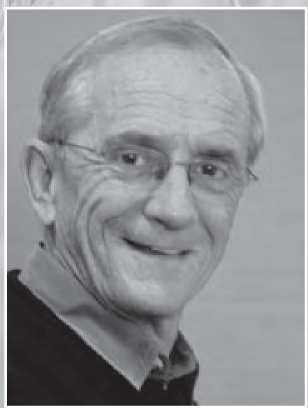
THE 2007 FARRER MEMORIAL ORATION



Improvements in wheat yield: Farrer, physiology and functional genomics

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1. Introduction

Most of my research and related activities have been with wheat, and much on the physiology of the wheat crop, so it is wise for me to focus this oration on wheat physiology, but it is a subject that can begin with Farrer, although I hope it doesn't end with functional genomics. Besides it is a subject not often taken up in previous Farrer Orations, although there are the notable exceptions from CMDonald in 1964, LTEvans in 1979 and WVSingle in 1984, all physiologists to whom I owe a considerable debt. Placing my subject in the larger framework of yield improvement is essential in these times of focus on impact, but it is also second nature to someone who grew up on a wheat farm, studied agriculture science in Melbourne under the likes of Tom Neales, Derek Tribe and Alan Lloyd, and later worked under Albert Pugsley, then Norman Borlaug, and alongside Rajaram and Passioura.

2. William Farrer

Farrer's life and achievements are well covered in Shelton (1925) and Russell (1949), and have been discussed by previous Orators, in particular Lloyd Evans in 1979 (Evans, 1980). But it is appropriate, indeed important, to recall a few highlights regarding this great Australian scientist, now dead 101 years and banished by inflation from our paper currency.

He was quite a remarkable person, the more so for us in Canberra, because he was a local:

1. Emigrating to Australia in 1870 after a top degree in mathematics at Cambridge University, he married Nina de Salis from Cuppacumbalong Station, just south of Canberra, and soon after settled at nearby Lambrigg Farm where he did most of his wheat breeding work, beginning about 1886, and where he died in 1906. For his last 8 years Farrer was an employee of NSW Department of Mining and Agriculture, as was I many years later, and for this reason during the talk I will refer to other NSW Agriculture employees where appropriate, for the Department has had a long and proud history in wheat improvement since it all began with William Farrer.
2. He was the father of wheat breeding in Australia and ranks amongst the first wheat breeders here (others were Hugh Pye in Victoria and E.M. Shelton in Queensland) and in the whole world. He first wrote about wheat breeding in 1882, and began breeding on his own initiative soon after. Influenced by Darwin, his methods were scientific, built up by painstaking observations and detailed record keeping. In the last year of his life he became aware of the work of Mendel, postulating units of inheritance; Farrer wrote that he himself had reached the same conclusions through observation and common sense (Shelton 1925)!
3. As an example of his innovation, his breeding techniques remain largely those of conventional breeding today. He carried out hybridization of parents and selection amongst progeny for desirable recombinants, but he crossed widely, even between species, sought parental material from all over the world, practiced backcrossing, and was aware of trangressive segregation, whereby trait expression in progeny could go beyond the range of parental values.
4. He was the first to breed wheat for disease resistance (rust, bunt), baking quality, and drought resistance especially through earliness. He released many varieties superior in these traits, but his greatest variety was Federation released in 1901 and popular because of its ability to yield under dry conditions. Federation quickly became the most widely grown variety in Australia (and was grown in significant acreage overseas). The five fold increase in Australian wheat production between 1890 and 1920, with the emergence of Australia as a major wheat exporter, was due to this and other Farrer varieties (in particular Bunyip, Firbank, Florence, Genoa and Thew), plus better cultivation methods according to Shelton (1925). It was accompanied by a large expansion of wheat growing into the drier inland parts of southeastern Australia permitted by Farrer's varieties.
5. Farrer was also an agronomist. He wrote about the importance of soil management, including attention to the physical, chemical and biological fertility of the soil. He was a strong advocate of leguminous green manuring, and had serious doubts about the practice of clean fallowing.
6. Farrer wasn't just a keen observer, he thought about the underlying theory arguing that "those who despise theory will do well to recollect that a function of theory is to examine the foundations of practice, and by this means, to modify it and extend it advantageously". Thus he had his theories about wheat yield in the Australian environment, recognizing the importance of earliness, of "scanty stooling and high tiller survival", and of short stature whereby wheats did not "spend too much of their strength producing straw" (Farrer, 1898).
7. It is clear that, working over 100 years ago, Farrer was able to embrace the whole of plant and crop science, something not so easy to do these days. Besides from his writings its clear he worked for humanity, not just for the Australian farmer, and he readily shared his materials and results with the whole world. I feel sure he would have got along very well with 1970 Nobel Peace Prize winner and wheat breeder Norman Borlaug, and I recall being at the International Wheat Genetics Congress in Canberra in August 1968 when Borlaug, and other greats of modern wheat breeders took time off to visit Farrer's grave at Lambrigg Farm.

