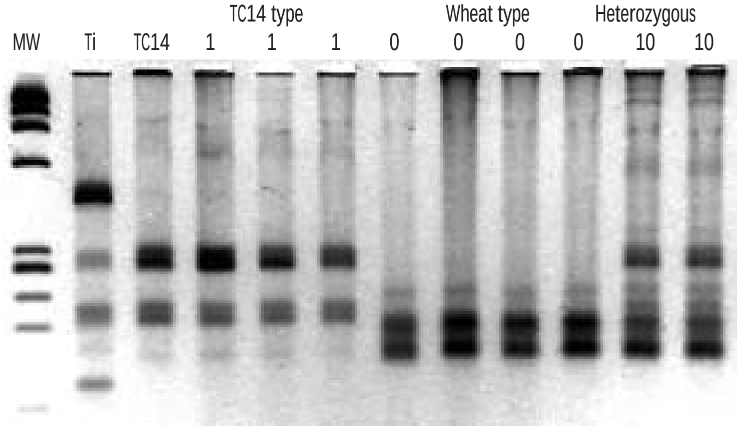


Figure 2. Agarose gel showing differentiation between lines homozygous for *gwm37* (1), heterozygous (10) or not carrying the diagnostic marker (0).

Each F_1 combination and three recombined lines where genes *Lr19*, *Bdv2* and *gwm37* were present together and possessed white flour were used for mitotic FISH preparations. The translocations present in this germplasm were characteristic of *Lr19* and *Bdv2* in the F_1 heterozygote (Figure 1c), and appeared to be of similar length as in the TC14 lines in the advanced progeny with white flour

Conclusions

- The *Th. elongatum* and *Th. intermedium* chromosome segments were recombined successfully.
- Recombined alien segments possessing genes *Lr19*, *Bdv2*, and white flour with or without the molecular marker *gwm37* were identified.
- The recombined translocations could be useful for transferring the *Bdv2* gene using leaf rust resistance as a marker, or vice-versa by using the *gwm37* molecular marker.
- The status of the gene that enhances yield potential has yet to be determined.

References

Ayala, L., M. Henry, D. González de León, M. van Ginkel, A. Mujeeb-Kazi, B. Keller, and M. Khairallah. 2001. A diagnostic molecular marker allowing the study of *Thinopyrum intermedium* derived resistance to BYDV in bread wheat segregating populations. *Theoretical and Applied Genetics* (accepted for publication).

Banks, P.M., P.J. Larkin, H.S. Bariana, E.S. Lagudah, R. Appels, P.M. Waterhouse, R.I.S. Brettell, X. Chen, H.J. Xu, Z.Y. Xin, Y.T. Qian, X.M. Zhou, Z.M. Cheng, and G.H. Zhou. 1995. The use of cell culture for subchromosomal introgressions of barley yellow dwarf virus resistance from *Thinopyrum intermedium* to wheat. *Genome* 38:395-405.

Islam-Faridi, M.N., A. and Mujeeb-Kazi. 1995. Visualization of *Secale cereale* DNA in wheat germplasm by fluorescent in situ hybridization. *Theoretical and Applied Genetics* 90:595-600.

Mujeeb-Kazi, A., Q. Jahan, and A. Vahidy. 1994. Application of a somatic and meiotic cytological technique to diverse plant genera and species in the *Triticeae. Pakistan Journal of Botany* 26:353-366.

Sharma, D., and D.R. Knott. 1966. The transfer of leaf-rust resistance from *Agropyron* to *Triticum* by irradiation. *Canadian Journal of Genetics and Cytology* 8:137-143.

Singh, R.P., J. Huerta-Espino, S. Rajaram, and J. Crossa. 1998. Agronomic effects from chromosome translocations 7DL.7Ag and 1BL.1RS in spring wheat. *Crop Science* 38:27-33.

Table 1. Mean meiotic metaphase I chromosomal associations observed in the F1 between two translocation germplasms (Oasis/ /TC14/2* Spear) with *Lrl9* and *Bdv2* genes.

	Metaphase I chromosome association					
No. of cells	I	oII*	rII*	III	TOT. II	%
5	0	21	0	0	21	16.7
3	0	20	1	0	21	10.0
2	2	20	0	0	20	6.7
6	0	19	2	0	21	20.0
5	0	18	3	0	21	16.7
1	2	18	2	0	20	3.3
1	4	18	1	0	19	3.3
1	1	18	1	1	19	3.3
2	0	17	4	0	21	6.6
1	4	17	2	0	19	3.3
1	1	17	2	1	19	3.3
1	3	16	2	1	18	3.3
1	0	15	6	0	21	3.3

* oII and rII = ring and rod bivalent associations.

Table 2. Distribution of F_3 lines homozygous for *Lr19* and for flour color in each cross.

	Lr19 homozygous F_3 lines (no.)	
Cross	Yellow flour	White flour
Simple		
Super Seri #2//TC14/2*Hartog	37	0
Super Seri #2//TC14/2* Spear	30	0
Oasis 86//TC14/2*Hartog	28	0
Oasis 86//TC14/2*Spear	15	16
Top		
Super Seri #2//TC14/2*Hartog/3/Seri.1B	3	0
Super Seri #2//TC14/2*Spear/3/Seri.1B	7	0
Oasis 86//TC14/2*Hartog/3/Yecora+*Lr34*	5	2
Oasis 86//TC14/2*Spear/3/Yecora+*Lr34*	6	3

Table 3. Examples of the F_5 recombinant lines with white flour and carrying *Lr19* (rust resistance) and/or *Bdv2* (barley yellow dwarf virus resistance) genes.

Cross	Line number	*gwm37*	BYDV response	IOD[1] – 10 days
Oasis 86//TC14/2*Spear	F5Lr19RG-34	1[2]	Resistant	0.211±0.062
Oasis 86//TC14/2*Spear	F5Lr19RG-74	1	Resistant	0.181±0.055
Oasis//TC14/2*Spear/3/Yecora+*Lr34*	F5Lr19RG -193	1	Resistant	0.216±0.067
Oasis 86//TC14/2*Spear	F5Lr19RG -27	1	Susceptible	0.986±0.127
Oasis//TC14/2*Spear/3/Yecora+*Lr34*	F5Lr19RG -233	1	Susceptible	1.399±0.327
Oasis//TC14/2*Hartog/3/Yecora+*Lr34*	F5Lr19RG -134	1	Susceptible	0.741±0.191
Oasis//TC14/2*Spear	F5Lr19RG-108	0	Susceptible	1.143±0.145
TC14/2*Spear (Check)	F5Lr19RG -237	1	Resistant	0.223±0.077
Oasis 86 (Check)	F5Lr19RG -236	0	Susceptible	0.637±0.132

[1] IOD = average ODs of infected individual assessed by ELISA, 10 days after inoculation.

[2] 1= Homozygous for marker, 0 = not carrying the diagnostic marker.

The Global Economic Impact of Nonspecific Leaf Rust Resistance in Modern CIMMYT-Derived Spring Bread Wheat: A Preliminary Report

C.N. Marasas, M. Smale, R.P. Singh, and P.L. Pingali

Introduction

Leaf rust caused by *Puccinia triticina* (Figure 1) is an important disease of wheat (*Triticum aestivum* L.) worldwide. The cultivation of resistant varieties is the most economical and environmentally friendly control method. Rust pathogens are able to mutate rapidly and form new races. Genes conferring race-specific resistance produce resistant reactions, but their effects are overcome within a relatively short time. In contrast, genes conferring race-nonspecific resistance have partial and additive effects, which appear to endure longer.

Figure 1. Leaf rust of wheat caused by *Puccinia triticina.*

Control of rust diseases of wheat through genetic resistance has been an important breeding objective at the International Maize and Wheat Improvement Center (CIMMYT) (Rajaram et al. 1988). Utilization of the nonspecific type of resistance to leaf rust, controlled by genes that confer slow rusting, has been the dominant breeding strategy used during the past 25 years. This study aims to estimate the global economic benefits of CIMMYT's decision to incorporate nonspecific, rather than specific resistance to leaf rust into spring bread wheat. The analysis is still in progress and the information presented here is therefore preliminary.

Methodology

Breeding for genetic resistance to rust diseases in wheat is an example of research aimed at maintaining crop productivity. Research benefits are valued in terms of the yield losses that would have occurred globally if a strategy for specific resistance, rather than nonspecific resistance had been employed.

A list of all major spring bread wheat varieties grown in the developing world was drawn from CIMMYT's latest Global Wheat Impacts Survey data, conducted in 1997 by the Economics and Wheat Programs (Heisey et al., forthcoming). Varieties released after 1970, when CIMMYT's nonspecific resistance breeding program was initiated, and for which seed could be obtained, were grown in a field trial in El Batán, Mexico. The varieties were classified using the modified Cobb scale (Peterson et al. 1948) for the type and the level of genetic resistance to the current Mexican population of leaf rust. The trial data, combined with information on leaf rust resistance mechanisms from various trials, were used to classify the varieties by slow rusting category (SRC). Each category was assigned different levels of potential yield savings by CIMMYT breeding mega-environment (ME). These results, combined with the variety area estimates in the Impacts Survey data, provide a sample estimate of the area currently planted by SRC in the developing world.

Historical logistic diffusion curves for each SRC and ME were fitted using 1) function parameters including ceilings, lags, initial and final years, which were estimated from historical CIMMYT Wheat Impacts data (Heisey et al., forthcoming; Byerlee and Moya 1993); 2) a time series of areas estimated by combining national data on wheat areas obtained from the Food and Agriculture Organization (FAO) with CIMMYT Impacts data on spring bread wheat areas by ME and country; 3) Wheat Program estimates of areas potentially affected by leaf rust in each ME; and 4) the sample estimate of 1997 percentage areas by SRC and ME.

The yield savings per SRC and ME were estimated for four different scenarios of yield losses using 1) the yield saving of each SRC over the losses suffered by susceptible varieties, and 2) a time series of average yields estimated by combining FAO national wheat yield information with CIMMYT Impacts data on spring bread wheat yields by ME and country.

Production savings are being calculated by combining the yield and area time series generated by the above two steps. The net present value and internal rate of return associated with these savings will then be computed using the real wheat export parity price. Scenarios will be simulated to represent different assumptions about actual yield savings, alternative investments, and the costs of the program in order to test the sensitivity of the results.

Preliminary Results and Discussion

Table 1 shows the percentage area of the sample varieties per SRC and ME.

The major proportion of the sample area was protected by genes conferring nonspecific resistance. Thirty seven percent of the area was planted with varieties showing moderate resistance (SRC 3) and a further 37% of the area was planted with varieties showing high levels of resistance (SRC 4 and 5). These varieties should survive most leaf rust epidemics.

Ten percent of the sample area was protected by genes conferring specific resistance (SRC 6). The percentage area planted with varieties in SRC 6 was the highest in MEs 4b and 3. Characteristics other than nonspecific leaf rust resistance might be more important in these MEs. However, these varieties comprise only a relatively small proportion of the total sample area.

Only 10–16% of the sample area was planted with varieties showing moderate to higher levels of susceptibility to the Mexican population of leaf rust (SRC 2 and 1, respectively).

Research conducted at CIMMYT thus far indicates that the economic benefits of breeding for nonspecific resistance to leaf rust in spring bread wheat should be substantial (Sayre et al. 1998; Smale et al. 1998). For the Yaqui Valley of Mexico alone, the

Table 1. Percentage area of each slow rusting category per mega-environment in the sample of major CIMMYT-derived wheat varieties grown in the developing world in 1997

	Slow rusting category (SRC)[1]					
Mega-environment	1	2	3	4	5	6
1	11.83	6.61	37.74	36.07	4.07	3.68
2	0.98	8.01	37.79	19.40	0	33.83
3	8.68	0	7.88	11.09	0.32	72.03
4a	1.09	2.93	53.62	25.21	0	17.15
4b	0	0	1.64	1.16	0	97.20
4c	8.65	5.02	36.78	41.41	4.33	3.80
5a	12.96	8.53	33.24	40.87	2.47	1.93
Total sample area per SRC						
(000 ha)	3,694	2,342	13,679	12,723	1,222	3,694
(%)	10%	6%	37%	34%	3%	10%

[1] Slow rusting categories correspond to the following percentages of disease relative to the susceptible check: 1: 80-100%; 2: 50-70%; 3: 30-50%; 4: 10-20%; 5: <10%; 6: <5%. SRCs 2-5 represent nonspecific gene resistance; SRC 6 represents specific gene resistance; and SRC 1 corresponds to the percentage disease suffered by susceptible varieties. Scoring was based on the modified Cobb scale (Peterson et al. 1948).

internal rate of return on the research investment over the period 1970-90 was estimated at 13% under the most conservative assumptions. The benefits expressed in 1994 real terms amounted to US$ 17 million. In enlarging the scale of analysis from the Yaqui Valley to CIMMYT's global mandate area, the benefits are expected to increase substantially.

References

Byerlee, D., and P. Moya. 1993. *Impacts of International Wheat Breeding Research in the Developing World, 1966-1990.* Mexico, D.F.: CIMMYT.

Heisey, P.W., M.A. Lantican, and H.J. Dubin. *Assessing the Benefits of International Wheat Breeding Research in the Developing World: The Global Wheat Impacts Study, 1966-1997*. Mexico, D.F.: CIMMYT (forthcoming).

Peterson, R.F., A.B. Campbell, and A.E. Hannah. 1948. A diagrammatic scale for estimating rust intensity of leaves and stem of cereals. *Canadian Journal of Research C* 26:496-500.

Rajaram, S., R.P. Singh, and E. Torres. 1988. Current CIMMYT approaches to breeding for rust resistance. In N.W. Simmonds and S Rajaram (eds.), *Breeding Strategies for Resistance to the Rusts of Wheat,* pp. 101-118. Mexico, D.F.: CIMMYT.

Sayre, K.D., R.P. Singh, J. Huerta-Espino, and S. Rajaram. 1998. Genetic progress in reducing losses to leaf rust in CIMMYT-derived Mexican spring wheat cultivars. *Crop Science* 38:654-659.

Smale, M., R.P. Singh, K. Sayre, P. Pingali, S. Rajaram, and H.J. Dubin.1998. Estimating the economic impact of breeding nonspecific resistance to leaf rust in modern bread wheats. *Plant Disease* 82:1055-1061.

