Book of Abstracts

Complementary strategies to raise wheat yield potential

Workshop held at CIMMYT, El Batán, Mexico
10-13 November 2009

Matthew Reynolds and Debra Eaton (Editors)

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The International Maize and Wheat Improvement Center, known by its Spanish acronym, CIMMYT® (www.cimmyt.org), is an international, not-for-profit research and training organization. With partners in over 100 countries, the center applies science to increase food security, improve the productivity and profitability of maize and wheat farming systems, and sustain natural resources in the developing world. The center's outputs and services include improved maize and wheat varieties and cropping systems, the conservation of maize and wheat genetic resources, and capacity building. CIMMYT belongs to and is funded by the Consultative Group on International Agricultural Research (CGIAR) (www.cgiar.org) and also receives support from national governments, foundations, development banks, and other public and private agencies.

Abstract: The abstracts herein are of presentations by world-renowned experts for the workshop "Complementary strategies to raise wheat yield potential" (10-13 November 2009, CIMMYT-El Batán, Mexico). Sponsored by the United States Agency for International Development (USAID), the event covered innovative methods to significantly raise wheat yield potential, including making photosynthesis more efficient, improving environmental adaptation, addressing the physical processes involved in lodging, and physiological and molecular breeding. The workshop also represented a key step in establishing an International Wheat Yield Potential Consortium that involves scientists working on all continents to strategically integrate research components in a common breeding platform, thereby speeding the delivery to farmers of new wheat genotypes.

Contents

Complementary strategies to raise wheat yield potential

CIMMYT, El Batan, Mexico
10-13 November 2009

- **8:30 Registration**

- **9:00 Opening Ceremony** (led by Tom Lumpkin)

Session 1: Imperatives for raising wheat yield potential (Chair: Sahara Moon Chapotin, USAID)
While wheat constitutes a major component of the human diet worldwide, population growth, climate change and unsustainable cropping practices threaten global food security. This session addresses issues impacting on supply and demand for wheat with emphasis on resource poor farmers in the developing world.

- **9:30 Socioeconomic factors determining the supply and demand of wheat**
  (Hans Braun, Director, Global Wheat Program, CIMMYT)

- **10:00 Climate change and global food production**
  (David Battisti, Chair of Atmospheric Sciences, University of Washington)

- **10:30 COFFEE**

- **11:00 Realizing the genetic yield potential of wheat through soil and crop management technologies based on the principles of conservation agriculture**
  (Patrick Wall, Director, Global Conservation Agriculture Program, CIMMYT)

- **11:30 New opportunities to harness photosynthesis for increasing wheat yield potential (**Stephen Long, Professor Crop Sciences, University of Illinois –by video link–)

- **12:00 Increasing wheat yield potential: new opportunities, challenges and bottlenecks**
  (Richard Richards, Program Leader, CSIRO, Plant Industry)

- **12:30 LUNCH** in the *Rincon Mexicano*

- **1:30 Food security in the developing world: imperatives for new investment**.
  (Panel discussion)
  • Hilda Buck, President, Bucks Seeds, Argentina
  • Abdolali Ghaffari Director General, DARI, Iran
  • Zhonghu He, representing Dr. Huqu Zhai, President of CAAS, China
  • A Mujeeb Kazi, NARC, Pakistan
  • Mousa Mosaad, National Wheat Coordinator, Egypt
- K.V. Prabhu, Head of Genetics Division, IARI, India

- **3:30 COFFEE**

- **4:00 Raising genetic potential of wheat: investment strategies**
  (Rollin Sears, Syngenta)

- **4:30 Monsanto's plans and prospects for wheat Improvement through breeding and biotechnology**
  (Joseph Shapiro, Monsanto)

- **5:00 CLOSE**

- **6:30 TRADITIONAL MEXICAN DINNER & LIVE *MARIMBA*** in the *Rincon Mexicano*

Session 2: Improving crop photosynthesis
(Chair, Ron Phillips)

Basic research in photosynthesis has confirmed that substantial improvements in radiation use efficiency are theoretically possible. Ideas for how to achieve this in wheat (based partially on outcomes of a recent ANU-CIMMYT-ACIAR workshop in Canberra) will be presented:

- **9:00 Systems modeling for identification of new approaches to gain higher photosynthetic energy conversion efficiency**
  (Xinguang Zhu, Chinese Academy of Sciences)

- **9:30 Improving photosynthesis at the canopy level**
  (Erik Murchie, Nottingham University)

- **10:00 Improving photosynthetic efficiency and capacity through CO_2 concentrating mechanisms**
  (Bob Furbank, CSIRO)

- 10:30 COFFEE

- **11:00 Genetic modification of Rubisco, Rubisco activase and RuBP regeneration**
  (MAJ Parry, Rothamsted Research)

- **11:30 C_4 rice: Supercharging photosynthesis to double rice yields**
  (Bob Furbank, CSIRO)

- **12:00 Discussion** led by Ron Phillips

- **12:30 LUNCH**
  in the *Rincon Mexicano*

- **1:30- 5:30 Trip to Pyramids of** *Teotihuacán*

- **1:30- 4:30 Finalization of sub-projects within research themes**
  (for WYC project writers)

- **6:30 COCKTAILS AND DINNER** at *Villas Arqueológicas*

Session 3: Optimizing adaptation, yield & lodging resistance
(Chair Tony Fischer)

To ensure that genetic gains in radiation use efficiency show impact at the agronomic level, other physiological traits must be optimized simultaneously including partitioning of assimilates to grain growth, adaptation –especially of reproductive growth– to distinct agroecosystems, and stem and root characteristics that minimize risk of canopy structural failure:

- **9:00 Optimizing developmental pattern to maximize spike fertility**
  (Gustavo Slafer, University of Llerida)

- **9:30 Optimizing harvest index through increasing partitioning to spike growth `and maximizing grain number**
  (John Foulkes, University of Nottingham)

- **10:00 Manipulating stress signaling to enhance grain production**
  (Bill Davies, Lancaster University)

- **10:30 COFFEE**

- **11:00 Identifying traits and developing genetic sources for lodging resistance**
  (Pete Berry, ADAS, UK)

- **11:30 Modelling tradeoffs and synergies between yield-determining traits of wheat**
  (Roger Sylvester-Bradley, ADAS, UK)

- **12:00 Discussion**
  led by Tony Fischer

- **12:30 LUNCH**
  in the *Rincon Mexicano*

- **1:30- 5:30 Tour of local archeological/historic sites**

- **1:30- 5:30 Finalization of sub-projects within research themes**
  (for WYC project writers)

- **7:00 CONFERENCE DINNER AND *BALLET FOLKLORICO*,**
  Guest House Gardens

Friday 13 November

Session 4: Combining complementary traits through breeding
(Chair: Calvin Qualset)

Genetic solutions must be developed to incorporate novel yield potential traits into a new generation of breeding lines that also encompass stock-in-trade agronomic traits.

- **9:00 Exploration of wheat genetic diversity**
  (Tom Payne, Head of Gene Bank, CIMMYT)

- **9:30 Broadening the genetic base of wheat to increase yield potential through wide crossing**
  (Ian King, Aberystwyth University)

- **10:00 Robust strategies for the identification and targeted deployment of genes controlling wheat yield**
  (Diane Mather and Simon Griffiths, ACPFG, Australia & John Innes Centre, UK)

- **10:30 COFFEE**

- **11:00 Genomics selection and prediction**
  (Jose Crossa, CIMMYT)

- **11:20 Trait based breeding to accumulate yield potential traits and their alleles**
  (Matthew Reynolds, CIMMYT & Tony Condon, CSIRO)

- **11:40 Modelling strategies in the application of QTL and trait information in breeding programs**
  (Scott Chapman, CSIRO and David Bonnett, CIMMYT)

- **12:00 Integration into a practical breeding platform**
  (Bill Angus, Nickerson, UK Ltd)

- **12:30 LUNCH**
  in *Rincon Mexicano*

- **2:00 Discussions and wrap-up**

- **4:00 Closing Ceremony**

Socioeconomic factors determining the supply and demand of wheat

H.-J Braun, J. Dixon, and P. Kosina
CIMMYT

For nearly half a century, the international wheat breeding system has delivered improved high yielding varieties of wheat that created (along with rice) the Green Revolution and underpinned strong growth in wheat productivity in irrigated and rainfed, developed and underdeveloped, regions. Future priorities for breeding and complementary sciences will still include yield but will also diversify in response to changing market demands and growing environments, particularly in developing countries. It is argued that in the coming decades research on wheat quality characteristics will become increasingly important to plant breeders, whose work will be supported by the development of markers and advanced tools from molecular biology. Breeders will have to contend with increased heat stress and variability stemming from climate change, which is expected to create regional winners, as the northern high latitudes grow warmer and moister, and losers, as the sub-tropics and tropics increasingly suffer from heat stress and drought. Yield response of improved varieties in farmers' fields depends to a very great degree on sustainable systems management, which also is essential to reverse the ongoing degradation of agricultural resources. Finally, the importance of expanding the systems lens from farmers to policy makers, and of linking farmers, commerce, science, and policy is illustrated for the rice-wheat farming systems of South Asia.