3. Past wheat yield progress and physiology

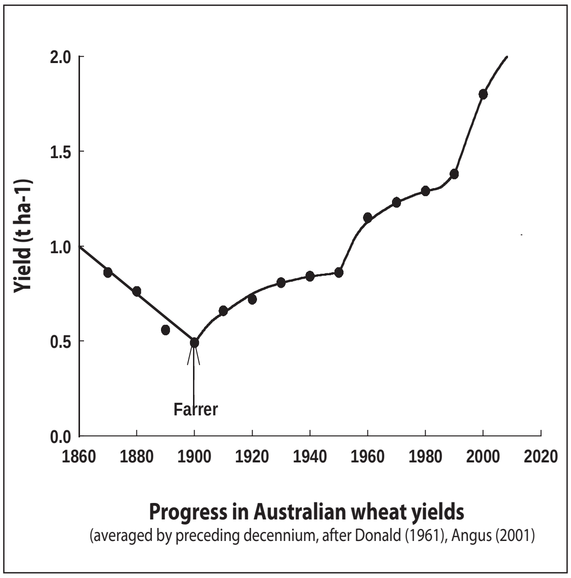
I would like now to return to the title of my talk, without breaking the link with Farrer whose work clearly drove the first wheat yield improvement in Australia and who urged attention to underlying theory. I will talk first about yield improvement in the 100 years since Farrer, then about future prospects, a field which for many is dominated by functional genomics. Throughout I will take the perspective of the discipline which I mainly practiced in my career, namely crop physiology. But what is crop physiology? Physiology is the function of plants at the cellular and higher levels of organization (organ, whole plant), and crop physiology is this function taken to the highest level, that of the crop community.

The latter is usually characterized by plants growing closely together with genetically-like neighbours (the monoculture), and in real soil under normal field environments: in other words, agricultural crops as grown by farmers. Functional genomics is plant functioning beginning at a lower level of organization than physiology, namely the nucleic acid level of the gene and proceeding upwards to the level of enzymes and their products, with the ultimate goal of reaching the crop level also. But more about that later (see Figure 6).

Agricultural economists might talk about total factor productivity growth in agriculture, while agricultural scientists worry about profit on farms and what is happening to their natural resource base; crop physiologists, on the other hand, are fascinated by yield progress. Let's look at wheat yield progress since Farrer's time in Australia. The Australian yield graph is probably well known to the audience (Figure 1), growth over the last 100 years has been quite impressive, average yield has increased almost four fold even as area has risen several fold with the spread of wheat cropping onto generally less favourable lands. The progress amounts to an exponential yield gain of about 1.3 % pa terms (Figure 1). The Australian example, an entirely rainfed crop, has been thoroughly analysed by crop physiologists and others: the only point that I would make here is that Farrer's breeding catalysed the beginning of this long process, a process involving both breeding better varieties and developing improved crop agronomy.