Monitoring Root Rot Diseases on Irrigated, Bed-Planted Wheat

M. Mezzalama, K.D. Sayre, and J. Nicol

Introduction

In the Yaqui Valley (Sonora, northwest Mexico) the most common crop sequence is wheat planted as a winter irrigated crop on conventionally-tilled raised beds, followed by maize as a summer crop. Tillage is often accompanied by burning of crop residues, although some maize and wheat straw is baled-off for fodder and some is incorporated during tillage.

Farmers are intensely interested in new production technologies that would markedly reduce tillage operations and retain crop residues, because they could reduce their production costs and lead to more sustainable soil management.

For all their benefits, these practices may introduce some problems. Reduced tillage and residue retention can foster build-up of soil-borne pathogens that cause root rot and plant parasitic nematodes. Poor root health is a major factor contributing to inefficient use of water and nitrogen fertilizer by wheat grown under reduced tillage.

In 1999 we started monitoring root rot on wheat in two long-term experiments initiated in 1992. The objective of these experiment was to investigate the production feasibility of growing wheat using farmers' practices versus wheat sown on beds initially formed for the first crop and then reused with only superficial reshaping (permanent beds) before planting each succeeding crop.

The aim of the monitoring is to assess the effect of adopting reduced-till bed planting in irrigated systems on wheat root rot pathogens.

Materials and Methods

The trials are sited at CIANO research station of Ciudad Obregon, Sonora, Mexico, and were initiated in 1992.

Experiment 402 was designed as a randomized complete block with four replications and a split-plot arrangement. Main plots consisted of two tillage treatments: permanent beds (PB) and conventionally tilled beds (CTB); two subplots of straw management: retention (PB-straw; CTB-straw) and burning (PB-straw burned; CTB-straw burned). The experiment involves a two-crop annual rotation with wheat planted in November and harvested in early May and maize planted in early June and harvested in October. Plot size is 8 m long x 8-10 beds wide (each bed 75 cm).

Experiment 209 was designed as a randomized complete block with three replications and a split plot treatment arrangement. Main plots consisted of five tillage straw treatments; seven subplots of N fertilizer applications of urea. The experiment involves a two crop annual rotation with wheat planted in November and harvested in early May and either soybean or maize planted in late May or early June respectively and harvested in October. Plot size is 13 m long x 8 beds (75 cm each).

Root rot evaluation was carried out on three out five main plots and three subplots as follows:

Treatments

- Conventional tilled beds with both wheat and maize residues incorporated (CTB-straw)
- Permanent beds reshaped as needed with both wheat and maize residues burned (PB-straw burned)
- Permanent beds reshaped as needed with both wheat and maize chopped and left in place (PB-straw chopped).

During 1999 and 2000, three months after planting, 15 plants/plot were sampled for fungal root rot lesion evaluation. Seminal, crown, and tiller roots were scored on a scale of 0 to 7 (Thomashow and Weller 1988). Plant parasitic nematode *Pratylenchus thornei* was extracted from soil (using one 200-g composite homogenous soil sample with the whitehead tray method) and from wheat roots.

Results

The mean yield of the experiment was significantly greater in 1999 than in 2000. In 1999 the yield obtained on PB-straw was significantly greater than burning straw, while in CTB-straw there was no significant difference. In 2000 yield was significantly greater under CTB than PB (Table 1; Figure 1).

In this experiment, root rot incidence was significantly greater in 1999 than in 2000, although always at a very low level (2.71 on 0-7 scale). In 2000 the incidence of root rot was greater under PB than CTB and in CTB-straw burned than CTB-straw. No other significant difference was found (Table 2; Figure 2).

Yield in 1999 was significantly greater than in 2000. In 1999 PB-straw burned yield was lower than in CTB- straw and PB-straw chopped. Also in 2000 yield was lower in PB-straw burned than in PB-straw chopped (Table 3; Figure 3).

Root rot incidence on seminals was higher in 2000 than 1999. In 1998 the summer crop was soybean, while in 1999 it was maize. This may explain the higher incidence of root rot on wheat in 2000, as maize can carry pathogens (i.e., *Fusarium* spp.) that may affect wheat roots. In 1999 the incidence was significantly higher in PB-straw burned than in CTB-straw incorporated. In 2000 the incidence was significantly higher in PB-straw chopped than in CTB-straw (Table 4; Figure 4).

Number of *Pratylenchus thornei* extracted from wheat roots

The population of *P. thornei* extracted from roots was significantly greater in 1999 than in 2000. In 1999 the population was significantly higher in PB–straw burned than in CTB-straw. No significant difference was found in year 2000 (Table 5; Figure 5).

Number of Pratylenchus thornei extracted from soil (0-20 cm)

The mean number of nematodes 200g-1 of soil$_{dw}$ was not significantly different in the two years of monitoring. In 1999 no significant difference was found among treatments, while in 2000 the population was higher in PB-straw burned than in CTB-straw and in PB-straw chopped (Table 6; Figure 6).

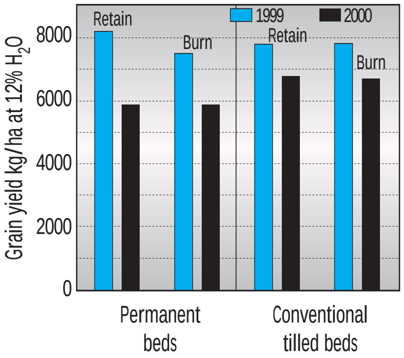


Figure 1. Experiment 402.

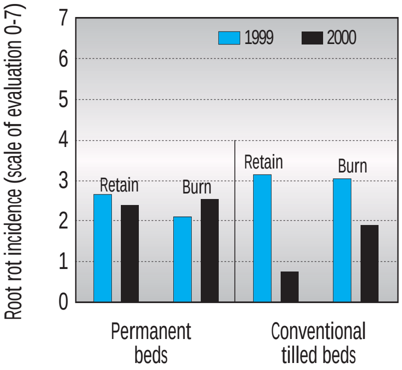


Figure 2. Experiment 402: evaluation of crown roots.

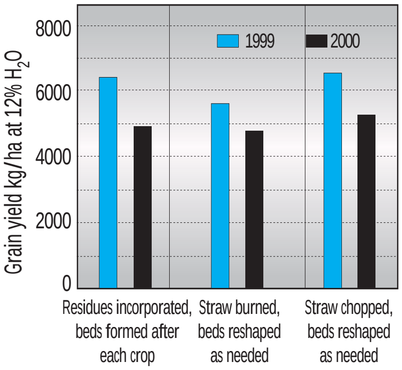


Figure 3. Experiment 209.

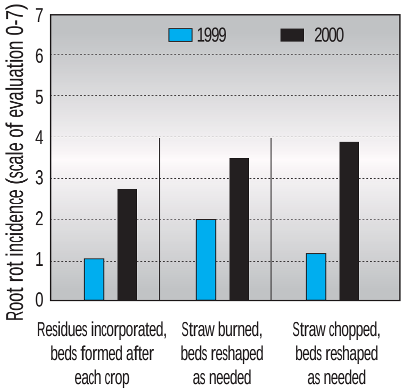


Figure 4. Experiment 209: evaluation of seminal roots.

Table 1. Yield in experiment 402.

Treatment	Grain yield at 12% H_2O
Mean yield in 1999	7,806.56
Mean yield in 2000	6,318.50 significantly different at $P<0.05$
Mean yield PB-straw in 1999	8,174.75
Mean yield PB-burn in 1999	7,464.5 significantly different at $P<0.05$
Mean yield PB in 2000	5,873.25
Mean yield CTB in 2000	6,763.75 significantly different at $P<0.05$

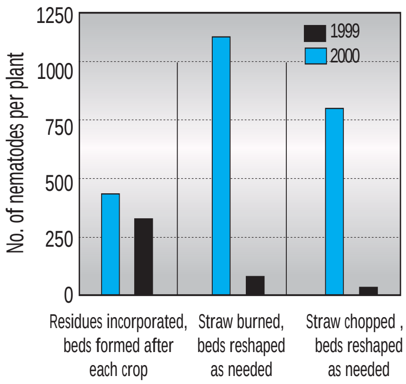


Figure 5. Experiment 209: *Pratylenchus thornei* extracted from wheat roots.

Table 2. Root rot incidence on wheat crown roots in experiment 402.

Treatment	Score (0-7 scale)
Mean score in 1999	2.71
Mean score in 2000	1.88 significantly different at $P<0.05$
Mean score PB in 2000	2.45
Mean score CTB in 2000	1.31 significantly different at $P<0.05$
Mean score CTB-straw in 2000	0.75
Mean score CTB-burn in 2000	1.87 significantly different at $P<0.05$

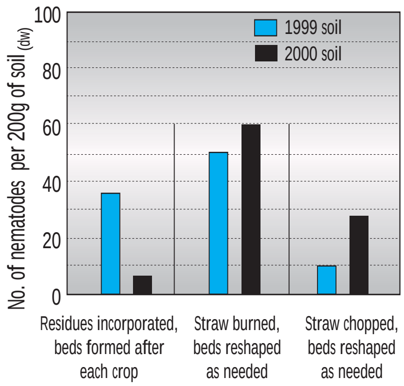


Figure 6. Experiment 209: *Pratylenchus thornei* extracted from soil (0-20 cm).

Table 3. Yield in experiment 209.

Treatment	Grain yield at 12% H_2O
Mean yield in 1999	6,183.14
Mean yield in 2000	5,000.25 significantly different at $P<0.05$
Mean yield PB-straw burned in 1999	5,625.77
Mean yield CTB-straw in 1999	6,399.88 significantly different at $P<0.05$
Mean yield PB-straw burned in 1999	5,625.77
Mean yield PB-straw chopped in 1999	6,523.77 significantly different at $P<0.05$
Mean yield PB-straw burned in 2000	4,7667.88
Mean yield PB-straw chopped in 2000	5,286.77 significantly different at $P<0.05$

Table 4. Experiment 209: root rot evaluation on seminals.

Treatment	Score (0-7 scale)
Mean score in 1999	1.19
Mean score in 2000	2.85 significantly different at P<0.05
Mean score PB-straw burned in 1999	1.70
Mean score CTB-straw in 1999	0.89 significantly different at P<0.05
Mean score CTB-straw in 2000	2.30
Mean score CTB-burn in 2000	3.31 significantly different at P<0.05

Table 5. Experiment 209: number of *Pratylenchus thornei* extracted from wheat roots.

Treatment	No. of *P. thornei* / plant
Mean number in 1999	776.88
Mean number in 2000	49.62 significantly different at P<0.05
Mean number PB-straw burned in 1999	1,099.77
Mean number CTB-straw in 1999	430.22 significantly different at P<0.05

Table 6. Experiment 209: number of *Pratylenchus thornei* extracted from soil (0-20 cm).

Treatment	No. of *P. thornei* / 200g soil$_{(dw)}$
Mean number PB-straw burned in 2000	60.11
Mean number in 2000	6.88 significantly different at P<0.05
Mean number PB-straw burned in 2000	60.11
Mean number CTB-straw chopped in 2000	27.7 significantly different at P<0.05

Conclusions

Under the environmental conditions of northwest Mexico it is possible to conclude that:

- Straw retention is a critical practice in the adoption of reduced tillage and of conventional tillage:
    - On yield to ensure long term production sustainability, increasing soil organic matter and improving soil physical conditions.
    - On fungal and nematode root rot agents increasing the beneficial soil microflora and enhancing natural biocontrol.
- Straw burning did not show a significant effect on the control of fungal root rot pathogens and nematodes; therefore, it does not seem justified, as it is in cooler and more humid areas, where moisture in soil can favor fungal pathogens (i.e., *Gaeumannomyces graminis tritici, Rhizoctonia solani, Pythium* spp.) not present in this area (Cook 1992).
- The low incidence of root rots in both experiments did not explain a yield reduction in 2000, considering also that in experiment 402 root rot incidence was higher in 1999 than in 2000 CTB.
- Although the evaluation of plant root pathogens shows some significant effects with management treatments, none of these are directly related to yield.

References

Cook, R.J. 1992. Wheat root health and environmental concern. *Canadian Journal of Plant Pathology* 14:76-85.

Thomashow, L.S., and D.S.Weller.1988. Role of phenazine antibiotic from *Pseudomonas fluorescens* in biological control of *Gaeumannomyces graminis* var *tritici. Journal of Bacteriology* 170:3499-3508.

Developing Molecular Markers for Phasic Development Genes in Wheat

**M. William, S. Ortiz, V. Garcia,
J. van Beem, and A.J. Worland**

Introduction

Wheat is cultivated in a wide range of agroclimatic regions of the world due to its ability to adapt to diverse environmental conditions. Wheat cultivars can be divided into spring and winter habit varieties, with a group of intermediate lines known as facultative wheats.

The vernalization response in wheat (Figure 1) is controlled mainly by a homeologous set of genes on Group-5 chromosomes known as *Vrn-A1*, *Vrn-B1*, and *Vrn-D1.* They are located on chromosomes 5A, 5B, and 5D, respectively. Besides major *Vrn* genes in homoeologous group 5 chromosomes, additional *Vrn* genes have been located on chromosomes 7A (*Vrn-A2*) and 7B (*Vrn-B4*).

Wheat is also photoperiod sensitive and requires long days for floral initiation. Photoperiod sensitivity in wheat is primarily determined by a set of homeologous genes located on the short arms of Group-2 chromosomes. These genes are known as *Ppd-A1*, *Ppd-B1*, and *Ppd-D1*, and are located on chromosomes 2D, 2B, and 2A, respectively.

Objectives

The objective of this study is to identify molecular markers associated with photoperiod sensitivity gene *Ppd-B1* and vernalization response gene *Vrn-A2.* This is a part of a larger project aimed at characterizing *Ppd* and *Vrn* genes, involving laboratories of John Innes Center, Technical University of Munich, and the International Maize and Wheat Improvement Center (CIMMYT). In this poster, we report progress achieved towards the molecular characterization of *Ppd-B1* and *Vrn-A2*.

Germplasm

Two single-chromosome recombinant line (SCRL) populations developed at John Innes Center were used for bulked segregant analysis. Eighty-nine SCRLs of a doubled haploid population from a cross between Chinese Spring X Chinese Spring (chromosome 2B substitution line from wheat cultivar Marquis) were used in characterizing *Ppd-B1.* Twenty-three SCRLs of a doubled haploid population from Chinese Spring x Chinese Spring (chromosome 7A substitution line from Ciano 67) were used in characterizing *Vrn-A2*. The populations were phenotyped at the John Innes Centre, and lines were characterized for flowering response.