Climate change and global food production

D.S. Battisti
University of Washington

Virtually all places on the planet have experienced a warming trend in the past 100 years that has been attributed, in large part, to increasing greenhouse gases (GHG) due to human activity. The 2007 report of the Intergovernmental Panel on Climate Change (2007) concluded the foremost cause of the warming trend is the increase in atmospheric GHGs, primarily the increase in CO_2 due to burning of fossil fuels and to a lesser extent land use and cement production. Other important GHGs that have increased over the 20th Century due to human activity include methane and nitrous oxide, mainly due to agriculture (rice production, changing wetlands and fertilizer use).

Using middle-of-the-road (less than business-as-usual) scenarios for GHG emissions for the next 100 years, climate models project a warming of the planet over the next 100 years that will greatly exceed that of the 20th Century. Some of the expected climate changes are both certain and large. These include less precipitation and reduced soil moisture throughout most of the subtropics and mid-latitudes, longer dry periods, and a reduction in the frequency of rainfall, but more intense rainfall when it happens. Seasonal average (growing season) temperatures throughout most of the tropics and mid-latitudes will be out-of-bounds compared to the historical record. The certain projected climate changes will greatly impact global food production through a myriad of effects that, without adaptation, will essentially erase the gains in yield made over the course of the Green Revolution.

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Realizing the genetic yield potential of wheat through soil and crop management technologies based on the principles of conservation agriculture

P.C. Wall, K.D. Sayre, B. Govaerts, and N. Verhulst
CIMMYT

Potential yield, when crop yield is limited only by temperature and/or radiation, requires crop and soil management techniques that ensure nutrients, water, oxygen (in the soil), pests and diseases do not limit crop production, and that the soil supports the standing crop. However, while true yield potential is largely of academic interest, the "economic potential yield" is of far more general interest – how close can the farmer get to the potential yield while still making a profit?

The availability of nutrients and water in the root zone depends just as much on soil structure, and the factors that affect soil structure, as it does on the overall supply of nutrients. Soil conditions that restrict root exploration restrict the entry of water into the soil (or the drainage of excess water) and the diffusion of oxygen into the soil from the atmosphere can prejudice crop growth and yield and therefore the attainment of optimum or potential yields. Soil organic matter provides the cohesive material that enables the formation of the stable soil aggregates necessary for a well structured soil, as well as loosely binding nutrients in a form more available to the plant than inorganic salts. Poor soil structure, resulting from depleted soil organic matter levels and intensive tillage, which breaks down soil aggregates mechanically, leads to many of the factors that limit crop yield: surface sealing and crusting (impede water infiltration, gaseous diffusion and seedling emergence); low soil porosity and discontinuous pore spaces (impede water infiltration and drainage, gaseous diffusion and root exploration); and compacted layers (limit root exploration and cause suspended water tables and soil saturation). Tillage also increases soil erosion losses and reduces biological activity (rapid decomposition of incorporated organic matter leads to "feast or famine" for soil organisms).

Conservation agriculture (CA) systems (based on the three principles of minimum soil disturbance, surface cover with crop residues and/or growing crops, and crop rotation) remove from productive conventional systems the factors that lead to soil degradation and yield decline. Not only do CA systems offer the possibility of sustainable production systems for field crops, they also offer greater productivity (of land, labour and capital), reduced risk, and lower risk of crop losses when stresses threaten crop productivity. Of course, CA practices, as do conventional practices, need to be accompanied by sound crop management practices, including adequate control of weeds, pests and diseases, and the supply of sufficient nutrients.

The crop residue cover component of CA also has a major effect on the evaporation of water from the soil surface. Under dryland conditions, evaporation accounts for a large part of the total evapotranspiration, and so reducing the evaporation component can markedly increase the total rainfall use efficiency under moisture limited conditions, helping the crop attain closer to its potential yield.

In summary, CA is important as it is the only system we have today for the extensive production of field crops that conserves or improves soil structure and increases soil organic matter content. These two factors are important indicators of biophysical sustainability. CA also reduces the levels of inputs required and increases the efficiency of use of applied inputs, thus tending to at least improve economic sustainability.

Raising genetic potential of wheat: Investment strategies

R.G. Sears
AgriPro

Historically, wheat improvement has been primarily a public sector activity, but to fight and win the war against hunger the private sector must become increasingly more involved. Doubling wheat yields in 40 years will require everything to go right, hard and dedicated work by many and luck, and "the harder you work the luckier you get". So what does good look like? First we need science based regulation. Wheat has been greatly affected by political based regulation which has greatly increased risk and diminished investment. Secondly, we need improved private–public partnerships, which will require a greater understanding of each institution's strengths and weaknesses, as well as a greater appreciation of established and developing markets. Thirdly, we'll need a much stronger appreciation of intellectual property, because greater investment will demand a balance between risk and reward. Fourthly, we will need to employ a full tool kit that involves seed health, crop protection, seeds and biotechnology and within these disciplines innovate at the interfaces. Fifthly, we will need to generate products that create sustainability and value to farmers, both are critical. Last, but not least, we'll need to establish confidence. Confident investment by the private sector will help bring improved agricultural technologies to the global market.

Monsanto's plans and prospects for wheat improvement through breeding and biotechnology

Y. Shapiro
Monsanto

Wheat is an important large-acre crop which is grown on more acres globally than any other and provides a major share of the nutritional requirements for the growing world population. However, improvement of yield, nutritive value, end-use quality and stress tolerance has been disadvantaged by under-investment in technology, relative to other major crops. Over the past several years, stakeholders in the wheat and agricultural development communities have increased their awareness, and advocacy, of the need for enhanced technology investment in wheat to fulfill future grain demand. Working in other crops, Monsanto has developed technical capabilities and intellectual property that can help to address the productivity challenges wheat farmers confront.

We see an opportunity to enhance the profitability and sustainability of wheat production by helping farmers to protect their crops and improve their yields while reducing inputs. Our recent acquisition of WestBred provides a platform on which we can apply our breeding advances to United States wheat in the near-term and establish a commercial presence, while we develop biotechnology traits. We recognize the critical role that public sector R&D has played in the enhancement of wheat to date, so as we define our direction and establish our presence, we are also seeking to develop collaborations with public sector breeding programs for mutual benefit and the advancement of wheat growers.

Systems modeling for identification of new approaches to gain higher photosynthetic energy conversion efficiency

X-G. Zhu
Chinese Academy of Sciences

Natural selection selects for survival and fecundity and does not necessarily select for maximal photosynthetic productivity. As a result, the current photosynthetic apparatus might not have the optimal photosynthetic energy conversion efficiency ($Є_c$). Though light energy is captured by photosynthesis; photosynthesis is influenced by a number of other regulatory, metabolic, and physiological processes, all these together control the actual $Є_c$. Over the past few years, we have identified a few approaches such that $Є_c$ can be substantially improved. In the presentation, I will summarize the current progress of identifying new approaches to engineer for higher $Є_c$. To further facilitate systematic identification of new approaches to engineer for higher $Є_c$, an integrated model of plant primary metabolism, which describes photosynthesis, respiration, nitrogen assimilation and water uptake processes, is required. During the presentation, I will introduce a general procedure to combine an evolutionary algorithm with systems models to systematically identify new approaches to engineer for higher $Є_c$.

Improving photosynthesis at the canopy level

E. Murchie
University of Nottingham

It is recognised that a rise in both leaf and canopy photosynthesis will be a prerequisite for future biomass increases in many crops, including wheat. Canopy photosynthesis may already have played an important role during crop evolution, increasing in parallel with features such as morphology, leaf area index and nitrogen application. The role of photosynthesis per unit leaf area (whether light-saturated or not) in the improvement of canopy photosynthesis has been more complex and the reasons are explored in detail in recent reviews (Long *et al.,* 2006; Murchie *et al.,* 2009). Until now breeding has been undertaken with the tacit assumption that canopy photosynthesis is optimised. However, a number of lines of study indicate that it is not and we cannot assume that improvements in other areas will 'release' any residual capacity for canopy photosynthesis.

Obviously any gains from an increase in single-leaf photosynthesis must be integrated to give rise to enhanced canopy photosynthesis. However, it has also become clear that leaf photosynthetic responses and canopy structure are inter-dependent: as explained here, the dynamic responses of the primary processes of light collection, electron transport and carbon assimilation within the crop canopy depend on the behaviour of the canopy as a whole. Previous studies of rice canopies indicate that photosynthetic rates of individual leaves fall significantly below capacity, almost certainly as a result of dynamic down regulation at various levels (Horton and Murchie, 2000). These represent a significant and un-tapped source of extra photosynthate. Thus, our working hypothesis is that photosynthesis is not optimised for agriculture and maximum crop yield under all climatic and environmental conditions. Our increasing understanding of the mechanisms, both molecular and physiological, of integrated leaf and canopy photosynthesis can enable us to exploit areas of 'lost' photosynthesis.

Final output at the canopy level requires the integration of an extremely large number of processes that balance often-conflicting constraints: for example transpiration and canopy temperature can be critical. Close attention to process modelling is always required. Here we take a focussed approach and consider mechanisms for improving the rate of closed canopy photosynthesis at a given developmental state:

- Canopy-level photosynthesis results from the combined assimilation rates of leaves or leaf-parts operating at differing levels of irradiance (and often temperature, humidity and development/acclimation state). As the top portion of the canopy is most likely to be light-saturated, many lower leaves are light-limited and these constitute a significant proportion of canopy leaf area. This results in a more linear relationship between canopy photosynthesis and light level. It is critical that this linearity is maintained and thus canopy light saturation is minimised. This can be achieved by increasing leaf erectness to improve light penetration and increase photosynthetic rate in lower regions. Wheat canopies are often an erectophile type; however, modelling suggests there could be scope for further improvement (Long *et al.,* 2006).