Figure 1

Australian average wheat yields (t/ha) between years 1850 and 2000 (average plotted at the end of each decennial period; after Donald (1965) and Angus (2001)).



Breeding and agronomy also drove the more recent yield progress in the UK, the highest yielding wheat-growing nation, and in India, with the additional comment that part of India's progress is linked to a big increase in the proportion of the crop irrigated (Figure 2). World wheat yields have grown similarly, such that even with little change in sown area since 1950, production growth has exceeded demand growth and real prices have been in general decline over the period and indeed for more than a century. One obvious question is whether this yield growth can continue, a question to which I shall return.

Figure 2

Progress in average wheat yields of the United Kingdom and India (source FAOStat).

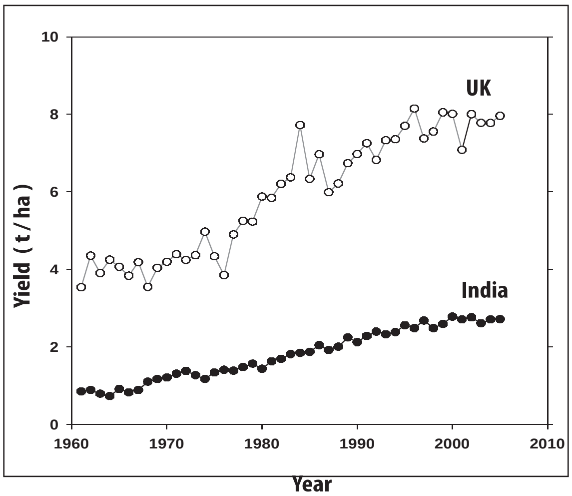
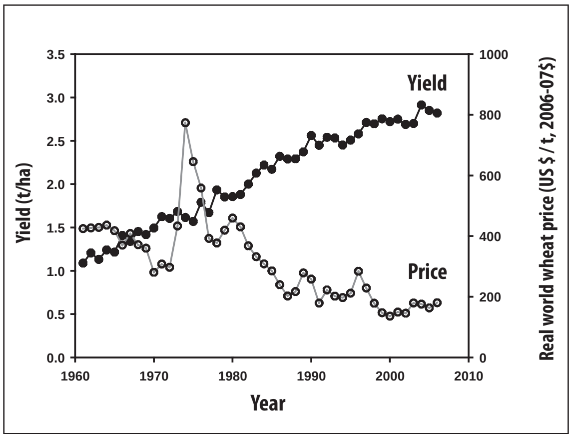


Figure 3
Progress in world average wheat yields and changes in the real price of wheat (Source FAOStat and ABARE).



Yield progress brings two relevant questions for physiologists: what role did physiology play in this progress and what are the future yield possibilities and limits. Physiologists love speculating about future yield possibilities, thinking about designs for better wheat plants, smarter techniques to breed them, as well as better ways to manage them. And as a guide to this future progress, a lot of work has been done on the past routes of progress, retrospective studies as they have sometimes been disparagingly called. It is useful to look briefly at the results of this body of research, which gives some clues as to the past role of physiology, and to future yield prospects.

3 .1 Genetic improvement and yield progress

Matching phenology, or crop duration, to the environment has been critical everywhere, in simple terms it means getting flowering time right. In Australia it started with Farrer's early flowering wheats like Federation. Physiologists have susequently dissected the controlling mechanisms, and understanding the wheat plant responses to photoperiod, vernalizing cold, and temperature, has undoubtedly helped breeders manage this key trait, a point strongly made by NSW Agriculture wheat breeder and 1953 Farrer awardee Albert Pugsley (Pugsley, 1983).