Bulked Segregant Analysis

Bulked segregant analysis (BSA) was used with a set of microsatellites and AFLPs. For AFLP analysis, 96 *Pst1/Mse1* primer combinations were used.

Ppd-B2

Of the 89 SCRLs, bulks were made by combining equal amounts of DNA from the 9 earliest lines to form the “early bulk” and 10 late lines to form the “late bulk”. Bulks and two parental controls were screened with microsatellite markers located on homoelogous Group-2 chromosomes as well as with 96 *Pst1/Mse1* primer combinations. When polymorphisms were observed, polymorphic markers were used to screen the entire population.

Figure 1. Near-isogenic lines differing for *Vrn* response.

Results

Bulked segregant analysis identified a number of AFLP markers and microsatellites that seemed to differentiate between the two bulks. These were first tested on all entries used to make up the bulks, and some AFLP bands were confirmed to be located on chromosome 2B by using cytogenetic stocks. Figure 2 shows the linkage group developed with some of the polymorphic markers utilizing the entries used for making the bulks. Figure 3 shows the mapping results using the 89 SCRLs with all polymorphic markers identified in the BSA.

Vrn-A2

This population consisted of 23 SCRLs from the Chinese Spring x Chinese Spring (7A. Ciano-67) population. The population was phenotyped and all entries were characterized as being "early" or "late". Bulks were made by taking equal amounts of DNA from 11 early entries and 12 late entries. No microsatellite polymorphisms were observed between the two bulks. Several polymorphisms were identified when testing the bulks with 48 *Pst1/Mse1* primer combinations. Figure 4 shows the linkage group established after mapping polymorphic AFLPs on the 23 individuals of the population.

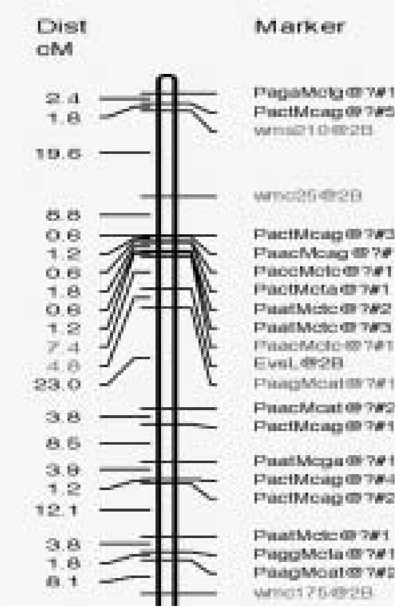


Figure 3. Molecular map around the *Ppd-B1* locus on wheat chromosome 2B with all polymorphic markers identified in the BSA.

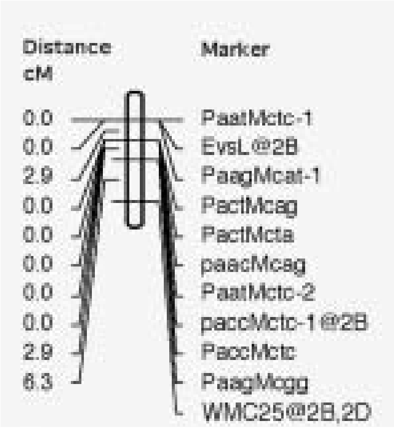


Figure 2. Partial linkage group associated with *Ppd-B2*.

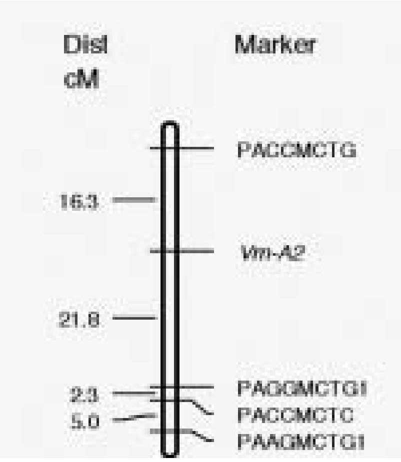


Figure 4. Partial linkage map around the *Vrn-A2* (*Vrn7A*) locus on chromosome 5B.

Conclusions

- We successfully identified AFLP markers presumably flanking the *Ppd-B2* with 7.4 cM and 4.8 cM in the SCRL population used. These markers are being converted with the objective of developing PCR-based markers.
- More AFLPS will be screened with the *Vrn-A2* population to find markers with closer linkages to *Vrn-A2.* Currently available data indicates that the closest marker is 16.3 cM from the likely genomic location of *Vrn-A2.* Population size is a significant limitation.

Identification of Highly Transformable Bobwhite Sister Lines for Mass Production of Fertile Transgenic Plants

A. Pellegrineschi, L.M. Noguera, S. McLean,
B. Skovmand, R.M. Brito, L. Velazquez, R. Hernandez, M. Warburton, and D. Hoisington

A group of 129 "Bobwhite" sister lines, generated at the International Maize and Wheat Improvement Center (CIMMYT) in the mid 1970s from the cross CM 33203 (pedigree: Aurora//Kalyan/Bluebird/3/Woodpecker), were used in this study. They are highly responsive materials, reported to be transformable.

The objectives of this study were: 1) to use transformation protocols and genotype data to screen 129 Bobwhite accessions for their transformation ability; and 2) to identify the most transformable and responsive accessions based on their ability to regenerate and adapt to tissue culture, and on their agronomic characteristics.

Materials and methods are described in Pellegrineschi et al. (forthcoming).

Results

Somatic embryo induction

Cultures transferred to selective medium were checked for somatic embryo formation. The effect of genotype on scutellum embryogenesis is summarized in Table 1. Most (111) of the 129 genotypes tested produced somatic embryos (Table 1). Eleven accessions showed the highest yield (nearly 100%) of embryos producing embryogenic callus. There were no distinct differences in stage development, with the exception of the number of scutella differentiating somatic embryos. Generally, the first globular stage somatic embryos were observed 4-5 days after transfer, and the globular stage usually formed directly from the scutellum. This was followed by a high frequency of repetitive somatic embryogenesis. Early globular stages were followed by full differentiation of the somatic embryo.

Transformation frequency and selection efficiency

Transformation efficiency was evaluated based on regeneration performance on selective medium. Healthy, fully differentiated embryogenic calli were scored (1 callus per embryo, Table 1) as number of regenerating calli divided by total number of immature embryos bombarded (one regenerating callus was scored as 1). Somatic embryo germination frequency was 0-89%. Accessions responded in four different ways to bombardment: 1) no regeneration, 2) herbicide tolerance and bombardment susceptibility, 3) herbicide sensitivity, bombardment tolerance, and high regeneration, and 4) herbicide sensitivity and bombardment tolerance but low regeneration (Table 1). Transformation efficiency was calculated as the effective number of transgenic plants obtained divided by the total number of immature embryos bombarded.

The most efficient lines were SH-98 26 and SH-98 56 (Table 1). Other accessions (SH-98 15, SH-98 88, and SH-98 121) gave higher regeneration frequency but less overall efficiency due to "escapes" (plants surviving the selection process but not transgenic). Accessions SH-98 26, SH-98 29, SH-98 56, SH-98 96, SH-98 97, SH-98 110, SH-98 128, and SH-98 129, the best lines for transformation, were tested further as described in Materials and Methods; results are shown in Table 2.

Molecular screening of transgenic plants

Shoot tissue harvested from Basta™ resistant plants was screened with PCR to verify the

Table 1. Regeneration and effective transformation efficiency of 129 Bobwhite lines.[1]

Bobwhite line	Embryogenesis		Regeneration		Transformation	
	Bombarded	Control	Bombarded	Control	Bombarded	Tr. / emb.
SH 98 01	50.35	51.86	49.15	1.20	47.94	1.05
SH 98 02	66.26	69.57	62.55	3.70	58.85	1.20
SH 98 03	33.91	34.59	22.31	11.59	10.72	2.10
SH 98 04	36.99	36.62	29.30	7.69	21.61	1.00
SH 98 05	33.83	34.17	28.99	4.84	24.16	1.02
SH 98 06	0.80	0.90	0.80	0.00	0.80	1.00
SH 98 07	40.98	42.30	40.98	0.00	40.98	1.04
SH 98 08	7.41	7.63	7.41	0.00	7.41	1.00
SH 98 09	61.79	64.88	55.77	6.02	49.75	1.00
SH 98 10	38.12	38.88	38.12	0.00	38.12	1.00
SH 98 11	39.20	38.80	28.22	10.98	17.25	1.00
SH 98 12	8.34	8.42	6.45	1.89	4.56	1.00
SH 98 13	23.25	26.13	20.78	2.47	18.31	1.00
SH 98 14	97.68	100.00	76.53	21.15	55.38	1.30
SH 98 15	109.15	100.00	71.65	37.50	34.15	1.00
SH 98 16	89.59	94.07	71.61	17.98	53.63	3.00
SH 98 17	24.34	24.83	5.19	19.15	2.05	1.00
SH 98 18	37.50	37.13	0.00	37.50	0.00	0.00
SH 98 19	48.52	49.00	39.90	8.62	31.28	1.20
SH 98 20	3.85	4.32	3.85	0.00	3.85	1.00
SH 98 21	43.64	45.03	43.64	0.00	43.64	1.00
SH 98 22	54.85	56.49	46.85	8.00	38.85	1.50
SH 98 23	47.89	50.28	47.89	0.00	47.89	1.02
SH 98 24	56.72	57.85	56.72	0.00	56.72	2.02
SH 98 25	20.00	19.80	20.00	0.00	20.00	1.00
SH 98 26	**73.81**	**74.55**	**73.81**	**0.00**	**73.81**	**2.40**
SH 98 27	16.39	18.42	8.70	7.69	1.00	1.00
SH 98 28	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 29	**62.16**	**64.03**	**62.16**	**0.00**	**62.16**	**1.40**
SH 98 30	48.12	50.53	48.12	0.00	48.12	1.00
SH 98 31	22.41	22.86	22.41	0.00	22.41	1.20
SH 98 32	61.79	61.18	45.13	16.67	28.46	1.00
SH 98 33	48.61	49.10	34.88	13.73	21.16	1.00
SH 98 34	30.62	34.42	24.56	6.06	18.50	2.20
SH 98 35	14.03	14.48	5.80	8.24	0.00	0.00
SH 98 36	22.92	23.60	22.92	0.00	22.92	1.00
SH 98 37	22.48	23.60	22.48	0.00	22.48	1.00
SH 98 38	57.03	58.17	42.32	14.71	27.62	1.00
SH 98 39	23.03	22.80	23.03	0.00	23.03	2.00
SH 98 40	38.88	39.27	11.96	26.92	0.00	0.00
SH 98 41	0.02	0.03	0.02	0.00	0.02	1.00
SH 98 42	0.03	0.04	0.03	0.00	0.03	1.00
SH 98 43	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 44	0.05	0.05	0.05	0.00	0.05	1.00
SH 98 45	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 46	0.26	0.26	0.26	0.00	0.26	1.00
SH 98 47	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 48	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 49	25.00	25.80	25.00	0.00	25.00	1.00
SH 98 50	0.16	0.17	0.16	0.00	0.16	1.00
SH 98 51	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 52	0.09	0.10	0.09	0.00	0.09	1.00
SH 98 53	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 54	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 55	24.91	28.00	24.02	0.89	23.13	1.10
SH 98 56	**73.47**	**75.82**	**73.47**	**0.00**	**73.47**	**2.10**
SH 98 57	34.28	35.31	28.66	5.62	23.04	1.00
SH 98 58	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 59	39.32	40.10	39.32	0.00	39.32	1.00
SH 98 60	48.20	47.71	34.20	14.00	20.20	1.10
SH 98 61	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 62	71.34	80.19	49.68	21.67	28.01	1.50
SH 98 63	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 64	58.28	60.03	47.37	10.91	36.46	1.00
SH 98 65	62.28	65.39	49.55	12.73	36.82	1.00
SH 98 66	41.90	42.74	28.26	13.64	14.62	1.00
SH 98 67	60.59	59.98	36.88	23.71	13.17	1.00
SH 98 68	29.60	29.89	26.09	3.51	22.58	1.00
SH 98 69	37.13	41.74	37.13	0.00	37.13	1.00
SH 98 70	41.35	42.67	41.35	0.00	41.35	1.10
SH 98 71	66.92	68.92	40.67	26.25	14.42	1.20
SH 98 72	88.09	92.49	32.20	55.88	0.00	1.00
SH 98 73	84.11	85.79	51.85	32.26	19.59	1.00
SH 98 74	61.64	61.02	53.57	8.06	45.51	1.00
SH 98 75	64.08	64.72	58.90	5.17	53.73	1.10
SH 98 76	67.77	76.17	59.26	8.51	50.75	1.25
SH 98 77	49.56	51.15	43.68	5.88	37.80	2.25
SH 98 78	47.01	48.42	35.90	11.11	24.79	1.00
SH 98 79	57.95	60.85	55.45	2.50	52.95	1.00
SH 98 80	32.57	33.22	32.57	0.00	32.57	1.00
SH 98 81	80.77	79.96	50.00	30.77	19.23	1.00
SH 98 82	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 83	79.14	88.95	54.55	24.59	29.96	1.00
SH 98 84	62.34	64.34	52.97	9.38	43.59	1.30
SH 98 85	43.72	45.03	35.38	8.33	27.05	1.10
SH 98 86	35.48	37.26	35.48	0.00	35.48	1.00
SH 98 87	46.04	46.96	43.82	2.22	41.60	1.00
SH 98 88	100.00	103.00	54.41	80.00	0.00	0.00
SH 98 89	95.45	100.00	50.00	45.45	4.55	1.00
SH 98 90	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 91	50.00	49.50	50.00	0.00	50.00	1.40
SH 98 92	94.75	95.70	68.09	26.67	41.42	1.00
SH 98 93	54.05	60.75	51.72	2.33	49.40	1.00
SH 98 94	42.29	43.14	35.54	6.76	28.78	1.00
SH 98 95	74.13	73.39	45.10	29.03	16.07	1.20
SH 98 96	**72.20**	**72.92**	**70.54**	**1.67**	**68.87**	**3.25**
SH 98 97	**90.92**	**100.00**	**77.19**	**13.73**	**63.47**	**1.00**
SH 98 98	68.93	71.14	44.44	24.49	19.95	1.00
SH 98 99	61.95	63.81	50.36	11.59	38.76	1.00
SH 98 100	37.95	39.84	28.57	9.38	19.20	1.00
SH 98 101	55.20	56.31	36.15	19.05	17.11	1.00
SH 98 102	81.00	80.19	57.60	23.40	34.20	1.00
SH 98 103	100.00	100.00	80.85	35.21	45.64	1.00
SH 98 104	79.99	83.99	62.14	17.86	44.28	1.00
SH 98 105	59.08	60.26	45.56	13.51	32.05	1.00
SH 98 106	67.12	66.45	55.36	11.76	43.59	1.00
SH 98 107	96.26	97.22	58.76	37.50	21.26	1.00
SH 98 108	98.81	100.00	66.46	32.35	34.10	1.00
SH 98 109	22.10	21.88	13.94	8.16	5.78	1.00
SH 98 110	**82.10**	**82.92**	**71.43**	**10.67**	**60.76**	**1.10**
SH 98 111	73.74	82.89	40.41	33.33	7.08	1.00
SH 98 112	81.87	84.49	51.26	30.61	20.65	1.00
SH 98 113	92.71	95.49	30.80	61.90	0.00	0.00
SH 98 114	94.35	99.07	71.28	23.08	48.20	1.20
SH 98 115	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 116	100.00	100.00	83.81	50.00	33.81	1.00
SH 98 117	100.00	100.00	89.47	47.06	42.41	1.00
SH 98 118	100.00	100.00	81.71	37.04	44.67	1.50
SH 98 119	100.00	100.00	80.87	40.91	39.96	1.00
SH 98 120	100.00	100.00	85.07	37.50	47.57	1.00
SH 98 121	100.00	100.00	87.50	41.67	45.83	1.00
SH 98 122	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 123	25.64	25.38	25.64	0.00	25.64	1.00
SH 98 124	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 125	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 126	**100.00**	**100.00**	**86.62**	**23.26**	**63.36**	**1.10**
SH 98 127	0.00	0.00	0.00	0.00	0.00	0.00
SH 98 128	**93.38**	**96.18**	**76.71**	**16.67**	**60.05**	**1.00**
SH 98 129	**82.92**	**87.06**	**72.92**	**10.00**	**62.92**	**1.00**