- There are a number of other aspects of photosynthetic physiology which need to be integrated with canopy architecture: for example leaves lower in the canopy should acclimate efficiently such that they have low respiration rates and low light compensation points but equally possess a high enough A_{max} and Rubisco content to exploit light transients. This is to be maintained in balance with the role of leaves as N stores, and the importance of re-allocation towards new growth and grain filling is a critical component of the canopy structure.

- Changes in solar elevation and leaf movement result in increasingly large short-term changes in irradiance within the canopy. It is imperative that photosynthesis exploits these as a resource in parts of the canopy that are usually not light-saturated. Increases in irradiance induce chloroplast photoprotective processes; here we will call it non-photochemical quenching (NPQ). These serve to regulate the redox state of the electron transport chain and to protect photosynthesis from damage, acting as a safety valve that gets rid of excess absorbed light energy. It also reduces quantum yield of CO_2 assimilation. Although field studies are incomplete, as much as 80% of absorbed radiation may be wastefully dissipated through this channel. The question is whether regulatory processes such as NPQ are optimised in crop canopies: there is evidence that they may represent a conservative over-protection response in many plants. For example, theoretical work calculates that the 'lag' in recovering from NPQ results in a 6.5–17% reduction in daily canopy carbon uptake at 30ºC rising to maximum of 32% at 10ºC (Zhu *et al.*, 2004). We have analysed a number of genes which alter the capacity and the kinetics for NPQ and have manipulated them in a suitable model species which is fast growing and forms a full three-dimensional canopy; rice. This is a sensible approach which allows the effect of these processes on canopy photosynthesis and growth to be isolated and quantified and should be extended to other crop species such as wheat.

Preliminary results show improved carbon assimilation during light transients at the leaf level, for example in rice in which the level of a critical molecular component of NPQ (the PsbS protein) has been reduced. These processes are found in all plant species and we fully expect this to be applicable to wheat. It is particularly relevant in that as canopy architecture improvements permit greater penetration of light, these short term responses will become more and more valuable.

The strategy for improvement at the crop level is not straightforward because it is expected to require identification and elimination of trade-off processes. In particular, there is a greater requirement for photoprotection during periods of abiotic stress. However, the possible benefits are large and this principle also extends beyond NPQ to a number of cellular events including Calvin cycle activation and partitioning of other photochemical processes.

Introducing these improvements to primary carbon assimilation in future wheat crops will require a combined effort in different disciplines including transgenic technology, systems modelling, physiology and efficient linkage with agronomists and breeders.

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Improving photosynthetic efficiency and capacity through CO_2 concentrating mechanisms

R.T. Furbank[1], S. von Caemmerer[2], M.R. Badger[2], and D. Price[2]
[1]CSIRO and [2]Australian National University

Under current and future atmospheric CO_2 concentrations, photosynthetic rate at non-limiting light intensities is primarily controlled by the amount and kinetic properties of Rubisco, the primary enzyme of CO_2 fixation in C_3 photosynthesis. The efficiency with which CO_2 is assimilated by C_3 crop plants is severely compromised by photorespiratory activity. In C_3 plants in air, almost one third of the flux through Rubisco results in the incorporation of oxygen rather than CO_2. The subsequent processing and recycling of the product of this reaction, phosphoglycolate, requires both energy and the loss of CO_2 (photorespiration). Reduced photorespiration and increased photosynthetic efficiency can be achieved by concentrating CO_2 at the site of Rubisco, either using a biochemical and anatomical "pump", such as that achieved in C_4 plants, or a biophysical pump, such as that present in algae and cyanobacteria, to directly pump CO_2/bicarbonate across the cell membrane or chloroplast envelope (known as CO_2 concentrating mechanism, CCM). Photosynthetic efficiency in C_4 plants, such as maize and sorghum, is almost double that of a C_3 plant, such as wheat, and similar or greater increases in efficiency could potentially be achieved by introducing a CO_2 concentrating mechanism into wheat.

In this presentation we discuss recent advances in the molecular genetics of CCMs and C_4 photosynthesis, strategies for how such mechanisms might be used to increase yield potential in wheat and the likely benefits of such an approach.

Genetic modification of Rubisco, Rubisco activase, and RuBP regeneration

M.A.J. Parry[1], M.E. Salvucci[2], C. Raines[3], and P.J. Andralojc[1]
[1]Rothamsted Research (RRES), [2]USDA and [3]University of Essex

Whole plant photosynthetic capacity determines crop growth, development and also yield. However, comparatively few studies have shown a positive correlation between photosynthesis on a leaf area basis and yield. Consequently photosynthesis has not been widely used to select for increased yield. Many field scale CO_2 enrichment experiments have unambiguously shown that increased rates of photosynthetic carbon assimilation can lead to increased biomass, highlighting manipulation of photosynthetic rate as a route to increase yield.

The rate of CO_2 assimilation is limited either by the carboxylation of the acceptor molecule RuBP, catalysed by Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) or by the capacity to regenerate RuBP. The balance between these contributory processes is significantly affected by environmental conditions (e.g. CO_2, light, temperature and water availability).

The catalytic properties of Rubisco are not optimal for current or projected environments. Rubisco is a slow catalyst and large amounts, up to 50% of soluble leaf protein, are needed to sustain high photosynthetic rates. Rubisco is also promiscuous and catalyses a competing and wasteful reaction between RuBP and oxygen which leads to the photorespiratory loss of fixed CO_2 and to the diversion of RuBP and energy from assimilation. In C_3 plants such as wheat, this wasteful oxygenase activity is most significant when photosynthetic rates are high, when prevailing temperatures are high, or both. Some of the limitations of Rubisco could be overcome if Rubisco had a higher carboxylase activity and/or had different relative affinities for its gaseous substrates. The widely reported inter-species variation in such catalytic properties of Rubisco could be applied to crop improvement. However, there are still major technological hurdles to overcome before foreign Rubisco genes can be expressed in wheat to form catalytically competent Rubisco.

Rubisco activity is regulated in response to short term fluctuations in the environment. Such regulation may not be optimally poised for crop productivity. Rubisco produces misfire products that can act as tight binding inhibitors that decrease its activity. The removal of such inhibitors requires another protein, Rubisco activase. Despite being relatively heat stable, Rubisco activity declines at elevated temperatures because Rubisco activase is thermally labile and no longer able to remove inhibitors from Rubisco under such conditions. Thus, there is potential to protect photosynthetic activity by increasing the thermal tolerance of Rubisco activase. Alternatively, decreasing the affinity of Rubisco for oxygen or altering the active-site chemistry to minimize side-reactions would also reduce the production of misfire products, thereby improving photosynthetic performance at high temperature.

Modelling studies suggest that over expression of some Calvin cycle enzymes can increase the regeneration of RuBP and photosynthetic carbon assimilation. There is also irrefutable experimental evidence that manipulation of one Calvin cycle enzyme, SBPase, can increase plant productivity in laboratory conditions and may also enhance stress tolerance. Here we describe our approaches to genetically modify Rubisco, Rubisco activase and RuBP regeneration in wheat.

C$_4$ rice: Supercharging photosynthesis to double rice yields

R.T. Furbank[1] and P. W. Quick[2]
[1]CSIRO and [2] International Rice Research Institute (IRRI)

There is now strong evidence that yield potential in rice is becoming limited by "source" capacity, i.e. photosynthetic capacity or efficiency, and hence the ability to fill the large number of grain "sinks" produced in modern varieties. One solution to this problem is to introduce a more efficient, higher capacity photosynthetic mechanism to rice; the C$_4$ pathway. The C$_4$ pathway has independently evolved more than 40 times and requires anatomical and biochemical specialisation where a biochemical "pump", localised in the mesophyll cells, concentrates CO$_2$ in the bundle sheath cells, where Rubisco is located. A major challenge is identifying and engineering the large, complex set of genes necessary to install C$_4$ photosynthesis in rice and indeed determining the minimal set of genes and traits required for an efficient C$_4$ system to operate. Recently, an international research consortium, funded by the Bill and Melinda Gates Foundation, was established to achieve this aim. Central to this project is phenotyping large populations of rice and sorghum mutants for "C$_4$-ness" to identify C$_3$ plants which have acquired C$_4$ characteristics or "revertant" C$_4$ plants which have lost them. This paper describes a variety of approaches being used in the C$_4$ rice consortium to identify these plants and the genes responsible, based on our detailed physiological knowledge of C$_4$ photosynthesis. Strategies to assess the physiological effects of the installation of components of the C$_4$ pathway in rice are also presented and synergies with a wheat yield potential program are identified.

Optimizing developmental pattern to maximize spike fertility

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[3]CONICET (Consejo Nacional de Investigaciones Cientificas y Tecnicas), [4]Universidad de Buenos Aires and
[5]INTA-Pergamino, Argentina.