Reducing plant stature through the use of dwarfing genes, minor and major, to prevent lodging, has enabled crops to respond to higher soil fertility without falling over. It seems the early Japanese wheat breeders were the first to understand this; later, as cheap nitrogen fertilizer became available, it was taken up by breeders almost everywhere, using various major and minor dwarfing genes: a classic example of agronomic innovation creating an opportunity for breeders. Retrospectively physiologists pointed out how reduced stature led to higher harvest index rather than more biomass (grain yield can be considered as the product of total biomass produced multiplied by the proportion of biomass in grain, namely the harvest index), a more efficient crop even in the absence of lodging, something Farrer also argued in his writings, and achieved in the variety Federation. But in Farrer's time, shorter varieties suffered because they produced less straw, since they were grown in a system where straw was valuable as, for example, horse fodder.

Today most varieties fall into the optimum height for wheat without water stress of around 80- 95 cm. But there have been further improvements in yield at this optimum stature. These have been associated with continued increases in harvest index and some increases in biomass. Studies over the last 20 years, in particular in Mexico, the UK, France, Australia and Argentina, point to a strong positive association between yield progress and grain number/m2 in the crop, with little change in seed size as yield has been improved. Recent work suggests that this is not just due to shorter stems, but that more efficient investment of dry matter in spikes and grains may also be related to more erect canopies and greater leaf photosynthetic activity improving crop photosynthesis around flowering, to more grain sites per unit spike dry matter, and to more stored carbohydrates in stems at flowering (Abbate et al 1998; Fischer et al 1998; Shearman et al 2005).

Again this elucidation of progress has mostly been retrospective, but the relationships discovered between yield and leaf physiological traits like photosynthetic activity, stomatal conductance and canopy temperature depression have been so strong, and the means to measure these traits in the field so efficient, that their use as early generation indirect selection criteria for yield has recently been investigated and looks promising; agricultural economist, John Brennan, another NSW Agriculture scientist was involved in this assessment (Brennan et al 2007).

These leaf traits appear also to be important under dry conditions, as in Australia. In addition, Farrer's scanty tillering and extra earliness have a special advantage. As well, we are starting to see the release of varieties specifically selected for physiological (ideotype) traits postulated by to help performance under drought. I refer to wheats which are specifically more water efficient at the leaf level (low delta, eg Drysdale and Rees), or have longer coleoptiles for a given optimum stature, or greater early vigour (Richards 1991). This ideotrait breeding for water productivity is found right here at CSIRO Canberra; it is still fairly unique in the world of wheat breeding and began in the late 1970s. It represents the most proactive role of crop physiological thinking in wheat variety development in the whole century of progress described. As such the time and money spent on this endeavour can be a guide to the likely cost of future breeding progress via the analytical route.

In summary breeding has led to substantial yield progress in the century since Farrer; breeding has also delivered other valuable components of progress but this not our subject here. There have been many studies of the rate of breeding progress, usually based on side by side comparisons of an historic set of varieties under appropriate agronomy. These have certain limitations, but those for Australia are shown in Table 1. Excluding the two shorter release periods, overly dominated by the one-off yield jump arising from introducing semidwarf varierties in the 1970s, the average rate of yield progress has been about 0.5% per annum, a number fairly typical for rainfed environments.

Rates elsewhere in the world, especially under wetter conditions, tend to be closer to 1% p.a.; the most recent study of winter wheat varieties released as late as 2004 in the UK actually produced 1.2% pa (Shearman et al 2005).

Table 1.

Studies in Australia measuring the rate of breeding progress for wheat yield by growing historic sets of varieties side by side and regressing natural log of yield against year of release.