---

[1] Accessions with high transformation efficiency highlighted. Transformation efficiency calculated by dividing total number of transgenic plants obtained by total number of embryos bombarded.

presence of the Bar gene in the plant genome. Results indicated that all plants analyzed from all experiments contained the Bar gene. Amplified DNA fragments (approximately 350 nucleotides) from transgenic plants were identical in size to the controls, and all hybridized with the plasmid probe. Fifty independently transformed plants were analyzed for copy number (Bar gene) by Southern blot analysis in which a gene copy reconstruction lane was included. Where the Southern analyses indicated there were multiple copies of the transgene (Figure 6: lanes 6 to 13 and 19 to 26), all copies appeared to cosegregate yielding progenies with all or no copies. This suggested that all copies of the transgene were inserted at the same genetic locus. The Bar transgene was inherited and expressed in the T_1 and T_2 generation lines tested. Most of the initial transgenic wheat plants were at least partially fertile. Fertility was usually restored in subsequent generations, indicating that partial sterility observed in the T_0 generation was not, in most cases, an inherited trait.

Inheritance of the marker gene

Selected progeny were evaluated again for resistance to Basta^{TM}. Resistant and sensitive seedlings were clearly distinguishable after spraying with 0.3% Basta^{TM}. A segregation ratio of 3:1 was observed for 500 of 600 independent transgenic events tested (randomly taken). The Basta^{TM} resistant (T_1) progeny of plants that gave a segregation ratio of 3:1 were analyzed by PCR and Southern hybridization. All Basta^{TM}-resistant progeny contained bands that hybridized with Bar probe; none of the sensitive progeny hybridized and may have been escapes (data not shown).

Statistical analysis

Results of the average, standard deviation, minimum and maximum of embryogenesis, regeneration, and transformation efficiencies are shown in Tables 1 and 2.

Table 2. Results of statistical analyses of the 8 best Bobwhite lines for embryogenesis, regeneration in selective medium, and transformation efficiency.[1]

	Embryogenesis		Regeneration		Transformation	
Bobwhite line	Bombarded	Control	Bombarded	Control	Bombarded	Tr. / emb.
SH 98 26	72.09±13.34	75.35±13.39	71.17±14.68	0.00	70.86±14.48	2.42
SH 98 29	59.23±15.56	63.49±18.22	61.90±11.29	0.00	60.92±11.58	1.34
SH 98 56	70.34±9.82	70.14±5.98	70.34±9.83	0.00	69.02±6.94	2.13
SH 98 96	69.17±9.92	69.97±4.73	69.17±9.93	2.43±1.55	66.96±6.14	3.2
SH 98 97	90.96±5.95	93.33±4.92	76.63±9.02	13.98±4.54	66.96±4.53	1.1
SH 98 110	81.07±7.15	81.25±5.23	70.95±6.32	10.77±4.87	60.80±6.28	1
SH 98 128	91.15±4.85	93.54±4.22	78.13±8.21	20.13±5.61	58.27±10.40	1
SH 98 129	80.55±7.01	85.59±6.11	71.82±9.61	10.08±3.58	60.04±9.61	1

[1] Data pooled from 3 repetitions with over 2000 embryos per transformation.

Discussion

The use in biolistic transformation of a highly responsive wheat genotype can enhance efficiency. To identify highly responsive genotypes, it is necessary to optimize and standardize tissue culture conditions and transformation efficiency, and to identify the physiological conditions of the material to be transformed.

Standardization of the physiological status of the donor plants was a critical factor for comparing transformation abilities of the Bobwhite accessions. After testing under various conditions (data not shown), a uniform non-stressed growth environment was selected for the optimal growth of the donor plants.

The choice of the zygotic embryo development stage was also important. Various development stages were screened for their response to the transformation process. The dimension of the embryo (1 mm on the longest side) was taken as standard in all accessions regardless of “days after pollination” because at this stage scutella are more responsive to tissue culture. In the transformation experiments, accessions SH-98 26 and SH-98 56 were slightly more efficient (overall efficiency: more than 70%), although their ability to differentiate somatic embryos was less than other accessions (Table 1). Their performance could be explained by their high sensitivity to herbicide selection (non-transformed controls were not able to produce plants under selection conditions).

Of the two high performing varieties, the variety SH 98 26 was selected as “super transformable” because it is early maturing, does not have the 1B/1R translocation, and may be a suitable parent in breeding programs. Genetic analyses of T_1 and T_2 progeny provided conclusive evidence of the incorporation of the Bar transgene into wheat chromosomes. In most cases the Bar gene was inherited with a Mendelian ratio of 3:1. However, in some progeny the phenotype “Basta^{TM} resistance” was expressed in the T_1 generation with an unusual pattern of segregation, but the T_2 generated from the Basta^{TM}-resistant T_1 plants segregated at the expected Mendelian ratio (3:1).

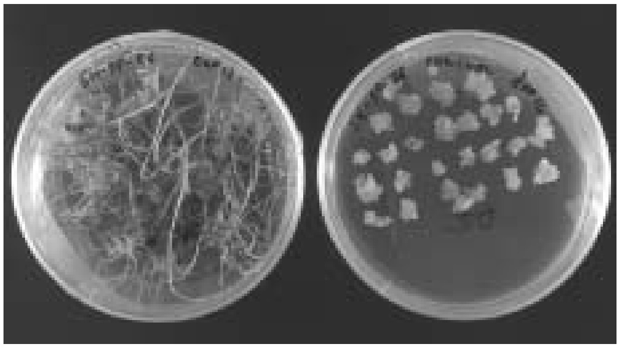


Figure 1. Response of Bobwhite line SH 98 26 to selection medium.

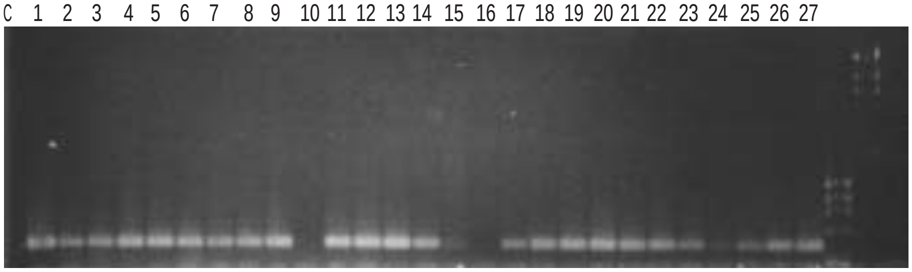


Figure 2. PCR analyses of transformants of line SH 98 26.
DNA was extracted from leaves. Each lane represents an independent event. Plants 10 and 16 did not survive the Basta^{TM} treatment.

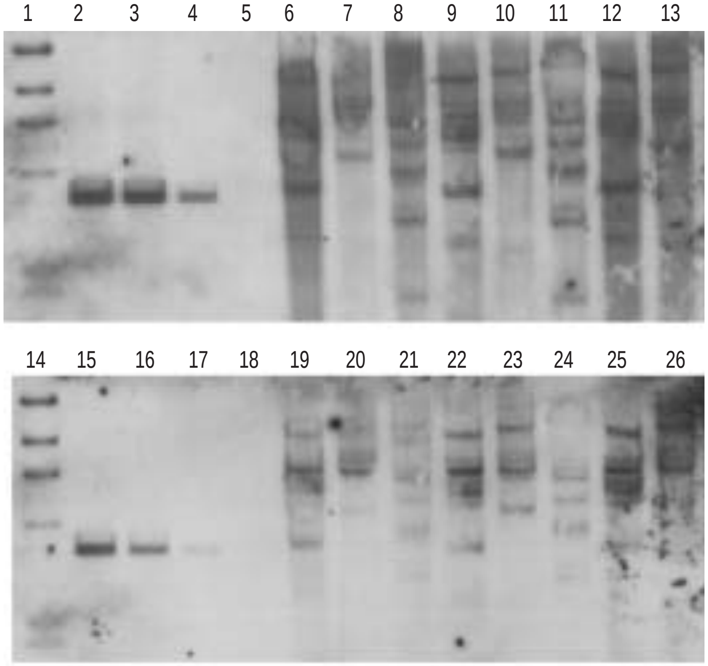


Figure 3. Southern blot analysis of regenerated T_0 plants from line SH 98 26 after SmaI restriction digest plasmid (unique site on UbiBar plasmid).
DNA digested with SmaI and probed with UbiBar plasmid Dig-labeled by nick translation.
Lanes 1 and 14 contain a 1 Kb ladder; Lanes 2, 3, 4 15, 16, and 17 represent copy number references (10, 5, and 1 copy number, respectively); lanes 5 and 18 are negative controls; and lanes 6 to 13 and 19 to 26 are from Basta^{TM} resistant plants.

Acknowledgments

This research is funded in part by the Australian Cooperative Research Center for Molecular Plant Breeding, in which CIMMYT is a participant. The “Bobwhite” family, developed by Dr. S. Rajaram, is stored in CIMMYT’s germplasm bank, as “in trust” material under the United Nation Food and Agriculture Organization (FAO) agreement.

References

Pellegrineschi A., L. M. Noguera, S. McLean, B. Skovmand, R. M. Brito, L. Velazquez, R. Hernandez, M. Warburton, and D. Hoisington . Identification of highly transformable wheat genotypes for mass production of fertile transgenic plants. Submitted to Plant Cell Reports.

Irrigated Wheat Production Systems: Too Much Tillage, Too Much Nitrogen, Not Enough Water

K.D. Sayre, J. Cruz, S. Sanchez, and M. Cano

Irrigated wheat production systems (spring, facultative and winter wheat) comprise nearly 55% of the wheat area and roughly 65% of wheat production in the developing countries. Between 35% and 45% of these production systems involve wheat in rotation with flooded paddy rice and the rest with wheat in rotation with a large number of potential upland crops like maize, soybean, and cotton. The vast majority of this area is characterized by 1) use of intensive tillage systems, often with crop residue removal or burning; 2) largely inefficient irrigation water delivery by gravity systems (mainly by flooding) and 3) use of comparatively high levels of N fertilizers.

Excessive tillage, especially when residues are removed or burned, is clearly contributing to a "wearing down" of the foundation for sustainable production through degradation of soil productivity and/or through creation of conditions leading to diminishing input use efficiencies. However, the problems associated with marked reductions in tillage combined with high levels of surface retained crop residues for surface/gravity irrigation water delivery systems (especially flood irrigation systems) have discouraged most irrigation researchers and farmers from trying to reduce tillage and retain residues. Agronomists at the International Maize and Wheat Improvement Center (CIMMYT), nonetheless, in collaboration with scientists from national agriculture research systems and farmers, have developed new technologies and machinery to allow zero/reduced till planting with crop residue retention, which are being extended in South Asia, including to small scale farmers. Furrow irrigated, bed-planting systems have greatly facilitated the scope to manage crop residues as well as dramatically reduce tillage.

There is a continuing need to improve the efficiency of irrigation water use in wheat production because water presents a major production cost to most farmers. Yet more importantly, there is worldwide, accelerating competition for scarce water resources and agriculture will undoubtedly lose the battle to maintain even its current share, especially since most irrigation systems and farmer irrigation practices are notoriously inefficient, wasting excessive amounts of water. It is a foregone conclusion that marked increases in the efficacy of irrigation water use must be achieved if production levels are to be maintained or increased, since we will need to produce more from less.

Similarly, N fertilizer use efficiency in irrigated wheat must be improved, not only in view of its increasing contribution to the cost of wheat production but also because of detrimental environmental effects associated with improper N management and its excessive use.

This presentation attempts to illustrate how breeders and agronomists can work together to develop needed management strategies to enhance water and nitrogen use efficiency and then identify suitable genotypes to fit these new reduced-till management strategies. To do this, management by genotype interactions must be understood and utilized to identify the right genotypes.

A key part of crop management strategies which CIMMYT agronomists are using to improve both water and N use efficiency entails the use of furrow irrigated bed planting systems. Farmer trials/observations as well as station trials have indicated up to a 25-50% saving of irrigation water as compared to typical flood irrigation systems in Mexico as well as in China, India, Pakistan, and Iran. This planting system allows new management opportunities for planting orientation on the beds as well as for N timing and placement. Opportune field access facilitates management operations by tracking in the furrows between the beds.