Improvements in crop performance will remain a major objective of agronomy and naturally, then, a focal aim of any breeding program. Since demand for wheat is predicted to increase at a faster rate than the annual genetic gains that are currently being realized, improvement in wheat productivity will need to be accelerated. In this context it is critical to understand better the physiological bases of wheat yield (i) to complement –increasing their efficiencies– empirical approaches commonly used in breeding, and (ii) to facilitate the use of molecular biology to improve wheat yields, as it seems to be rather naive to expect genuine contributions to complex traits (such as yield) from genetics ignoring the physiological bases of those traits (Slafer, 2003; Reynolds and Tuberosa, 2008).

Crop-physiological studies aimed at identifying the attributes that were modified when yield potential was raised, largely coincide in that increased partitioning of assimilates to reproductive organs has had the single greatest impact on improving yield potential in wheat (e.g. Calderini *et al.*, 1999) not only under high-yielding conditions (e.g. Shearman *et al.*, 2005) but also under stressful conditions such as those of Mediterranean regions (e.g. Acreche *et al.*, 2008). This reflects that ancestral wheats did conservatively use resources to produce offspring, determining that photosynthetic capacity during grain filling was clearly underutilised in terms of grain production. Even though breeding has increased yield potential almost only by increasing sink strength, there are clear indications that yield of modern wheats is still far more sink- than source-limited during grain filling (e.g. Borras *et al.*, 2004). A mirror image of this sink-limitation is that current photosynthetic capacity may not even be utilized efficiently if not matched by adequate spike fertility (Reynolds *et al.,* 2005), as photosynthesis (both at the leaf and canopy levels of organization) seems to be responsive to the strength of the sink, even in modern cultivars with high numbers of grains (e.g. Acreche and Slafer, 2009).

It is critical in this context to find out opportunities to further rise spike fertility. Although papers describing genotypic variation in the number of grains per m^2 are abundant in the literature, sources of evidence on whether the differences are associated to the processes of generation or degeneration of floret primordia are rather scarce. Differences in floret fertility have been found in comparisons between tall and semi-dwarf wheats (e.g. Miralles *et al.*, 1998), but to identify useful traits for future gains we must identify further sources of partitioning (see John Foulkes contribution to this meeting) as well as other likely sources of genetic gains in spike fertility. One of those alternatives in which we have been working is the optimization of the partitioning of developmental time between phases occurring before and after the onset of stem elongation (SE).

The SE phase has been identified by many authors as the most important phase for grain number and yield determination (Slafer *et al.*, 2009 and many references quoted therein). Since during SE, yield is strongly limited by source strength (Fischer, 1985; and many experiments conducted worldwide afterwards have proven the universality of the finding), any trait allowing more assimilates to be allocated to the growing spikes during that period would result in increases in the number of fertile florets (at anthesis) and grains (at maturity) per m^2. Lengthening the duration of the SE phase may be an alternative way to achieve this goal (Slafer, 2003; Miralles and Slafer, 2007). Manipulating the duration of SE in field plots, we found repeatedly that the number of grains per m^2 increased with increasing duration of SE (e.g. González *et al.*, 2005a), as under relatively short photoperiod the proportion of floret primordia that develops towards fertile florets is consistently increased (e.g. González *et al.*, 2005b). The physiological basis of this overall response has only started to be studied and we definitely need more detailed studies to determine to what degree the floret developmental

rates, in connection with the duration of SE, are the cause of the change in the number of fertile florets, if at all. Elucidating these sorts of physiological processes and determining the number of fertile florets and grains may also be instrumental in understanding the causes behind floret abortion in wheat (see Bill Davies contribution to this meeting).

Determining a strong relationship between the duration of SE of a particular cultivar (through manipulating photoperiod during SE) and its number of fertile florets and grains has been consistent. Identifying genetic bases for this trait has been, unfortunately, more elusive (González *et al.*, 2005c). More recently, there have been incipient approaches to attempt to detect genetic factors controlling the duration of SE both through detecting genes up- or down-regulating when SE duration is altered (Ghiglione *et al.*, 2008) or through evaluating mapping populations in barley (Borràs *et al.*, 2009). The knowledge we have on the genetic control of the SE phase is only in its infancy. In the near future, we expect to be able to further elucidate the physiological and genetic bases of spike fertility. Achieving such elucidation will permit the breeding of cultivars with better utilization of the canopy's photosynthetic capacity, and, therefore, increased biomass and yield potential.

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Optimizing harvest index through increasing partitioning to spike growth and maximizing grain number

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For improvements in photosynthesis to result in additional crop yield, extra photo-assimilates must be partitioned to developing spikes and grains. The degree of partitioning of assimilates to yield – i.e. harvest index (HI) – is genetically complex. Although the introduction of dwarfing genes had a major impact on HI, yield improvement in the post Green Revolution period was also attributable to increased HI, the genetic basis of which is not established. To design a new generation of physiologically improved genotypes that are also maximised for HI, it will be necessary to determine its genetic and physiological components. Increased partitioning to grain yield could theoretically be increased by reducing competition from alternative sinks, especially during stem elongation when grain number is determined. These competing sinks include roots, leaves, stems and infertile shoots. The literature reports considerable genetic range for partitioning at anthesis, for spikes (0.12–0.27), leaf lamina (0.19–0.30), stems and leaf sheath (0.48–0.63) as a proportion of above-ground biomass; as well as for roots (0.10–0.15) as a proportion of total biomass (Reynolds *et al.*, 2009).

These data suggest the possibility for increasing partitioning to spikes at the expense of other plant organs. Although reducing partitioning to roots or leaves may result in suboptimal resource capture, reduced partitioning to the stem and infertile shoots, on the other hand, may not have negative effects. Fine-tuning stem partitioning by further optimizing plant height may be one strategy to increase spike growth, for example, by reducing peduncle length whilst maintaining the height of the leaf canopy. More recent work suggests that trade-offs between tiller number associated with the *tin1A* gene (Spielmeyer and Richards, 2004) and spike size and architecture may be important targets in designing new ideotypes with

improved HI; significant genetic variation has been established for the latter (Gaju *et al.*, 2009; Table 1) and molecular markers are in development (Ribas-Vargas *et al.*, 2008).

Optimizing the balance between structural and stem water soluble carbohydrate (WSC) will also need to be addressed in terms of maximizing grain number in general, without sacrificing grain size in specific contexts where assimilate availability during grain filling may be limited by high temperature or light (Beed *et al.*, 2007). However, since spike growth occurs during the same developmental stage as root, leaf and stem growth, genetic solutions must be identified which optimize trade-offs between competing processes. Different models will have to be tested both theoretically and empirically so that improvement in one trait is not at the expense of the other.

Table 1. Performance of large-spike phenotypes (LSP), LSP1 and LSP2*, as a percentage of Bacanora (=100) in growth room and field experiments for spike fertility and related traits (after Gaju *et al.*, 2009).

	Growth-room (GR) experiment 2005		Field experiments at Ciudad Obregon, mean 2004-06		Probability G × E (= GR vs field) int'n
	LSP1	LSP2	LSP1	LSP2	
No. spikes/plant	118.8	68.7	89.0	74.4	***
Rachis length	114.4	136.6	128.1	112.1	***
Spikelets/spike	114.5	131.2	104.9	103.8	***
Grains per spike	107.7	119.7	104.1	104.0	†
Grain weight	107.9	119.2	111.9	119.0	ns

*** Significant at 0.001 probability level; ns = not significant; † = significant at the 0.10 probability level.

* LSP1 and LSP2 for CMH80A.763 (non *tin1A*) and CMH79A.955/4/ AGA/3/4*SN64/ CNO67//INIA66/5/NAC (*tin1A*), respectively.

A high priority will be to identify genetic sources expressing favourable values of HI and related traits (grain number, partitioning to developing spikes, etc.) through screening genetically diverse germplasm to determine natural thresholds of variation under different agronomic environments. Simple quantitative frameworks can be applied (e.g. Eqn 1) relating partitioning traits to grain number to test for synergies and trade-offs with duration of stem elongation (linking with SP2.2 led by Gustavo Slafer), crop growth rate and the grains/spike DM ratio.

$$GN = SEP \times CGR \times SI \times GSR \qquad \text{(Eqn 1)}$$

GN = grains m^{-2}; SEP = duration of stem elongation phase (d); CGR = crop growth rate (g m^{-2} d^{-1}); SI = DM partitioning to the spike; GSR = grains to spike DM (at anthesis) ratio (grains g^{-1}).

The genetic basis of these traits will need to be established for easier deployment in breeding and to better understand the degree to which apparent trade-offs are genetically independent. In this respect it will be important to assemble a population of diverse but agronomically acceptable materials for association mapping to gain a better understanding of the range of potential loci and alleles that influence these traits and as well as their interactions with environment and in terms of epistasis. Further understanding of these complex processes can be gained by studying the effects of major genes that have been already deployed in breeding (*Rht, Ppd, Vrn*) as well as alien introgressions (7Ag/7DL, 1B/1R etc) all of which have well documented effects on yield potential. For example, isoline pairs can be used to quantify some of the trade-offs, while their widespread occurrence in conventional gene pools – coupled with availability of perfect markers – will also permit their interactions to be quantified experimentally.