Location	Variety release Period	Rate of gain % pa	Source
Victoria	1886-1973	0.41	O'Brien (1982)
NSW 1	1956-1974	1.03	Martin (1981)
ACT	1884-1978	0.72	Richards (1991)
NSW 2	1926-1984	0.60	Antony and Brennan (1987)
NSW 3	1956-1984	0.90	Antony and Brennan (1987)
WA	1884-1982	0.44	Perry and D'Antuono (1989)
Average	Long period	0.54	Excluding NSW 1 and 3

3.2 Crop management and yield progress

Restoring and/or increasing soil fertility to match the yield potential of the variety, as governed by genotype, climate and especially water supply, has been a major agronomic factor in yield improvement over the last century. It has interacted with reduced stature in varieties to give an extra yield jump. Much of the fertility increase initially involved the introduction and use of superphosphate fertilizer, followed by legume ley farming starting in the 1940s, and in the last 20 years, N fertilizer use has increased markedly. We are now moving to supply other elements as they become exhausted by ongoing cropping (eg K, Zn etc), to the use of lime to counter the build up of soil acidity, and to using N fertilizer more tactically and more efficiently, the latter advances stimulated by crop physiological research on pattern of N uptake, on the response of yield components to nitrogen, and on the phenomenon of "haying off" (Angus and van Heerwarden 2001).

Mechanization has obviously massively substituted for labour in farming over the century, but it has also driven yield increases, especially through better timeliness of sowing and harvesting, something achieved even as crop area per farm family has grown greatly. Sowing within the optimum window is a major benefit, and this window, even with the right rainfall, may only be a few weeks (eg Kohn and Storrier, 1970). When I was a child, land preparation after the break and sowing with horse drawn equipment, could take months not weeks. Since the 1970s the move to reduced and even zero tillage, has brought further yield gains through soil water conservation ahead of planting where crop residue is retained on the soil surface and in terms of timeliness of wheat sowing, as well as significant cost cuts. It is not unusual now for one set of equipment to sow 1000 ha in a week.

Herbicides derive from international plant physiological research commencing in the 1950s. The impact of selective (broad leaf and then grass ones) and of knockdown herbicide has been huge: it is partly cost saving and partly yield increasing through both better weed control and less delays in sowing through not having to rely on traditional weed control, namely preseeding tillage. Riding the spray cart in the 1950s, as my father conquered our worst enemy skeleton weed (Chondrilla juncea), has given me a lifelong nostalgia for the slightest scent of 24D. Integrated weed management is now the name of the game, but without herbicides I believe the Australian wheat industry would be uncompetitive globally and/or unsustainable.

The final agronomic advance has come from improved crop rotations and sequences in which the wheat is grown; I refer to alternative land uses breaking the earlier cycles of continuous wheat, or wheat-fallow, or wheat oats barley. Firstly it was the introduction of clover and medic ley farming, meaning managed legume pastures preceding the wheat crop. This practice goes back to the famous Norfolk rotation of the 19th Century in the UK; it was foreshadowed in Farrer's writings , and the benefits are multiple including net addition to soil nitrogen, soil disease mitigation, and greater options for weed control. But it was slow to reach Australia (Henzell 2007), and it was not until impact in the early 1950s of the Korean War on wool prices, that legume ley farming really took off. Incidentally the wool price boom surely put me through boarding school and onto the long road which has led me here today. Legume ley farming still predominates in parts of the wheat belt, and lucerne has lately become a common feature of this. It is estimated that even now the Australian wheat crop gets only 30% of its nitrogen from fertilizer, whereas elsewhere in the world this figure is over 50% (Angus 2001). As well, new alternative broad leaf crops have risen in the last 30 years to occupy about 15% of the cereal acreage; this includes grain legumes (lupins, peas, chick peas, faba beans) and oilseeds, especially canola. The rotational benefits for wheat are multiple, including net addition to soil nitrogen, soil disease mitigation, and greater options for weed control; they were also foreshadowed in Farrer's writings. Plant introduction and breeding has catalysed these rotational innovations in the wheat system, and breeding of these relatively new economic plant species in Australia remains especially critical. The whole wheat cropping system is quite flexible, responding quickly to the relative prices of the various products (wool, meat, wheat, pulses, oilseeds, hay), and to technological setbacks and advances. This is meaningful agricultural diversity!