Irrigation Strategies

Figure 1a presents the two-year (1998/99 and 1999/00) averaged yield results for seven bread and seven durum wheat genotypes grown with five (554 mm H_2O applied) or four irrigations (392 mm H_2O applied). Performance of durum wheat lines over the two irrigation treatments was decidedly different from bread wheat lines. Average yield for the durums was not affected by reducing the irrigation whereas a small but significant yield reduction occurred in bread wheat. However, there were significant irrigation x crop and irrigation x genotype within crop interactions indicating differential performance patterns which can offer positive selection opportunities for breeders. Only small year alone or interactions of the other treatment factors with year were noted.

Figure 1b presents results from a similar trial where two durum and two bread wheat genotypes were produced in the 1998/99 and 1999/00 crop cycles with either five irrigations (508 mm H_2O applied) or 4 irrigations (392 mm H_2O applied). The genotypes were planted using either 3 rows/bed (20 cm between rows) or 2 rows/bed (40 cm between rows) on 80 cm beds (width from furrow center to furrow center). As can be observed, average grain yield was higher with 2 rows/bed using five irrigations whereas yield for four irrigations was higher for 3 rows/bed. However, there were highly significant irrigation x genotype and row #/bed x genotype interactions indicating that differential genotypic performance patterns must be carefully considered in order to be utilized in developing new lines that will provide higher water use efficiencies under the most feasible planting methodology.

Nitrogen Management Strategies

Nitrogen rates that many farmers use for irrigated wheat tend to be markedly higher that those used by most rainfed wheat producers because of higher yield potential expectations. However, this can be exorbitant, as in the Yaqui Valley of Sonora where the current average N application to wheat by farmers is over 275 kg/ha. As in most irrigated wheat situations, farmers in the Yaqui Valley tend to apply a large part of the N pre-plant or at planting (commonly between 50-80% of

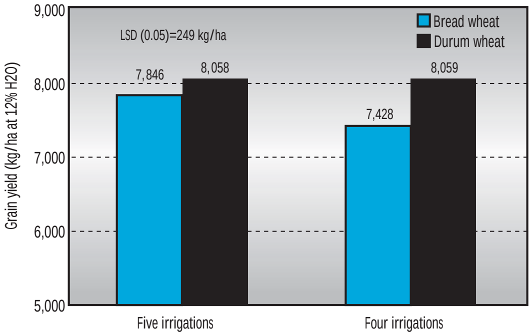


Figure 1a. Effect of irrigation frequency on the average grain yields of seven bread wheat and seven durum wheat genotypes common to both the 1998/99 and 1999/00 cycles at CIANO/Obregon. Both irrigation x crop and irrigation x genotype within crop interactions were significant at the 0.01 level.

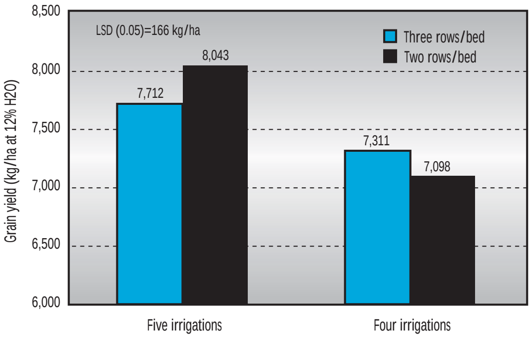


Figure 1b. Effect of irrigation frequency and row number per bed on the average grain yield of bread wheat and durum wheat genotypes (2 each) planted on beds with conventional tillage during the 1998/99 and 1999/00 crop cycles at CIANO/Obregon. Irrigation x row #/bed, irrigation x genotype, row #/bed X genotype and the three way interaction were all significant at the 0.01 level.

the total N applied). Our research has consistently demonstrated that when there is a marked reduction in the amount of fertilizer N applied at or before planting combined with the bulk applied at near the 1st node growth stage, yield is normally enhanced and remarkable grain quality improvement occurs.

Figure 2a presents the yields for four durum wheat varieties grown for two years (1998/99 and 1999/00) at CIANO where 225 kg N/ha were applied using three different timing patterns. Altar 84 currently is the most widely grown durum wheat in the Yaqui Valley and can be considered as a check. Applying all N at planting (similar to farmer practice) was grossly inferior to the other two application strategies using split applications. A small year x genotype interaction for yield was observed but no other interactions were significant.

Figure 2b presents the % flour protein for the same varieties and N management treatments and serves as a quality indicator. The figure clearly indicates the exceptional advantages of split applications in quality expression. There were large yield and quality differences between the varieties. Concerning the split application treatments, applying 1/3 N at planting and 2/3 at 1st node provided the highest yields and increases in % flour protein compared to applying all N at planting. Applying 2/3 at 1st node and 1/3 at boot stage provided an intermediate yield increase but a greater increase in % flour protein. There was a significant N management x variety interaction while all other interactions were not significant.

Figures 3a and b present similar information for a series of bread wheat genotypes grown during the 1999/00 crop cycle at CIANO on which 225 kg N/ha was applied with different timing. Rayon 89 is currently the most widely grown bread wheat in the Yaqui Valley and is the check. Also included are the mean yields for four genotypes obtained from the rust resistance program and five from the bread wheat program.

Yield performance illustrated in Figure 3a also indicates the inferiority of applying all N at planting. Yields were higher for the two split application treatments, which were at par. The splits were 1/3 at planting and 2/3 at 1st node versus 1/3 at planting, 1/3 at 1st node and 1/3 at boot stage. Large genotypic differences occurred but there was a significant N management x genotype interaction.

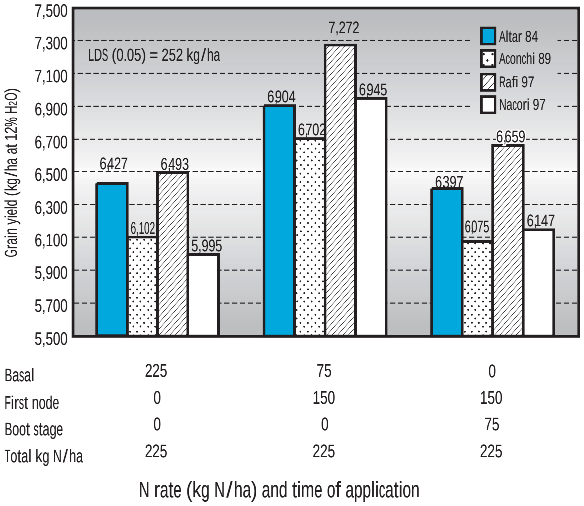


Figure 2a. Effect of nitrogen management on grain yield of four durum wheat varieties averaged over the 1998/99 and 1999/2000 crop cycles at CIANO, Cd. Obregon.

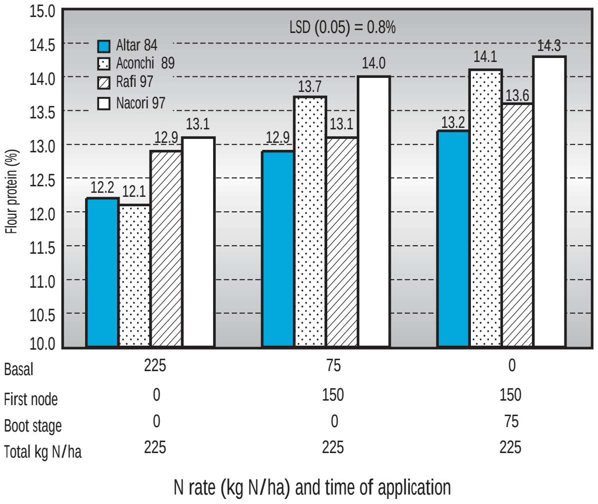


Figure 2b. Effect of nitrogen management on percent flour protein of four durum wheat varieties averaged over the 1998/99 and 1999/2000 crop cycles at CIANO, Cd. Obregon. The year x N management and year x variety interactions were not significant. The N management x variety interaction was significant at the 0.01 level.

Figure 3b presents the % grain protein values for the same N management and genotypes. As observed for durum wheat, split applications not only increased bread wheat yield but markedly increased grain protein content as compared to applying all N at planting. All genotypes responded in a similar manner for protein content although there were large genotypic differences. The 3-way split was better for both yield and protein for all genotypes except yield of Rayon 89. The N management x genotype interaction for protein was not significant.

The three examples given above indicate the sharp differences in crop and genotype performances that can be obtained with different crop management strategies. Furthermore, they illustrate differential management and genotype interactions that can occur and could be exploited in variety development. Breeders and agronomists have not worked closely enough to exploit these kinds of elements to more efficiently develop the varieties farmers need. This is especially true when faced with new technologies like reduced / zero till planting systems with residue retention, bed planting systems or the inevitable constraints imposed by less available irrigation water or more costly fertilizers. CIMMYT wheat program breeders and agronomists are trying to improve how we develop better germplasm and to provide a purposeful example for our colleagues in national agricultural research systems.

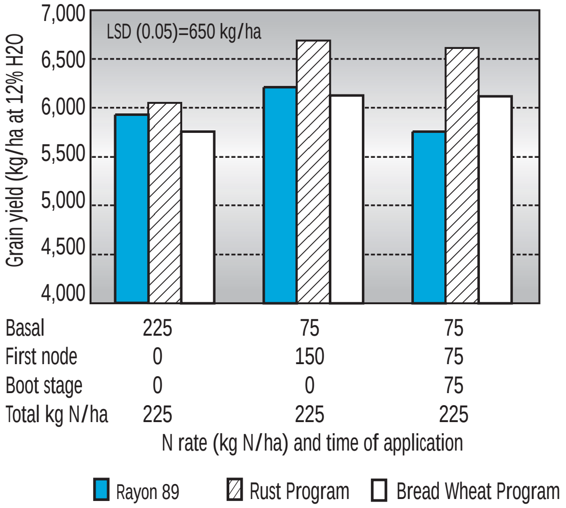


Figure 3a. Effect of nitrogen management on grain yield of Rayon 89, five advanced lines from the bread wheat program, and four advanced lines from the rust resistance program at CIANO, Cd. Obregon, during the 1999/00 crop cycle.

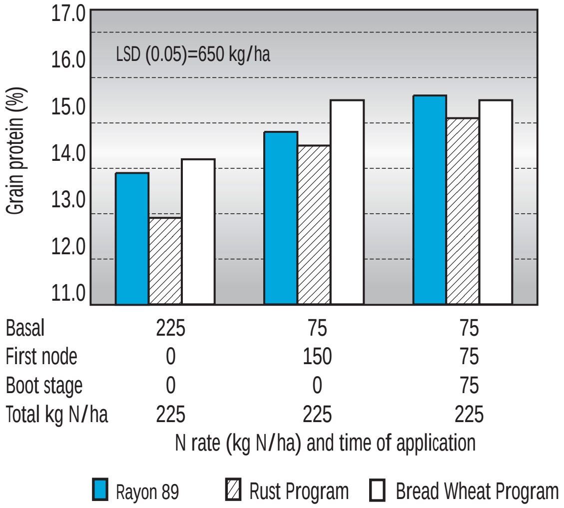


Figure 3b. Effect of nitrogen management on % grain protein of Rayon 89, five advanced lines from the bread program, and four advanced lines from the rust resistance program at CIANO, Cd. Obregon, during the 1999/00 crop cycle.

Triticale for Feed and Forage: Case Studies from Mexico and Ecuador

**A.R. Hede, J. Lozano-del Rio, M. Bejar-Hinojosa,
M. Rivadeneira, and M. Mergoum**

Introduction

Over the next 20-50 years, global demand for cereals will grow dramatically due to increased demand for grain for direct human consumption, and for animal feed (to satisfy, in turn, a growing demand for meat products). Though a newly cultivated crop, triticale is expanding in several production systems due to its ability to produce high biomass and grain yield over a wide range of soil and climatic conditions. According to an estimate given at the 4th International Triticale Symposium in Canada in 1998, triticale is cultivated on approximately 2.9 million hectares in more than 30 countries.

Most triticale is grown for animal feed and fodder and only a little is used for human consumption. Consequently, the International Maize and Wheat Improvement Center (CIMMYT) is emphasizing the development of triticale types targeted for feed grain, dual-purpose forage/grain, and grazing. Several studies have demonstrated that triticale provides better nutritional profiles for animal consumption than conventional grains or forage crops (triticale has better amino acid composition, fiber content, palatability, and more metabolizable energy). One of triticale's competitive niches may be as a crop to feed to livestock. This paper will discuss results and experience obtained in Mexico and Ecuador, where experiments have demonstrated triticale's potential as an alternative feed and forage crop.

Mexico

For several years CIMMYT, Universidad Autonoma Agraria Antonio Narro (UAAAN) in Saltillo, Cuahuila, and Centro de Investigacion para los Recursos Naturales (CIRENA) in Salaices, Chihuahua, have been working together to evaluate triticale's potential as an alternative forage crop in the winter months in northern Mexico. The northern region of Mexico, which includes the States of Coahuila, Durango, Chihuahua, and Sonora, is very important for livestock production, mainly beef and dairy cattle. Irrigated pasture crops are widespread and used for grazing, hay, silage, and cut-forage production. In La Laguna, the most important dairy area in Mexico (in 1997 milk production surpassed one billion liters), the most common feed use of pasture crops is for hay or cut forage, while in other areas, especially Chihuahua, grazing is more common (Bejar-Hinojosa et al. 2000). Whatever system is practiced, maize and sorghum are the traditional summer forage crops, while the dominant winter forage crops are oats (*Avena sativa* L.) and ryegrass (*Lolium* sp.). Farmers in this region rapidly accepted tricale as a forage crop, basically due to its high biomass production, but also because of its cold tolerance. Low temperatures often damage or restrict the growth of oat and ryegrass, but does no harm to triticale (Figure 1).

Results of experiments in which triticale was evaluated for dry matter production and nutritional value demonstrated that winter/facultative triticales significantly

Figure 1. Ice-covered triticale field, Cuatro.

outperformed traditional forage crops like oats and ryegrass (Lozano et al. 1998). Results of the 1998/99 crop cycle, in which wheat, rye, and barley were included as checks, were similar, i.e., triticale showed higher dry matter yields and better quality than the other forage crops (Figures 2-5). Furthermore, experiences from the La Laguna area have shown that triticale is far more water use efficient than oat and ryegrass, an important factor in a region where irrigation is a major constraint for forage production.