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Manipulating stress signalling to enhance grain production

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Seed number is a major yield component of grain yield, mainly determined at anthesis and slightly after it. In most species, the number of ovules largely exceeds the number of seeds. Water deficit generally reduces still further the ratio seed/ovule via abortion. This is an adaptive mechanism which allows seeds to be appropriately filled in spite of reduced photosynthate supply. The effect of this on grain yield can be positive or negative, depending on circumstances. In maize, abortion is generally considered a negative trait and breeders attempt to reduce it. In wheat, however, abortion is considered a positive trait which improves seed quality in a severely stressful environment and breeders have attempted to increase it.

Carbon availability and carbon transfer are essential for early seed growth and abortion. Boyer and co-workers have used sucrose feeding and simple metabolic experiments to demonstrate the importance of C supply (e.g. Zinselmeier *et al*., 1995; McLauglin and Boyer, 2007). Grain abortion is probably linked to a disruption of the distribution of sugars in the plant. Other processes, such as delayed silk growth (anthesis-silking interval; ASI) in maize, can also greatly increase abortion and seed number, and have been improved genetically in recent years (Duvick, 2005).

In maize, a body of evidence has mounted that accumulation of the plant hormone abiscisc acid (ABA) results in grain abortion (reviewed in Wang *et al*., 2002). The mechanism of this response has not been fully elucidated; it is uncertain whether ovary abortion is a direct hormonal response, or whether increased ABA concentrations throughout the plant inhibit photosynthesis (due to stomatal closure), and decreased photosynthate flux to the developing organs triggers ovary abortion.

In rice, the situation is apparently different. Spikelet sterility was significantly reduced when exogenous ABA was applied to the panicles of water-stressed plants at the early meiosis stage (Yang *et al*., 2007). It was suggested that this additional ABA down-regulated production of the plant hormone ethylene (which is generally regarded as a growth inhibitor) and its precursor 1-aminocyclopropane-1-carboxylic acid (ACC), and that this hormonal interaction may mediate spikelet fertility under water stress. Consequently, a higher ratio of ABA to ethylene in developing grains may be a selectable trait of rice adaptation to water stress (Yang *et al*., 2007).

There is little information on changes in hormone content of developing wheat grains in response to water stress, thus whether grain ABA accumulation in wheat is a desirable trait (as in rice) or undesirable trait (as in maize) requires further investigation. However, that excessive ethylene production results in wheat grain abortion under high temperature stress (Hays *et al*., 2007) suggests that wheat may belong in the former category.

Ethylene accumulates in plants in response to a range of stresses and recent reports suggest deleterious effects on the plant's capacity to control water status via effects on roots and on stomatal behaviour and accelerated senescence (Wilkinson and Davies, 2009).

As well as a focus on hormone balance as a trait in plant improvement programmes, there is scope to manipulate these variables with considerable success using management techniques based on novel understandings in plant science (Belimov *et al*., 2009; Zhang and Yang, 2004).

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Identifying traits and developing genetic sources for lodging resistance

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Lodging is a persistent phenomenon in wheat which reduces yield by up to 80% as well as reducing grain quality. Therefore, any comprehensive strategy to improve wheat yield potential should include lodging resistance. A validated model of the lodging process has identified the characters that determine the stem and root lodging risk of wheat (Berry *et al.*, 2003a). The risk of stem and root lodging is calculated in terms of the wind speeds required to cause failure of the stem base and the anchorage system. Stem lodging is predicted when the wind-induced leverage of a single shoot exceeds the strength of the stem base. Root lodging is predicted when the wind-induced leverage of all shoots belonging to a single plant exceed the anchorage strength. The wind-induced leverage of a shoot is calculated from its height at centre of gravity, the rate at which the shoot sways (natural frequency), the area of the ear and the wind speed. In turn, these plant characters can be calculated from the height to the ear tip, grain yield per unit area and shoot number per unit area (Berry *et al.*, 2004). The strength of the stem is calculated from the diameter, wall width and material strength of the stem wall. Root anchorage strength is calculated from the spread and depth of the root plate and the strength of the surrounding soil.

The lodging model described above has been used with preliminary datasets describing the dry matter costs of improving lodging traits to estimate the dimensions of a wheat plant to make it lodging-proof for the least investment of biomass in the supporting stem and root system (Berry *et al.*, 2007). The characteristics required to give a 8 t ha^{-1} yielding crop, with 500 shoots m^{-2} and 200 plants m^{-2}, a lodging return period of 25 years in a UK environment, include a height of 0.7 m, a root plate spread of 57 mm and for the bottom internode, a wall width of 0.65 mm, a stem diameter of 4.94 mm and a material strength of 30 Mpa (Fig. 1). Observations of a wide range

of varieties grown in the UK showed that the root plate of the best variety was 7 mm less than the ideotype target, the stem character targets were achieved but not all in one variety, and the height target was achievable with the use of plant growth regulators.

It is estimated that this lodging-proof ideotype will require 7.9 t ha^{-1} of stem biomass and 1.0 t ha^{-1} of root biomass within the top 10 cm soil, which will give an above-ground harvest index of 0.42. The development of the root and stem characters associated with lodging continues until anthesis and may therefore compete for resources with the development of grain number and the production of soluble stem reserves. The extent to which structural requirements compete with grain yield must be investigated to quantify possible trade-offs, e.g. it may be necessary to accept a lodging return period more frequent than 1 year in 25 to maximize grain yield. One
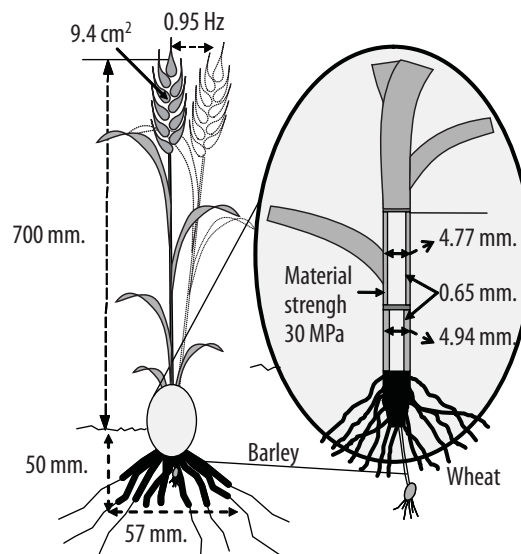

Figure 1. Dimensions of a lodging-proof wheat plant for the UK environment.

of the key assumptions within the lodging-proof ideotype analysis of Berry *et al*. (2007) was that the minimum height compatible with high yields is 0.7 m. Many empirical observations support this (e.g. Richards, 1992). Crop height has a major impact on the structural dry matter requirements for lodging resistance with each additional centimetre in height increasing the stem dry matter required by 0.23 t ha^{-1} (Berry *et al*., 2007). Further work must investigate why there appears to be a minimum height for high yield, whether this barrier can be overcome and whether the minimum height varies between environments. Preliminary work has indicated that dry matter density is positively related to the material strength of the stem wall which means there is a significant dry matter cost associated with increasing this strength parameter. Investigations are required to verify the dry matter cost of increasing material strength in a range of environments.

To increase lodging resistance, plant breeders must increase the spread of the root plate, stem thickness and the material strength of the stem wall, whilst minimising the width of the stem wall. The exact values of the traits will depend on further investigations to assess and validate the minimum crop height, the dry matter costs associated with the lodging traits and the possible trade-offs with yield formation. It is likely that some of the lodging traits, e.g. the spread of the root plate, will not be found within elite germplasm and wide crosses with novel germplasm will be required to achieve them. Broad sense heritabilities of the lodging traits have been estimated from Berry *et al*. (2003b) to range

from 0.68 for the spread of the root plate to 0.90 for stem diameter. A recent analysis of bi-parental mapping populations has identified more than one quantitative trait locus for each of the traits and indicated that they are controlled by several genes. Further work will be required to better understand the genetic control of the traits and to investigate whether reliable genetic markers can be identified which work across a range of genotypes and environments. Phenotypic screens must also be investigated to assess whether they can offer an alternative method for selecting germplasm in case genetic markers with a large effect prove difficult to identify.

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Modelling tradeoffs and synergies between yield-determining traits of wheat

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This paper uses a modelling approach to identify for discussion feasible synergies and tradeoffs in yield determination, focussing particularly on wheat physiology pre-anthesis. Conventional wheat models seek to simulate development, growth and yield of a particular cultivar in a particular environment. A new prototype Crop Design Tool (CDT) inverts this approach (Sylvester-Bradley and Riffkin, 2008) so that an optimum phenotype, or ideotype, can be estimated for any particular environment, the initial case being the High Rainfall Zone (HRZ) of Southern Australia. Thus, heritable trait values are only constrained by observations across the species as a whole. The logic underlying the CDT is that (i) due to abiotic constraints, each environment dictates an optimum life-span for wheat, (ii) depending on inherent photosynthetic efficiency, a maximum amount of DM can be formed in that life-span, (iii) a maximum of this DM should be partitioned to harvestable grain, but (iv) DM must be allocated for 'support' by roots (for anchorage, and capture of water and nutrients), leaves (for photosynthesis), chaff (to hold the grain), and stems (to maintain stature), and (v) for partitioning, the CDT assumes that, through future breeding, full inter-changeability will be achievable between DM allocated to root, leaf, stem and chaff during crop construction (between the start of stem extension and anthesis). From initial use of the CDT, indications of tradeoffs and synergies are as follows:

Phenology: The crucial yield-determining role of the construction phase (Sylvester-Bradley *et al.,* 2008) is evident and synergies are predicted from prolonging this phase at the expense of the foundation phase (Slafer *et al.,* 2005). Longer construction should allow increased DM allocation to the ear to increase floret survival. Additionally, in some environments, surplus DM to that required for support (as discussed below) may be allocated (e.g. as fructan) for subsequent redistribution to grain (Beed *et al.,* 2007).