The breeding and agronomic advances of the last century should not be considered separately, because there have been many positive interactions between new varieties and new agronomy such that taken together yield response has been more than their individual effects. This is evident in the well known Figure 4, which again shows Australian wheat yield progress, but now lists the major advances associated with this progress, like flags on the roof of the Sydney Opera House.

4. Future prospects for yield progress

As we look at an undiminished growth in demand for wheat due to the increase in world population and in per capita wealth, which indirectly increases feed wheat demand, and the serious limits on crop area expansion in most places, the importance of continuing to increase wheat yield is painfully obvious (The land used for cropping actually has some potential to increase given favourable prices and policies eg CRP and CAP set aside land in USA and EU, respectively, and abandoned decollectivized land in the exUSSR, plus new lands in Africa and South America, but there are also land losses due to urbanization in India and China).

Yield growth is not a sufficient condition for a better world with less poverty but it certainly is a necessary one. A figure of between 1.0 and 1.5% pa has been nominated by various authors: 1.0% across all cereals under a progressive policy scenario would hold real prices and crop areas relatively steady out to 2030 according to the IFPRI Impact model (von Braun et al 2005); this number was for all cereals, with feed grain demand a little stronger than that for wheat, and it did not consider the impact of a grain biofuel industry.

I conclude that the world must grow wheat yields at the very least at 1.0% pa for many years to come if the poor wheat eaters are not to suffer worse hunger. Besides competition from biofuel production could take land from food wheat production, and increase feed wheat demand, increasing the need for yield growth, while higher energy costs, irrigation water shortages and climate change, will make achievement of any yield growth goal more difficult.

Forecasters are now looking to stable or slightly increasing real wheat prices as a consequence of these more recent developments (Brown et al 2007 cf Figure 3). Besides in the longer term, I believe there is a particular need to increase the yield of rainfed wheat, because the very pressures I mentioned above will gradually displace wheat from the favoured and irrigated lands of the world, relegating it to the drier rainfed lands, the Great Plains of North America, the steppes and adjacent forests of Asia, the pampas of Argentina, and the drylands Australia, all places where it's comparative advantage is greatest.

Before commencing on the future, I would like to take another look at recent yield progress, to see whether there are signs of slow down and how rates compare to the projected 1.0-1.5% pa demand increase. This is a tricky business because yields fluctuate from year to year. Let's start with yields in the irrigated Yaqui valley in northwest Mexico, the most immediate target of CIMMYT's wheat research (Figure 4). Progress looked great, until a second order polynomial was fitted to the data: it's a good fit (r squared = 0.914, better than linear) and suggests that progress has almost ceased! But I believe this is deceptive, and to find out what is happening now, I prefer a linear fit to the most recent data, going back in time only far enough to get reasonable accuracy on the slope estimate, but not so far as to loose touch with the current situation. This is a compromise, and for the Yaqui Valley I chose 30 years to derive a relationship (line on Figure 5) which had a highly significant slope, amounting to 0.8% p.a. relative to current yield.