After evaluating several advanced triticale lines, four superior triticales were identified for northern Mexico and will be released during 2001. Multiplication plots of these four lines have been established to provide sufficient seed for farmers to plant by October 2002.

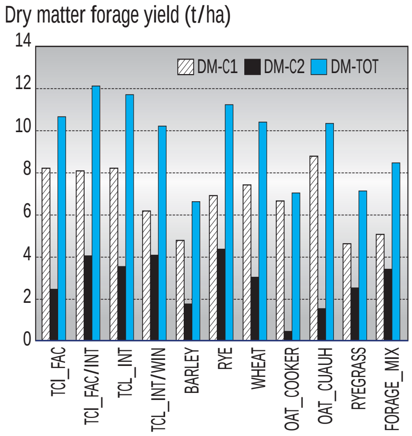


Figure 2. Dry matter (DM) forage yield in two cuts (C1 and C2) and total (TOT) of triticale (TCL) and other cereals at Salaices, Chihuahua, Mexico, 1998/99.

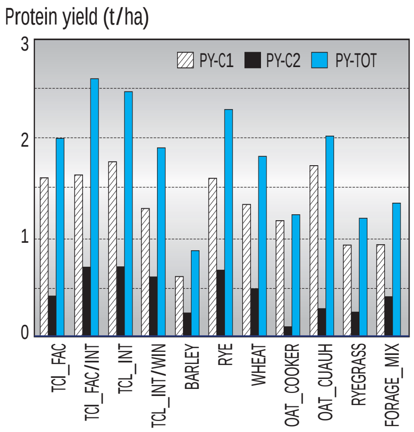


Figure 3. Protein yield (PY) in two cuts (C1 and C2) and total (TOT) of triticale (TCL) and other cereals at Salaices, Chihuahua, Mexico, 1998/99.

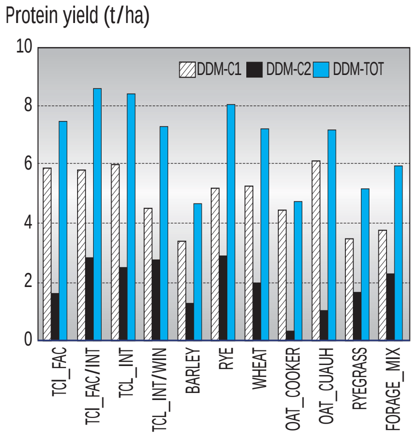


Figure 4. Digestible dry matter (DDM) yield in two cuts (C1 and C2) and total (TOT) of triticale (TCL) and other cereals at Salaices, Chihuahua, Mexico, 1998/99.

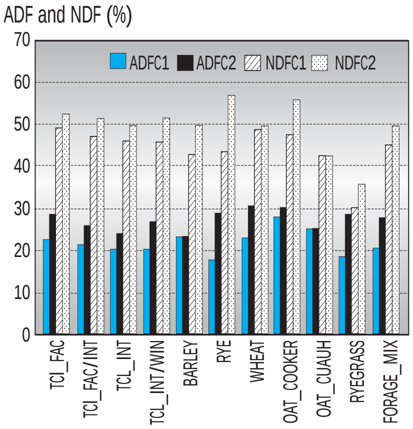


Figure 5. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) in two cuts (C1 and C2) and total (TOT) of triticale (TCL) and other cereals at Salaices, Chihuahua, Mexico, 1998/99.

Ecuador

In Ecuador, as a result of longtime collaboration between CIMMYT and Instituto Nacional Autónomo de Investigaciones Agropecuarias (INIAP), two triticale varieties, INIAP-Mana 82 and INIAP-Promesa 85, were released. However, due to agronomically unfavorable traits (e.g., shriveled grain) and a long vegetative period, these varieties were never planted over large areas in Ecuador. After several years of testing new advanced lines, INIAP has identified a new high yielding triticale that is early maturing and has high test weight. It was introduced from CIMMYT in 1991 under the cross name 'FARAS 1*2//BUCH'S'/CHRC'S' (selection history: CITM88-135-1RES-11M-1Y-0PAP), and will be released under the name INIAP-Triticale 2000.

INIAP-Triticale 2000 has been evaluated for its nutritional value as a feed grain for cows and calves; this evaluation will later be supplemented with data on its value for feeding pigs and poultry. Results of feeding trials where a concentrate containing triticale was fed to grazing cows are summarized in Figure 6. It was found that the increase in milk production from start of the lactating period to peak production time was higher in cows that had been fed triticale in the concentrate than in cows that ate concentrates containing grains other than triticale. Furthermore, cows having triticale included in the concentrate maintained maximum milk production over a longer period (2-3 months). Milk production at the end of the lactancy period was 12-14 L/

day for cows fed the triticale concentrate, while cows fed other concentrates produced 10 L/day. Similarly, higher weight gain per day was observed in calves fed rations in which maize had been replaced by triticale. A weight gain of 1 kg/day is favorable (Figure 7).

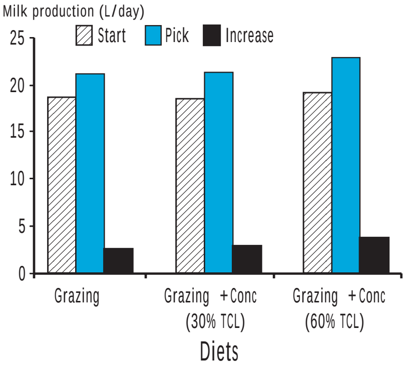


Figure 6. Initial and peak milk production in cows receiving triticale as a concentrate in different amounts. Results from Instituto Nacional Autónomo de Investigacines Agropecuarias, Ecuador.

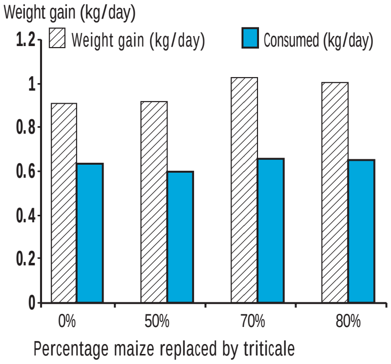


Figure 7. Weight gain of calves receiving feed concentrates with different proportions of maize replaced by triticale. Results from Instituto Nacional Autónomo de Investigacines Agropecuarias, Ecuador.

A complete analysis of the nutritional profile of the new triticale line compared to other crops demonstrates triticale's potential as an animal feed (Table 1). Of special importance is its high protein level (higher than barley and maize and the same as wheat) and favorable amino acid composition with a high content of lysine and tryptophan, which fit the nutritional requirements of monogastrics and poultry very well.

Conclusions

Results obtained in Mexico and Ecuador demonstrate triticale's great potential as a feed and forage crop. Farmers in many other countries have expressed great interest in growing triticale. In Canada, for example, triticale has expanded from 34,000 ha in 1998 to over 110,000 ha in 2000. However, although triticale has been widely accepted as a feed and forage crop, more information needs to be collected on a wide range of feeding situations in both monogastric and ruminant species.

References

Bejar-Hinojosa, M., A.J. Lozano, and A. Hede. 2000. El triticale, una alternativa forrajera para el norte de Mexico. Boletin tecnico No. 3. Salaices, Chihuahua, Mexico.

Lozano, A.J., V.M Zamora, H.D. Solis, M. Mergoum, and W.H. Pfeiffer. 1998. Triticale forage production and nutritional value in the northern region of Mexico. In: P. Juskiw (ed.), Proceedings of the 4th International Triticale Symposium, pp. 259-263.

Table 1. Nutritional characteristics of the variety INIAP-Triticale 2000, compared to other crops.

Crop	Protein %	Ash %	Fiber %	Ca %	P %	Amino acids Lysine	Amino acids Tryptophan	Total energy[1]
INIAP-Triticale 2000	13.43	1.88	3.24	0.03	0.38	5.04	0.67	44.24
Barley	11.80	3.15	6.66	0.05	0.38	2.94	0.37	44.17
Wheat	13.94	1.72	3.29	0.06	0.37	4.30	0.74	44.51
Maize (yellow, hard)	10.10	1.53	2.96	0.02	0.20	2.27	0.12	41.90

[1] Expressed as calories per gram of whole grain.

Utilization of *Aegilops geniculata* Diversity in the CIMMYT Wheat Program

M. Zaharieva and A. Mujeeb-Kazi

Why *Aegilops geniculata*?

Among the 22 species of the genus Aegilops, Aegilops geniculata Roth (syn. =Ae. ovata L.) is particularly interesting as a source of resistance to diseases and pests (Friebe and Heun 1989) and tolerance to drought and salinity (Rekika et al. 1998). This suggests that the species may be a valuable reservoir of genes for improving wheat resistance to both biotic and abiotic stresses.

What is *Ae. geniculata*?

Ae. geniculata (Figure 1) is an annual, self-fertile, allo-tetraploid species (2n=4x=28) with MU genome (Van Slageren 1994). It is widely distributed around the Mediterranean region.

Figure 1. *Aegilops geniculata* Roth.

Integrated Management and Use of *Ae. geniculata* Genetic Resources

Collection and study of diversity

A collection comprising 160 *Ae. geniculata* accessions originating from different eco-geographical regions (Figure 2) was established. Their genetic diversity was analyzed on the basis of molecular markers (RAPD, RFLP) and morphological traits (Zaharieva et al. 1999; Zaharieva et al. 2001a) (Figure 3).

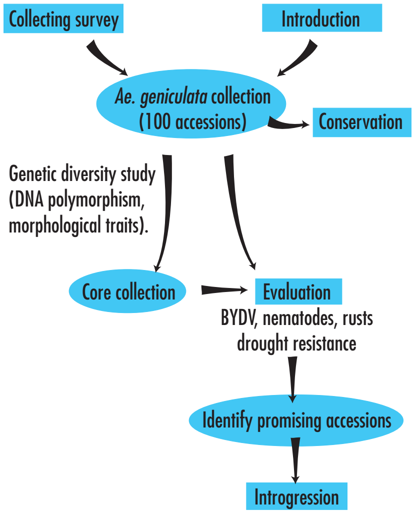


Figure 3. Management of *Aegilops geniculata* resources.

Figure 2. Origin of *Aegilops geniculata* accessions.

Evaluation

Resistance to barley yellow dwarf virus, rusts, and cereal cyst nematodes has been identified in the collection (Zaharieva et al. 2000). The accessions were evaluated for resistance to leaf and stripe rusts and root lesion nematodes at the International Maize and Wheat Improvement Center (CIMMYT). The collection was also studied for physiological traits related to drought and heat stress (Zaharieva et al. 2001b). A set of promising accessions possessing resistance traits was then selected for use in our wide hybridization program (Table 1).

Introgression of useful traits

Resistant *Ae. geniculata* accessions were crossed with susceptible high-yielding bread and durum wheats (Table 2) with priority currently given to transfers for BYDV resistance. F_1 hybrids produced have been cytologically analyzed and validated to be n=5x=35 (ABDUM) or n=4x=28 (ABUM). For each cross, some F_1 hybrids shall be doubled and amphiploids evaluated for the targeted diseases. The other F_1 hybrids will be backcrossed to the wheat parents for advancing the desired cross combination (Figure 4). A crossing program is also underway to hybridize Chinese Spring (*phph*) and Capelli (*ph1c*) with *Ae. geniculata* accessions and promote F_1 homoeologous pairing. A parallel strategy will be utilized in bread wheat-based F_1 hybrids or amphiploids where a backcross of these materials will be made by Chinese Spring *phph* and advanced using the protocol of Mujeeb-Kazi (1998).

Molecular markers will also be used to follow the introgressed alien material. Microsatellite DNA markers detecting genetic differences even among closely related individuals are useful for characterizing *Triticum* and *Ae. geniculata* genotypes and their progenies. Furthermore, molecular markers related to resistance traits or genes coming from the wild species could be explored.

Table 2. Bread and durum wheat cultivars to be used in the crosses.

Triticum aestivum	*T. durum*
Baviacora	Sooty 9/Rascon 37
Pastor	Cado/Boomer 33
Prinia	Dukem 12/2*Rascon 21
Babax/Lr42//Babax	Kucuk
Weebill 1	Topdy 18/ Focha 1//Altar 84
SRMA/TUI	Altar 84
Chinese Spring (*phph*)	Capelli (*ph1c*)

Table 1. ***Aegilops geniculata*** **accessions resistant to barley yellow dwarf virus (BYDV); stem, leaf, and stripe rusts; and cereal cyst nematodes (CCN).**

Biotic stress	Resistant accessions and origin
BYDV	MZ 20 (France), MZ 21 (France), MZ 97(Cyprus), MZ141 (Italy), MZ 149 (Greece)
Rusts	MZ 6 (Bulgaria), MZ 27 (Morocco), MZ 48 (France), MZ 79 (Lebanon), MZ 96 (Cyprus)
CCN	MZ 1 (Bulgaria), MZ 61 (Tunisia), MZ 63 (Libya), MZ 77(Jordan) , MZ 124 (Spain)

References

Friebe, B., and M. Heun. 1989. C-banding pattern and powdery mildew resistance of *Triticum ovatum* and four *T. aestivum – T. ovatum* chromosome addition lines. *Theoretical and Applied Genetics* 78:417-424.

Mujeeb-Kazi, A. 1998. An analysis of the use of haploidy in wheat improvement. In: M.M. Kohli and M. Francis (eds.), *Application of Biotechnologies to Wheat Breeding,* pp. 33-48. La Estanzuela, Colonia, Uruguay: CIMMYT-INIA.

Rekika, D., M. Zaharieva, P. Stankova, X. Xu, I. Souyris, and P. Monneveux. 1998. Abiotic stress tolerance in *Aegilops* species. In: M.M. Nachit, M. Baum, E. Porceddu, P. Monneveux, and E. Picard (eds.), *SEWANA Durum Research Network,* pp. 113-128. Aleppo, Syria: ICARDA.

Van Slageren, M.W. 1994. Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub and Spach) Eig (*Poaceae*). Agricultural University, Wageningen, and ICARDA, Aleppo, Syria. 512 pp.

Zaharieva, M., J. David , D. This, and P. Monneveux. 1999. Analyse de la diversité génétique d'*Aegilops geniculata* Roth en Bulgarie. *Cahiers Agricultures* 8:181-188.