Roots: In addressing DM partitioning to roots, surface roots should be the initial focus because these determine plant anchorage and their DM requirements are likely to have synergies with phosphorus capture.

Leaf: Leaf area is mainly governed by nitrogen supply (Lemaire, 2007), so the optimum leaf canopy (Sylvester-Bradley *et al.,* 1997), hence leaf DM requirement, is an economic trait based on the N:grain price ratio, the marginal return in grain from increased canopy, and empirical data on specific leaf weight (g DM m^{-2} leaf) (Stapper and Fischer, 1990). Direct measures of optimum 'leaf' DM appear small (2–3 t ha^{-1} in the UK, Sylvester-Bradley and Riffkin, 2008) compared to 'stem' DM (6–7 t ha^{-1}). However, leaves are usually measured as lamina only whilst leaf sheaths are included with stems. Recent data (Pask, 2009) show sheath biomass as similar to lamina biomass (Fig. 1), hence it will be important to determine the function of sheaths; if they have no clear structural or light intercepting role, it is possible that sheath DM could be reduced (perhaps by shortening), thus, increasing DM available for more vital organs.
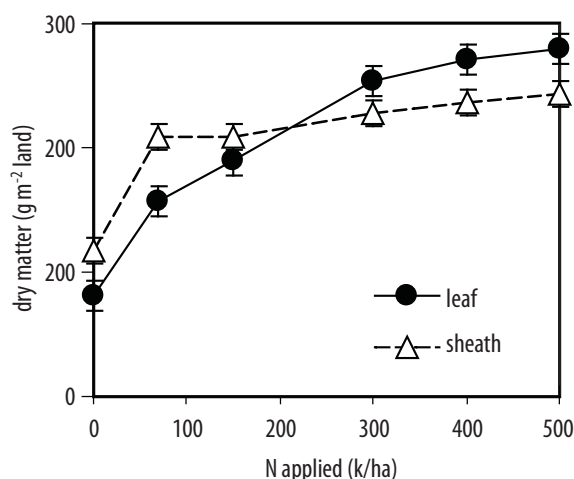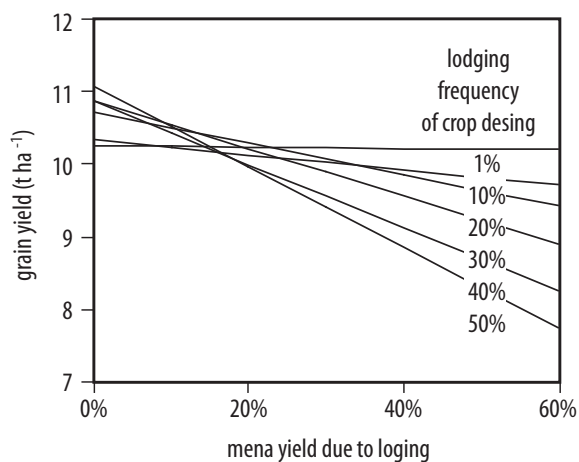

Figure 1. Effect of applied N on components of leaf DM. (Data from Pask, 2009).

Stem: The CDT measures stem DM required for lodging resistance, based on the model of Berry *et al.* (2003, 2004). Height is crucial in setting stem DM requirements, so it will be important to examine what minimum height (700 mm) is needed to maximise grain yield (Richards, 1992; Flintham *et al.,* 1997). Possibly stem length sets the capacity for storage of fructan which ultimately transfers to the grain (Beed *et al.*, 2007). Ultimately stem DM costs must be balanced against grain DM costs of lodging itself (Stapper and Fischer, 1990); it is possible that high lodging resistance will not be worthwhile in some conditions (Fig. 2).

Inflorescence: Empirical observations show (the reciprocal of) ear index for high yielding crops to vary from about 9 (Fischer, 1985) to 12 (Gaju *et al.,* 2009) mg chaff grain[-1]. Much of this variation remains unexplained but it clearly indicates significant promise for improvement of ear fertility.

In conclusion: Initial design work with wheat shows that, because support DM must first support itself, optimum harvest indices increase with total DM, thus increased photosynthetic efficiency could cause disproportionate increases in grain DM. But to achieve this, some key design questions must be addressed: By how much can crop construction be prolonged at the expense of the foundation phase? What are leaf sheaths for? How far can height be reduced compatible with high yields? What is the lower limit to chaff DM grain[-1]? Why do stem DM requirements appear large? Answers to some of these questions should help to identify and prioritise opportunities for synergies in wheat yield improvement.

Figure 2. Mean grain yield of crop designs for Hamilton, Victoria with a set lodging frequency, after lodging losses. (Data from Pask, 2009).

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Exploration of wheat genetic diversity

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Due to the strategic importance of wheat in food security and trade in many countries, and the critical importance of breeding in ensuring national industries remain competitive, over 80 autonomous germplasm collections holding in excess of an estimated 800,000 accessions have been established globally. These collections vary in size; the largest have over 100,000 accessions and the smallest a few hundred. They also vary greatly in coverage. Most collections evolved from breeders' working collections and carry predominantly local or regional cultivars – advanced, obsolete or landrace– as well as introduced cultivars of interest to national or regional breeders. Genetic resources suited for finding genes that will contribute to yield potential increases in wheat will first focus on the primary pool that consists of the biological species (*Triticum* spp., × *Triticosecale* spp., *Secale* spp. etc.) including cultivated, wild and weedy forms of the crop. Gene transfer in this group is considered to be easy. In the secondary gene pool there are species from which gene transfer is possible but difficult, while the tertiary gene pool is composed of species from which gene transfer is possible only with great difficulty. Selection within collections for appropriate germplasm sources is aided through approaches that use geo-referenced passport data (e.g. Focused Identification of Germplasm Systems, FIGS), advanced stochastic local search algorithms (e.g. Core Hunter) and through serendipitous random selections.

Broadening the genetic base of wheat to increase yield potential through wide crossing

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The most effective strategy by which world food security issues can be addressed at a time of climate change, coupled with the requirement for the development of environmentally friendly agricultural practises, is through the genetic improvement of crop species. This firstly involves the identification of germplasm from primary, secondary and tertiary genepools carrying beneficial phenotypic variation for target traits followed by the determination of the underlying genetic control of the trait, i.e. how many genes control the trait and their genomic location? Once the genes have been identified they can then be transferred into elite lines of crops via normal sexual hybridisation, or other means. However, the transfer of genetic variation to crop species and the identification and isolation of the genes responsible via forward genetic approaches, i.e. genetic mapping, chromosome landing, etc. requires the presence of sufficient phenotypic variation for the trait in question, e.g. yield, disease resistance, drought tolerance. In inbreeding species such as wheat, very little genetic variation exists in cultivated genotypes.

However, wild hexaploid wheat landraces and wild and distant relatives (alien species) (e.g. rye, *Thinopyrum bessarabicum*) provide a key source of variation for target traits. Wild and cultivated relatives of wheat, i.e. alien species, provide a vast and largely untapped reservoir of genetic variation for target traits. The process for the transfer of target genes from alien species into wheat requires 1) hybridisation of wheat with an alien species, 2) induction of recombination between the chromosomes of wheat and those of the alien species via suppression of the pairing control gene Ph1, and 3) production and identification of wheat progeny, that contain a small alien chromosome segment carrying the target alien gene but lacking deleterious genes.

In the past, there have been two major factors that have reduced the effectiveness of wheat/alien gene transfer. The first is that insufficient markers have been available to screen large enough populations of wheat for the presence of alien chromosome segments. However, by combining comparative mapping with next generation sequencing technology it is now possible to develop an excess of markers for any part of the genome. These markers are now being used to screen large populations for specific introgressions in monocot species. The second factor is that once an alien segment has been introgressed into wheat, although it carries the target gene, it can also carry deleterious genes resulting in a reduction in yield and/or fitness. Unfortunately, it is also very difficult to reduce the chromosome segment further, even by additional suppression of pairing control genes.

An alternative approach to reduce the size of a chromosome segment involves the inter-crossing of two lines with different but overlapping alien chromosome segments that carry the same target gene. As a result of recombination between the two overlapping alien segments, in the presence of pairing control genes, some of the progeny produced will carry a reduced alien chromosome segment; the target gene but lack the deleterious genes. However, this approach described by Sears for two *Aegilops umbellulata* chromosome segments carrying a gene for stem rust resistance requires the identification of lines possessing overlapping alien chromosome segments in the first place. Thus, this strategy has rarely been followed due to the lack of markers available to identify individuals carrying overlapping alien chromosome segments. However, the combination of comparative mapping, the sequencing of the model genomes and the development of next generation sequencing technology provides a means by which the whole genome of an alien

species can be transferred to wheat in overlapping alien chromosome segments. Furthermore, through recombination, a genome wide series of small alien introgressions that carry target genes but lack deleterious genes will be generated, thus leading to a significant increase in the gene pool available to breeders for selection and variety development.