Zaharieva, M., E. Gaulin, M. Havaux, E. Acevedo, and P. Monneveux. 2001a. Drought and heat responses in the wild wheat relative *Aegilops geniculata* Roth: potential interest for wheat improvement. *Crop Science* (in press).

Zaharieva, M., P. Monneveux, M. Henry, R. Rivoal, J. Valkoun, and M. Nachit. 2000. Evaluation of a collection of wild wheat relative *Aegilops geniculata* Roth and identification of potential sources for useful traits. In: Proceedings of the 6th International Wheat Conference.

Zaharieva, M., S. Santoni, and J. David· 2001b. Genetic diversity using RFLP of the wild wheat relative *Ae. geniculata* Roth (*Ae. ovata* L.) around the Mediterranean basin. Efficiency of molecular markers to build core collection. *Genetic Selection Evolution* (in press).

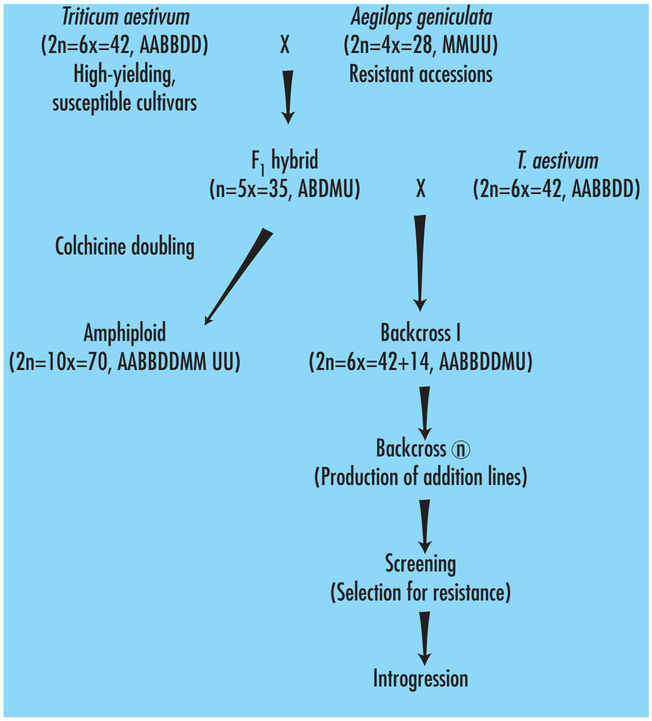


Figure 4a. Scheme of alien transfers from *Aegilops geniculata* to *Triticum aestivum* via the addition line production route.

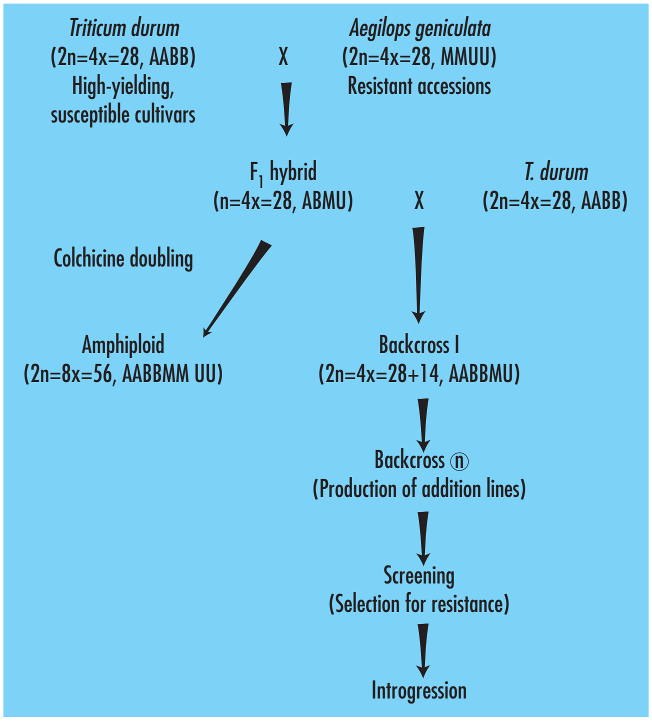


Figure 4b. Scheme of alien transfers from *Aegilops geniculata* to *Triticum durum* via the addition line production route.

Newly Accumulated Resistance in CIMMYT Bread Wheat Germplasm

M. van Ginkel, L. Gilchrist, and C. Velazquez

In the bread wheat breeding effort at the International Maize and Wheat Improvement Center (CIMMYT), we generate materials intended for higher rainfall areas in the developing world, among other mega-environments. In high rainfall environments, the major wheat production constraints are diseases plus certain abiotic stresses, such as waterlogging, sprouting-prone conditions, and, sometimes, nutrient imbalances (both deficiency and toxicity). However, the most observable stresses are the biotic ones. Of these, yellow or stripe rust (*Puccinia striiformis*) and leaf or brown rust (*P. recondita*) are often obvious, in particular the former, plus foliar blights such as *Septoria tritici*, tan spot (*Pyrenophora tritici-repentis*), and very occasionally *Septoria nodorum* and Fusarium *nivale* on the leaves. The main virus disease is barley yellow dwarf virus (BYDV).

Among diseases affecting the spike, fusarium head scab (FHS), induced by various *Fusarium* species, is the number one problem. The recent increase in this disease globally is probably due to the expansion of what are ironically called (from a disease standpoint) more sustainable production methods, such as zero, minimum, or reduced tillage, plus the intensification of rotations, in particular those including corn (maize), an alternate host of *Fusarium* spp.

As FHS spreads and causes damage by reducing the amount of harvested seed and contaminating the grain with toxins, joint efforts to combat this scourge have increased. This symposium is witness to such efforts. The key approach to controling the disease is through the incorporation of genetic resistance.

The CIMMYT program requests, receives, and specifically develops genetically diverse germplasm with FHS resistance. Various reports documenting these sources are available (Gilchrist et al. 1997a, 1997b; 1999). Also, genetic studies aimed at determining modes of inheritance have been carried out and published (Singh et al. 1995; Van Ginkel et al. 1996). In recent years, efforts by the pathology group have concentrated on differentiating germplasm in regard to the four types of resistance commonly applied in FHS (I, II, III, and IV). Our breeding strategy has focused on combining different resistances in adapted backgrounds (Singh and van Ginkel 1997). Two areas of recent research on FHS are reported here.

Three crosses were made among three resistance sources considered likely to be different, based on their genealogy. We chose two parents (1 and 2, below) whose pedigrees contain no Chinese germplasm. The three parents were:

1. Gov/Az//Mus/3/Dodo/4/Bow
2. Bau/Milan
3. Catbird

Though the study continues, data from the first cycle of artificial inoculation with *F. graminearum* isolates from Mexico have shown the following: It has proven very easy to select F_5 lines that have twice the resistance of either parent in all three possible intercrosses. Although two of the parents were not derived from Chinese germplasm, progress could easily be made. This indicates that different genes with accumulative effects (additive or multiplicative) are available in “common” germplasm. In fact, all parents have a very desirable agronomic type, combine readily, and, in many respects, are rather good parents to use in a breeding program, aside from their FHS resistance.

Finally, we have recently confirmed a group of relatively new CIMMYT bread wheat lines to have high levels of FHS resistance, which, until now, have not yet been commonly used around the world in breeding programs targeting scab (Table 1).

References

Gilchrist, L., S. Rajaram, A. Mujeeb-Kazi, M. van Ginkel, H. Vivar, and W. Pfeiffer. 1997a. Fusarium scab screening program at CIMMYT. In: H.J. Dubin, L. Gilchrist, J. Reeves, and A. McNab (eds.), *Fusarium Head Scab: Global Status and Future Prospects*, pp. 7-12. Mexico, D.F.: CIMMYT.

Gilchrist, L., S. Rajaram, M. van Ginkel, A. Mujeeb-Kazi, and J. Franco. 1997b. Characterizing *Fusarium graminearum* resistance of CIMMYT bread wheat germplasm. *Cereal Research Communications* 25(3-2):655-657.

Gilchrist, L., S. Rajaram, M. van Ginkel, C. Velázquez, and J. Crossa. 1999. Transferring fusarium head blight resistance from bread wheat sources to high yielding advanced lines. In: National Fusarium Head Blight Forum, 1999, pp. 162-163.

Singh, R.P., and M. van Ginkel. 1997. Breeding strategies for introgressing diverse scab resistances into adapted wheats. Pp. 86-92 In: *Fusarium Head Scab: Global Status and Future Prospects.* H.J. Dubin, L. Gilchrist, J. Reeves, and A. McNab (eds.). Mexico, D.F.: CIMMYT.

Singh, R.P., Hong Ma, and S. Rajaram. 1995. Genetic analysis of resistance to scab in spring wheat cultivar Frontana. *Plant Disease* 79:238-240.

van Ginkel, M., W. van der Schaar, Y. Zhuping, and S. Rajaram. 1996. Inheritance of resistance to scab in two wheat cultivars from Brazil and China. *Plant Disease* 80:863-867.

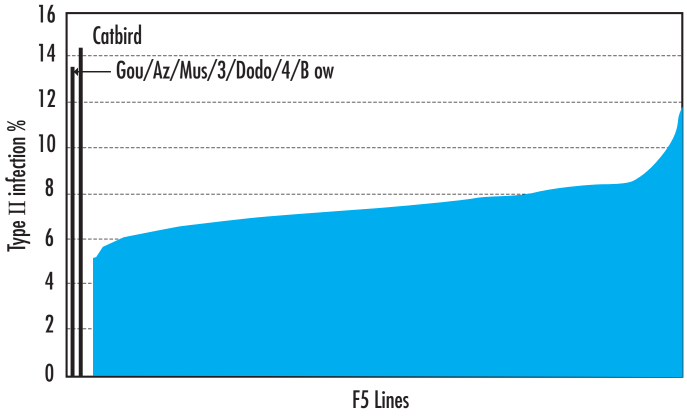


Figure 1. Cross of Gov/Az//Mus/3/Dodo/4/Bow with Catbird. Both parents and 197 derived F_5 lines are depicted against their response to infection to *Fusarium graminearum*, measured as Type II resistance.

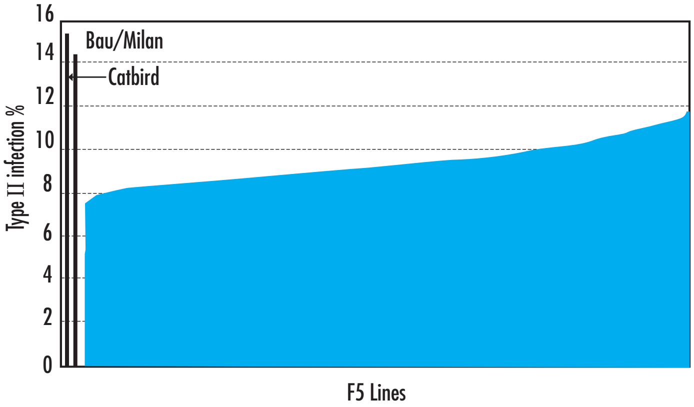


Figure 2. Cross of Bau/Milan with Catbird. Both parents and195 derived F_5 lines are depicted against their response to infection to *Fusarium graminearum*, measured as Type II resistance.

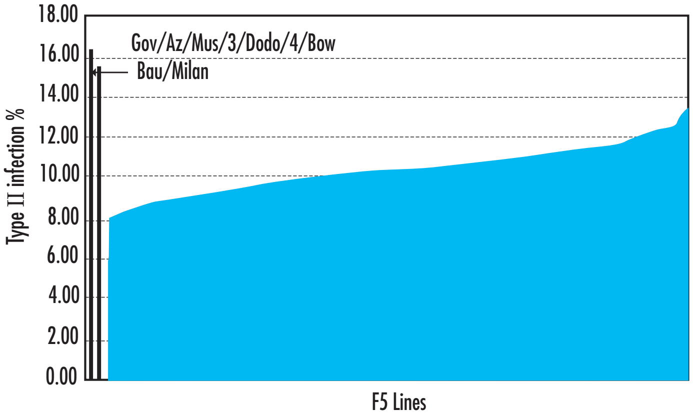


Figure 3. Cross of Gov/Az//Mus/3/Dodo/4/Bow with Bau/Milan. Both parents and 195 derived F_5 lines are depicted against their response to infection to *Fusarium graminearum*, measured as Type II resistance.

Table 1. Newly confirmed CIMMYT bread wheat lines carrying Type II resistance to FHS with infection values of less than 6%. The first five entries are comparative checks.