In fact, wide crossing has already been used to increase the yield potential of wheat through the introduction of whole or parts of alien genomes. Examples of the latter include the widespread occurrence of the *1B/1R* translocation from rye whose yield benefits are realized on around 40m ha of spring wheat in the developing world, or the *7Ag.7DL* translocation from *Lophopyrum elongatum* which increases yield as well as biomass and radiation use efficiency by 10% or more in optimal growing environments. Fusion of whole genomes within the Triticeae tribe to create synthetic polyploids is also a routine procedure in wheat breeding which results in improved yield and biomass in favourable as well as drought-stressed conditions. The procedure has even been used to create a totally new species, triticale, a wheat × rye hybrid, which is cultivated on 3.6m ha worldwide and has yields comparable with the best wheat cultivars, good yield stability, and often exceptional biomass. Traits that would be considered high priority for raising yield potential and which can be considered relatively easy targets –since genetic variation exists in the Triticeae– include spike fertility (*L. elongatum*), improved root capacity (rye), stem strength (triticale), drought tolerance (rye) and heat tolerant metabolism (*Triticum dicoccoides*). While the introduction of genes from outside of the Triticeae tribe is not a routine procedure in wheat breeding, the feasibility of introducing traits from C_4 species is supported by the fact chromatin from several C_4 species –including maize, sorghum, millet and wild grasses– has been introduced into wheat, and other cereals, including the construction of complete set of maize addition lines in oat. These precedents suggest that with appropriate investment, wide crossing may even be used to introduce all of the chromatin required into wheat for full expression of C_4 photosynthesis.

Robust strategies for the identification and targeted deployment of genes controlling wheat yield

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In any specific environment, the highest-yielding wheat varieties are those that are able to optimally exploit resources during vegetative development and grain filling, whilst avoiding stresses that limit grain production. Genetic advance for grain yield has been driven largely by crossing among high-yielding advanced lines that differ in their genetic constitution, followed by phenotypic selection of plants and lines with superior new gene combinations. Specific allelic variation has been deployed only for disease resistance genes, for loci that determine grain quality, and for a handful of cloned genes that contribute to mega-environmental adaptation through major effects on photoperiod response, vernalisation response and plant stature. 'Fine-tuning' of varieties for specific eco-geographic regions has relied more on phenotypic selection, to accumulate favourable alleles at quantitative trait loci (QTL) that influence micro-environmental adaptation. The production of near-isogenic lines (NILs) allows such QTL to be handled as discrete Mendelian loci, and leads to QTL cloning. Once the genes are cloned, functional analysis is possible, leading to knowledge of the mechanisms by which the genes act. Further, it becomes possible to analyse the sequence diversity of alleles, leading to the development of diagnostic ('perfect') markers.

During the first decade of the 21st century, the availability of rice genome sequence led to an upsurge of positional cloning of wheat genes. In the coming decade, this will be accelerated by increases in the production of wheat sequence data, decreases in genotyping costs and increases in genotyping throughput. Through rapid dissection of germplasm collections, new and useful genetic variation will be discovered, feeding the wheat breeding pipeline with new alleles which in turn will be cloned and characterised for maximum exploitation.

The technological advances that facilitate gene cloning also create new opportunities to apply molecular methods in wheat breeding; for individual genes, for gene combinations and networks, and for the entire genome. For individual genes, 'perfect' diagnostic markers improve the precision and predictability of plant breeding. For multiple genes, they make it possible to understand gene interactions and gene networks, to estimate the value of specific gene combinations and to design crosses and selection strategies to deliver the next 'step change' in yield potential. At the level of the entire genome, genomic selection may accelerate genetic gain through selection based on breeding values estimated from genomic profiles.

Genomics selection and prediction

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The selection of plants or animals, based on traits of economic importance, can be achieved by combining, in a selection index (SI), phenotypic values and molecular markers (MMs) scores closely linked to QTLs, or by using information from all available MMs to predict a total genetic value. This second method is a form of marker assisted selection (MAS) in which genetic markers, covering the whole genome, are used such that all QTLs are in linkage disequilibrium with at least one MM. This is termed genome wide selection (GWS) (or genomic selection). Within GWS, two selection methods can be distinguished; those that propose to incorporate MMs into the SI, as additional random variables, and use all available phenotypic and MM information, and those that propose to first estimate, from a base population (sometimes called training population), the effects of the MMs and later use them for (1) estimating the genomic breeding value of the individuals that have only been genotyped, and (2) selecting them prior to further phenotyping. This reduces the duration of the breeding cycle, increases the accuracy of selection, and speeds up genetic gains. Several authors have proposed a linear mixed trained model for estimating the Best Linear Unbiased Prediction (BLUP) of each MM and have used them in subsequent breeding cycles. Simulation results for GWS will be presented and some models for genetic value prediction will be discussed.

Trait based breeding to accumulate yield potential traits and their alleles

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Trait selection is the cornerstone of plant breeding and the process has become progressively more sophisticated with time. Plant breeding owes its success largely to deployment of simply inherited agronomic traits, disease screening, multi-location yield trials and testing for end use quality. However, the next generation of cultivars will be designed to encompass combinations of both complex and simply inherited traits based on understanding of adaptive processes and their genetic make-up. Just as agronomic traits have been selected to be complementary, such as combining yield potential with disease resistance, adaptive traits must be combined in a strategic fashion. For example, in the water-limited environments of Australia, lines have been developed that combine both early ground cover –to protect surface moisture from wasteful evaporation– with high transpiration efficiency so that water harvest is maximized (Richards *et al.*, 2002). Although the composition of traits involved in determining superior yield potential among cultivars is not well established, it has been shown that improvements in yield potential itself –yield expression in relatively optimal environments– is expressed across a wide range of environments including those affected by heat, drought, salinity and suboptimal levels of nitrogen (see Reynolds *et al.*, 2009)

Trait based breeding relies upon the ability to identify and measure traits of economic value and estimate their impact on yield across target regions. This is facilitated by development of conceptual models which are validated by hypothesis testing with different trait combinations in fixed lines, the quantification of genetic gains associated with trait expression in populations of related progeny and inferences from simulation studies that extrapolate and interpolate empirical data. Precision phenotyping is fundamental to these approaches since complex traits show a high degree of plasticity in response to environment. Once suitable conceptual models have been established,

they can be applied in the following crop improvement strategies: (i) trait-based crossing to combine complementary traits in progeny, (ii) high-throughput phenotyping to enrich for desirable alleles in segregating generations, (iii) exploration of genetic resources to broaden the genetic base for hybridization, and (iv) precision phenotyping of mapping populations to determine the genetic basis of complex traits. The last of these interventions can lead to the development of molecular markers that may either complement phenotypic selection traits, or replace them altogether with more efficient marker assisted selection (MAS) approaches (especially for difficult-to-phenotype traits) or genome wide selection. Furthermore, information generated in the processes of measuring trait expression in multi-location trials and mapping populations helps to understand the complex interactions between genes, genetic background, and environment; leading to more sophisticated conceptual models of adaptation.

Continual reselection within restricted gene pools is likely to lead to diminishing returns, so it is imperative to introduce new allelic diversity by exploiting non-conventional gene pools. For example, stress adapted landraces can be crossed freely with wheat, while closely related genomes are used in inter-specific hybridization. While it may be difficult to assess the value of a genetic resource based on the expression of agronomic traits, their physiological trait expression can be used as a basis for investing in wide crossing, assuming traits do not interact strongly with agronomic type. For example, deeper rooting under drought is a trait that has been incorporated into modern wheat from both landraces and wild relatives (Trethowan and Mujeeb-Kazi, 2008). As molecular markers for physiological traits are developed they will facilitate allele mining from genetic resource collections.

Physiological trait based breeding approaches have been used successfully by CSIRO in Australia to release drought adapted cultivars (Rees and Drysdale), and by CIMMYT leading to international distribution of a new generation of drought adapted lines (~25% of the 27th SAWSN and 17th SAWYT, respectively). In both cases, breeding research led also to the identification of quantitative trait loci (QTLs) associated with physiological traits (namely for transpiration efficiency, early vigour, canopy temperature and water soluble carbohydrate storage capacity). It is expected that a similar approach can be used to raise the yield threshold of wheat (Fig. 1) using a conceptual model for yield potential traits that will be validated and refined by the Wheat Yield Consortium (WYC). Traits and molecular makers identified by WYC members associated with improved yield potential will be introduced into elite backgrounds as needed, and combined through a series of hybridization steps that may include complex crosses and backcrossing. Crosses will include (i) *generic crosses* to bring together complementary traits with expected value across all environments, including superior photosynthetic potential, improved partitioning to yield and lodging resistance, and (ii) *regionally targeted crosses*, that will incorporate generic traits with alleles for adaptation to specific photoperiod regimes (including winter and spring wheat habitats), and adaptation to moderate levels of a range of abiotic stress factors including extremes of temperature and mild periodic water deficit. Progeny in which the full array of yield potential traits combine to express superior yield potential will be tested in international yield trials to establish robustness of its expression. The best material will then be made available to extant breeding programs to incorporate resistance to a spectrum of diseases and end use quality characteristics.