Cross	Selection history	Resistance Type II (%)
MAYOOR	Check: Moderately resistant	7.91
SUMAI#3	Check: Moderately resistant	9.20
SERI/CEP80120	Check: Moderately susceptible	14.84
FLYCATCHER	Check: Moderately susceptible	21.04
BCN//DOY1/AE.SQUARROSA (447)	Check: Susceptible	32.93
SHA3/CBRD	CMSS92Y00595S-1SCM-0CHN-015Y-3SCM	2.50
NG8675/CBRD	CMSS92Y00639S-1-5SCM-2M-6Y-010SCM-0Y-0SCM	2.52
HXL8088/DUCULA	CMSS93Y02492S-2Y-010M-010Y-010M-10Y-1M-0Y-3SJ-0Y	2.59
CROC_1/AE.SQUARROSA (205)//BORL95	CIGM90.250-4Y-3B-4Y-0B-2M-24M-0Y-010SCM-0Y-0Y-0Y	3.41
GUAM92//PSN/BOW	CMSS92M01860S-015M-0Y-050M-0Y-11M-0Y	3.64
TNMU/3/JUP/BJY//SARA	CMBW91M02016S-0M-040Y-1AL-2AL-7Y-0M-3SJ-0Y	3.70
R37/GHL121//KAL/BB/3/JUP/MUS/4/2*YMI #6/5/CBRD	CMBW91Y01575S-4Y-010M-010Y-015M-2Y-0M-1SCM-010Y-010SCM-1PZ-0Y	4.31
MILAN/DUCULA	CMSS93B01075S-74Y-010M-010Y-010M-8Y-0M-2SJ-0Y	4.72
THB//MAYA/NAC/3/RABE/4/MILAN	CMSS92Y02157T-50Y-015M-010Y-010Y-9M-0Y	4.84
NG8319//SHA4/LIRA	CMBW90M2302-6M-010M-010Y-015M-6Y-0M-0ECU-0Y	4.84
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-9Y-0M-0URY	4.85
R37/GHL121//KAL/BB/3/JUP/MUS/4/2*YMI #6/5/CBRD	CMBW91Y01575S-4Y-010M-010Y-015M-5Y-0M	4.92
NG8319//SHA4/LIRA	CMBW90M2302-6M-010M-010Y-015M-8Y-0M-5SJ-0Y	4.92
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-6Y-0M-3SJ-0Y	5.00
KAUZ/TNMU	CMSS93B01069S-54Y-010M-010Y-010M-8Y-0M-3PZ-0Y	5.00
MAYOOR//TK SN1081/AE.SQUARROSA (222)	CASS94Y00009S-18PR-2M-0M-1Y-0M	5.00
SHA3/SERI//G.C.W 1/SERI	CMBW91Y01596S-2Y-010M-010Y-015M-6Y-0M-1SJ-0Y-010SCM-2PZ-0Y	5.26
HXL8088/DUCULA	CMSS93Y02492S-2Y-010M-010Y-010M-10Y-1M-0Y-2PZ-0Y	5.26
SHA3/CBRD	CMSS92Y00595S-4GH-0M-0SCM-0Y	5.26
TNMU/TUI	CMBW89M3847-64M-0AL-5AL-2B-0Y	5.30
ALUCAN/DUCULA	CMBW89M3764-36M-0AL-2AL-2B-0Y-5PZ-0Y	5.36
IAS64/ALDAN//URES/3/TNMU/4/TNMU	CMBW90M4487-0TOPY-14M-11AL-0AL-07Y-1M-0Y-1SJ-0Y	5.36
SABUF/5/BCN/4/RABI//GS/CRA/3/AE.SQUARROSA (190)	CASS94Y00042S-9PR-1M-0M-1Y-0M	5.51
793.3402//BUC/PVN/3/KAUZ/4/NJ8611	CMSS92Y02234T-7Y-015M-015Y-010M-2Y-0M-1SCM-010Y-010SCM-0Y	5.56
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-9Y-0M-2SCM-010Y-010SCM-0Y-0SCM	5.61
SHA3/SERI//SHA4/LIRA	CMBW90M2468-12M-010M-010Y-015M-10Y-0M	5.65
TNMU/MUNIA	CMSS93B01052S-18Y-010M-010Y-010M-6Y-1M-0Y	5.66
NING8745/3/2*CHUM18//JUP/BJY	CMBW91Y02939M-030TOPM-9Y-010Y-015M-1Y-0M-0E-0ECU	5.74
R37/GHL121//KAL/BB/3/JUP/MUS/4/2*YMI #6/5/CBRD	CMBW91Y01575S-4Y-010M-010Y-015M-2Y-0M-1SCM-010Y-010SCM-3SJ-0Y	5.74
NG8675/CBRD	CMSS92Y00639S-1-5SCM-2M-6Y-010SCM-0Y	5.74
THB/CEP7780//SHA4/LIRA	CMBW90M2456-9M-010M-010Y-015M-10Y-0M	5.77
SHA3/CBRD	CMSS92Y00595S-5GH-0M-0Y-0SCM-0Y	5.85
NL456/VEE#5//PASA/3/BOW/GEN//KAUZ	CMSS93Y03376T-44Y-010Y-010M-010Y-8M-0Y	5.88
TUI/MILAN	CMSS92Y00540S-030Y-015M-0Y-0Y-18M-0Y	5.88
ISD-75-3-1/MO88//PRL/VEE#6	CMBW90M4731-0TOPY-42M-3Y-010M-3Y-9M-2KBY-05KBY-0B-0KEN	5.93

Invited Speakers

Dr. Norman E. Borlaug
Emeritus Consultant
CIMMYT
Apdo. Postal 6-641
06600 Mexico, D.F.
Mexico
Tel: +52 (55) 5804 2004
Fax: +52 (55) 5804 7558
Email: n.borlaug@cgiar.org

Dr. Hans Braun
Principal Scientist
Turkey/CIMMYT/ICARDA
International Winter
Wheat Improvement Program
PK 39 Emek
06511 Ankara
Turkey
Fax: +90 (312) 287 8955
Email: h.j.braun@cgiar.org

Dr. Paul Brennan
Consultant (Plant Breeding and
Biotechnology)
P.O. Box 144
Lennox Head, NSW 2478
Australia
Tel: +61 (02) 6687 5288
Fax: +61 (02) 6687 5911
Email: paul.brennan@bigpond.com

Dr. Fred Cholick
Dean
College of Agriculture and Biological
Sciences
South Dakota State University
Box 2207
Brookings, SD 57007
U.S.A.
Tel: +1 (605) 688 4148
Email: cholick.fred@abs.sdstate.edu

Dr. Dana Dalrymple
Research Advisor
Office of Agriculture and Food
Security
Bureau for Economic Growth,
Agricultural
Development, and Trade
U.S. Agency for International
Development
Washington, D.C.
U.S.A.
Tel: +1 (212) 712 5596
Fax: +1 (212) 216 3010
Email: ddalrymple@usaid.gov

Dr. Ron DePauw
Head
Cereals Section
Semiarid Prairie Agricultural Research
Centre
P.O. Box 1030
Swift Current, Saskatchewan S9H 3X2
Canada
Tel: +1 (306) 778 720
Fax: +1 (306) 773 9123
Email: depauw@em.agr.ca

Dr. Russ Karow
Head
Department of Crop and Soil Science
107 Crop Science Building
Oregon State University
Corvallis, OR 97331-3002
U.S.A.
Tel: +1 (541) 737 5857
Fax: +1 (541) 737 1589
Email: russell.s.karow@orst.edu

Dr. Arthur Klatt
Professor of Wheat Breeding
Department of Plant and Soil Science
Oklahoma State University
274 Ag Hall
Stillwater, OK 74078
U.S.A.
Tel: +1 (405) 744 9604
Fax: +1 (405) 744 5269
Email: aklatt@okstate.edu

Dr. C. James Peterson
Professor of Wheat Breeding and Genetics
231 Crop Science Building
Department of Crop and Soil Science
Oregon State University
Corvallis, OR 97331-3002
U.S.A.
Tel: +1 (541) 737 3728
Fax: +1 (541) 737 0909
Email: cjp@orst.edu

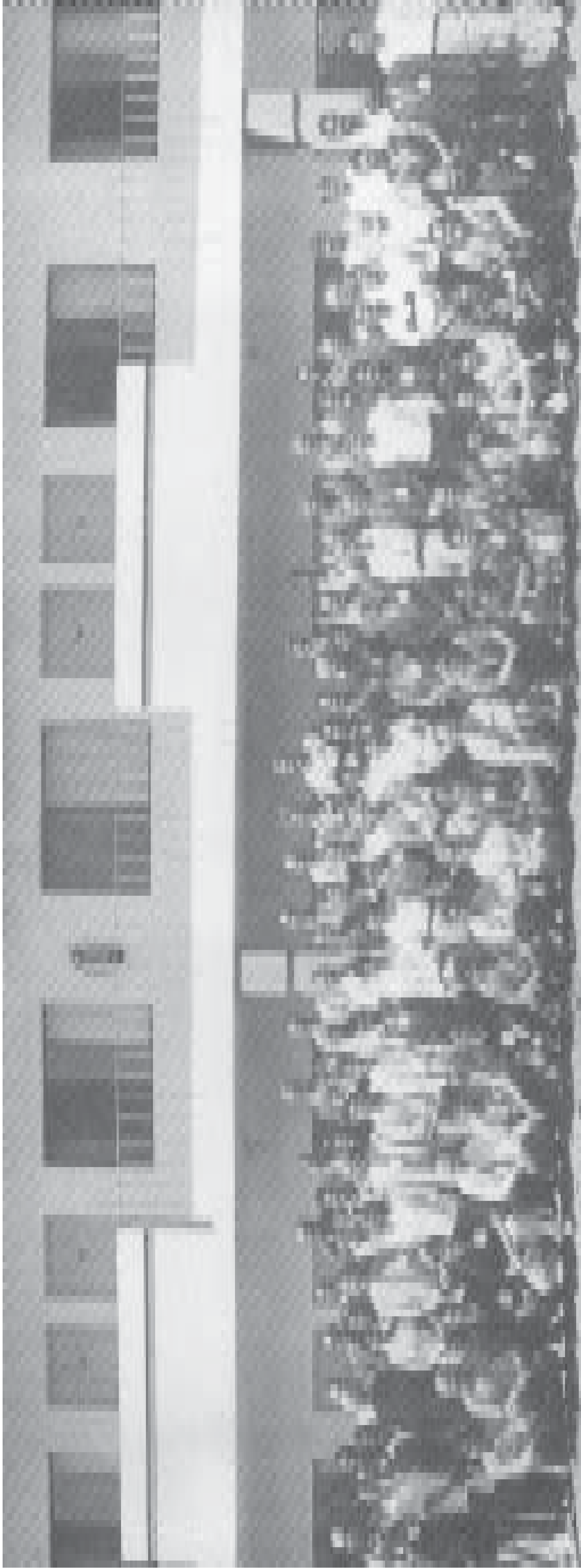
Dr. Prabhu Pingali
Director
Economics Program
CIMMYT
Apdo. Postal 6-641
06600 Mexico, D.F.
Mexico
Tel: +52 (55) 5804 2004
Fax: +52 (55) 5804 7558
Email: p.pingali@cgiar.org

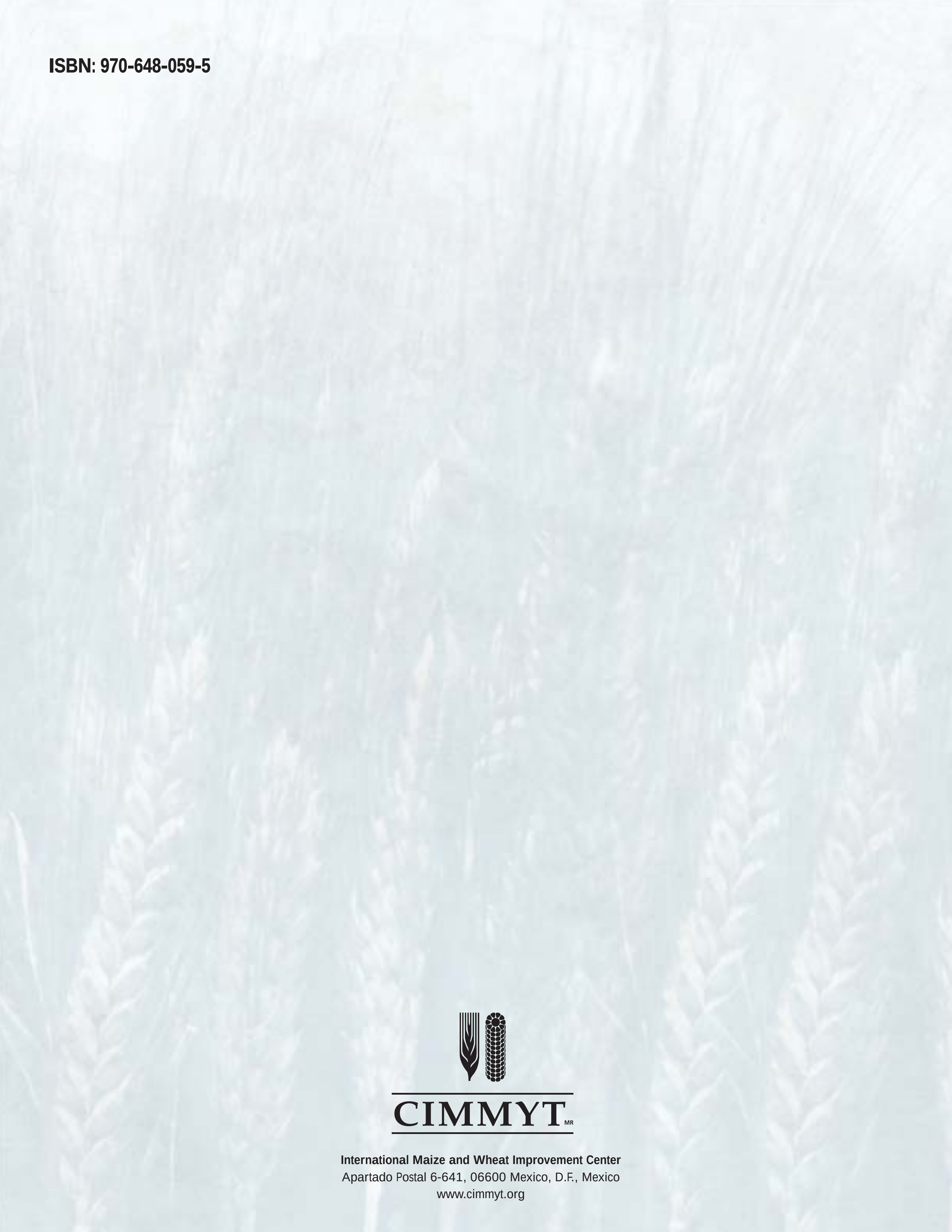
Dr. Sanjaya Rajaram
Director
Wheat Program
CIMMYT
Apdo. Postal 6-641
06600 Mexico, D.F.
Mexico
Tel: +52 (55) 5804 2004
Fax: +52 (55) 5804 7558
Email: s.rajaram@cgiar.org

Prof. Timothy Reeves
Director General
CIMMYT
Apdo. Postal 6-641
06600 Mexico, D.F.
Mexico
Tel: +52 (55) 5804 2004
Fax: +52 (55) 5804 7558
Email: t.reeves@cgiar.org

Dr. Hubert Spiertz
Professor of Crop Ecology
Department of Plant Sciences
Wageningen University and Research Center
P.O. Box 430
6700 AK Wageningen
The Netherlands
Tel: +31 (317) 482 678/485 315
Fax: +31 (317) 485 572
Email: Huub.Spiertz@cwe.dpw.wau.nl

Dr. John Witcombe
Manager
DFID Plant Sciences Research Programme
Centre for Arid Zone Studies
University of Wales
Bangor LL57 2UW
Wales
Tel: +44 (1248) 382 116
Fax: +44 (1248) 371 533
Email: j.r.witcombe@bangor.ac.uk





ISBN: 970-648-059-5

CIMMYT

International Maize and Wheat Improvement Center
Apartado Postal 6-641, 06600 Mexico, D.F., Mexico
www.cimmyt.org