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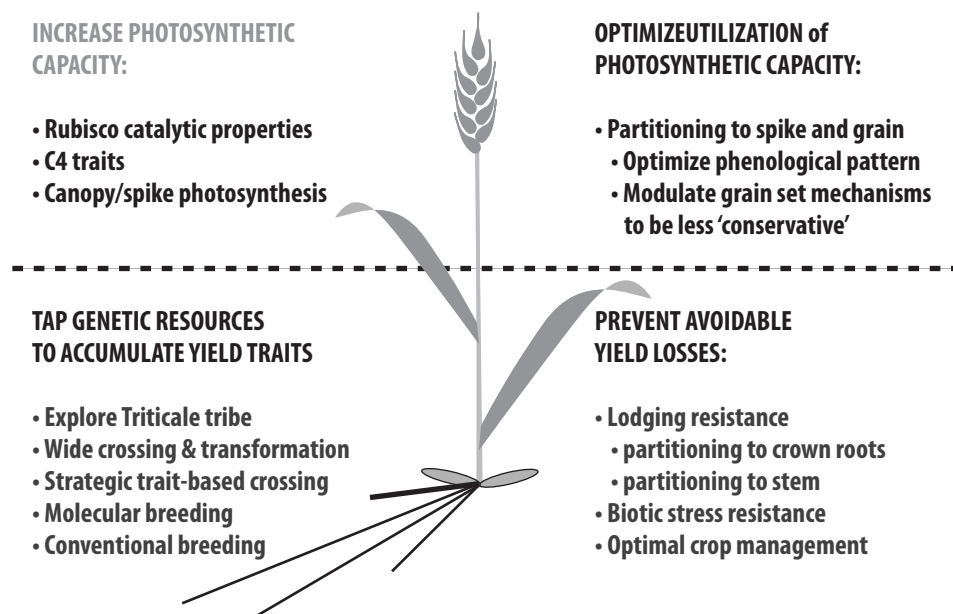
INCREASE PHOTOSYNTHETIC CAPACITY:

- **Rubisco catalytic properties**
- **C4 traits**
- **Canopy/spike photosynthesis**

OPTIMIZEUTILIZATION of PHOTOSYNTHETIC CAPACITY:

- **Partitioning to spike and grain**
  - **Optimize phenological pattern**
  - **Modulate grain set mechanisms to be less 'conservative'**

TAP GENETIC RESOURCES TO ACCUMULATE YIELD TRAITS

- **Explore Triticale tribe**
- **Wide crossing & transformation**
- **Strategic trait-based crossing**
- **Molecular breeding**
- **Conventional breeding**

PREVENT AVOIDABLE YIELD LOSSES:

- **Lodging resistance**
  - **partitioning to crown roots**
  - **partitioning to stem**
- **Biotic stress resistance**
- **Optimal crop management**

Figure 1. A multidisciplinary research platform to raise wheat yield.

Modelling strategies in the application of QTL and trait information in breeding programs

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With the increased availability of molecular marker and gene sequence information, a major challenge for plant breeders is how to best utilise this information to increase genetic gain. For water-limited environments, breeding decisions based on phenotype and quantitative trait loci (QTL) detection, crossing and selection, are further complicated by how yield is realised as a consequence of short-term and long-term interactions of genes, traits and environments.

As in many other industries, simulation allows the testing and trial of new methods, i.e. even before many breeding programs have the data or capability to apply such methods. To assist such decisions we utilise a platform where a genetic simulation model of gene effects and breeding schemes (Qu-Gene - www.uq.edu.au/lcafs/qugene/; Podlich and Cooper, 1998) interacts directly with a bio-physical simulation model (APSIM - www.apsim.info). This is the first platform that accounts for the complex interplays of genetic controls, physiological traits and environmental conditions throughout the crop cycle and the consequences for crossing and selection (Hammer *et al.,* 2006; Chenu *et al.,* 2008). This platform enables the construction of thousands of 'desktop breeding programs', where different parent lines, type of crosses, evaluation environments and selection criteria can be evaluated. The paper illustrates how this platform can be used to:

- Evaluate the expected selection response of different breeding strategies, e.g. in the design of the CIMMYT wheat program (Wang *et al.,* 2003);
- Create complex crosses among diverse parental lines while accounting for gene linkage and additive, epistatic, environmental and error effects, e.g. selection for diagnostic genes and QTL for recombination of traits among wheat lines (Wang *et al.,* 2009);
- Evaluate the interaction of environment and genotype effects to influence the estimation and utility of QTL detection experiments, e.g. comparison of outcomes of >500 QTL experiments in terms of realized yield response to selection for QTL (Hammer *et al.,* 2005; Chapman, 2008);
- Generate *in silico* datasets to test the impact in breeding programs of QTL for traits observed at different times or organ scales (e.g. hourly leaf growth, maximum leaf area index or grain yield), e.g. examining how the genetic control of leaf and silk elongation rates in maize can affect selection response for yield (Chenu *et al.,* 2009).

These tools still require further refinement in terms of the detail in which they capture the genetic information and the physiological relationships among traits. However, they have demonstrated how to improve the efficiency of breeding strategies (in terms of time and resources), and in the optimization of real-world examples for the pyramiding and re-combination of diagnostic genes and QTL. Their development is continuing via direct collaborations with public and private breeding programs, and the tools are freely available for use in public research and breeding.

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Integration into a practical breeding platform

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A key part of the successful strategy of the Green Revolution centred upon the development of novel wheat germplasm which optimised selection of crop ideotypes to meet local environmental constraints. Alongside this germplasm development, agronomic support strategies were conceived which allowed the optimisation of yield potential for the new ideotype. Future strategies will need to retain much of this philosophy, but the speed of development and integration will need to be faster and more efficient than previously – primarily because of the rapid rise in the world population, but also because global warming is leading to a more rapid change of the current environments in which wheat is grown. To maximise the impact of this consortium it is essential that expertise from both the public and private sectors are brought together to exploit the genetic material for the benefit of mankind.

The breeding objectives set by the Wheat Yield Consortium (WYC) demand improvements in key physiological and phenological traits of very high importance. Imperatives to increase biomass, enhance lodging resistance and broaden the genetic base as well as opportunities to develop genetically modified wheat crops are well understood. Only some of the traits associated with high value physiological characters are understood and there is much to be done to identify those which impact upon the phenology of the crop – essential if varieties are to be sown in their correct environments. Whilst much of the phenotyping work will be handled by physiologists, the delivery mechanism to the 'market place' will be through the plant breeding community, both the private and public sectors, and most importantly the combination of both. The WYC provides an opportunity to initiate breeding strategies to encompass the various disciplines necessary to increase the efficiency of this translation process. Whilst historically breeders have concentrated large amounts of resource to empirical approaches, the last ten years have seen a 'silent revolution' in the take up of new technologies to increase selection efficiency and it is this experience which needs to be brought to bear if rapid progress is to be made.

Exploitation of the range of 'new traits' currently under discussion will depend on the strong relationships that currently exist between the public and private sectors. Public sector breeding is highly efficient at developing germplasm for trait discovery but less efficient in translating this into the market place. Future progress will depend on integrating the technologies available from these bodies efficiently and with speed.

Current selection efficiencies are high – particularly in the developed world where new field technologies such as high speed seeding, automatic computerised weighing of trial plots and more recently the introduction of GPS technology are now used routinely. Laboratory based techniques for rapid throughput markers have also been developed. The current relationship within the UK between the John Innes Centre and the private sector winter wheat breeding companies (represented by the consortium known as British Wheat Breeders*) is a valuable working model for the consortium.

A key requirement for any breeder is the opportunity to assess the trait of value. Field based selection schemes have the benefits of low cost and high throughput. However for many physiological traits the characters and their inheritance will be complex demanding an understanding of how genes interact to produce the phenotype. To this end diagnostic markers associated with these traits will be essential. Breeders will be well placed to be able to discriminate between the efficiencies of field or marker based selection strategies. Private breeders have at their disposal high throughput marker technologies.

Sophisticated and rapid systems to incorporate new characterized genetic variation into breeding streams will be essential. For spring wheats, shuttle breeding was a major part of the previous strategy, but unless phenological traits are fixed, it is possible that the fine nuances of the different environments used will distort the frequency of the desired trait. Single Seed Descent and Doubled Haploid production will be key requirements for winter wheat breeding. Both of these have been developed in the public and private sectors and can be made available to the consortium.

Once genes of interest have been identified these can be fixed by 'genetic enrichment' – particularly valuable if bringing together multiple traits from a range of parental types or wide crossing. This form of marker assisted selection (MAS) is now used routinely to fix genes associated with intransigent traits. The range of traits forthcoming from this consortium will be broad and must be incorporated into a strategy which will encompass the many characters already being selected for.

Physiology/ phenology traits have the benefit of being able to be fixed in perpetuity in germplasm and a first step will be to fix these in adapted germplasm represented by the major wheat growing areas of the world. Once fixed these traits will be transferred via the use of efficient selection strategies, encompassing both field and laboratory based MAS, will be transferred to commercially valuable advanced lines.

In order to achieve these demanding targets there will be an imperative for the development of sophisticated bioinformatics programmes which are able to direct the selection process and optimise selection efficiency. Resources will need to be put aside to meet this demand.

* British Wheat Breeders (BWB) represents the major UK wheat breeding companies who currently occupy over 90% of the UK wheat acreage. This is a non exclusive arrangement with all breeders invited to join on the basis of equal access and investment.

Complementary Strategies to Raise Wheat Yield Potential Symposium

CIMMYT, El Batan, 10-13 November, 2009

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