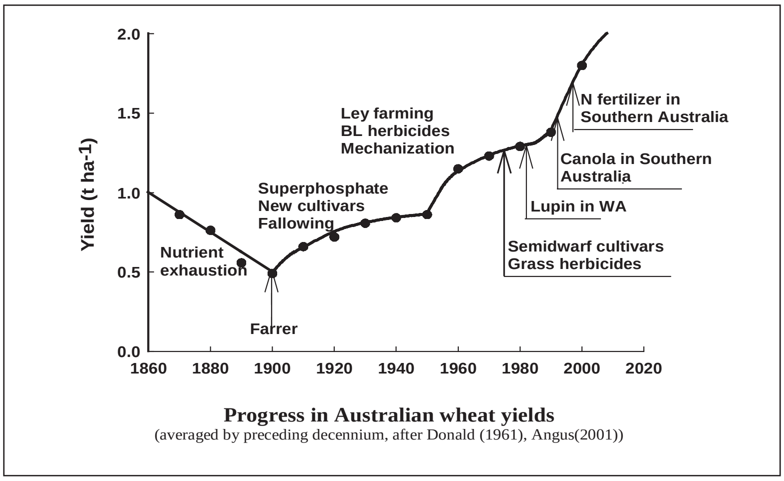
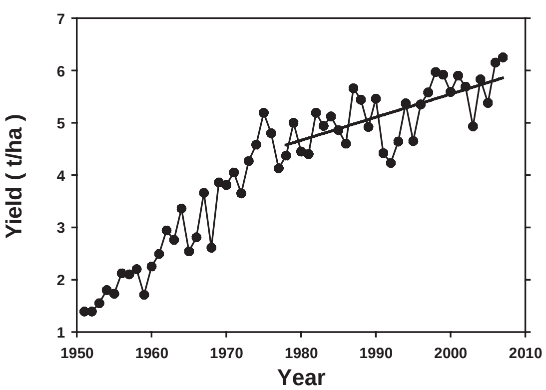


Figure 4
Australian average wheat yields (t/ha) between years 1850 and 2000 (average plotted at the end of each decennial period). After Donald (1965), Fischer (1999), Angus (2001) and others.

Figure 5
Average wheat yield in the Yaqui Valley of northwest Mexico. Courtesy Ken Sayre, CIMMYT. Linear egression fitted to last 30 years (see Table 2)



(Source Ken Sayre CIMMYT)

Using the procedure described above for the Yaqui Valley I have looked at the other regions mentioned earlier, choosing the time period according to the data (Table 4). For example Australian yield fluctuates so much from year to year that over the last 20 years the linear trend is not significantly different from zero (cf Figure 1); I had to go back 30 years. For the other examples I used 20 years, except for Indian and world yields with their much lower annual fluctuations, when 15 years seemed safe. All slopes in Table 4 are remarkably close to 1.0%. This is my best estimate, based on the raw statistics, of the current rate of progress of farm wheat yields around the world. The only thing I would add is that these slopes are all lower than those for earlier periods embracing the 60s and 70s and 80s: in other words the rate of progress as a % of actual yield is slowing gradually.

So, having understood the need for continuing yield progress and the elements involved in past wheat yield progress, what can we say about the burning question of future yield prospects. This depends on raising the best yields (yield potential whether water limited or not) and closing the current yield gap (the difference between yields with best practice, or attainable yield, and average farmer yields), which in some parts of the world and maybe even in Australia, is still substantial. Sadras and Angus (2006) estimate, based on water use efficiencies, that this could be more than 50% of best practice yields even in south-eastern Australia and the Great Plains; I suspect the average gap is not so high, and when the irrigated of India and China are included, a world average figure of one third (33%) is more likely. In anycase there is important scope for gap closing, discussion of which could however involve another paper. In the remainder of this one, I wish to focus on what we can foresee for yield potential, whether water unlimited or water limited, and I again look separately at agronomy and breeding, but especially the latter.

4.1 Agronomic innovations

Just as some argue that breeding offers better prospects for the future, others argue for a greater future impact from new agronomy (eg Anderson and Angus 2007). This agronomic impact can come from increasing yield, better managing for grain quality (and hence price), or from reduced production costs and improved sustainability. Important as the other wheat systems are, this discussion concerns advancing the yield possibilities in Australia's water limited wheat environment.

Most of the agronomic innovations I listed for the last century have been adopted and offer little opportunity for further yield gain (eg once weeds are controlled and nutrition optimized these are no longer yield constraints), although there is scope for cost saving and sustainability enhancing agronomic innovations. As I look forward, I may lack imagination for I can only foresee three areas of yield gain.

Table 2 Linear rate of yield progress in various regions for most recent period giving reliable slope estimate.

Region	Period	Slope kg/ha/yr	Std error slope	Slope as % Current Yielda	R squared
Yaqui Valley	78-07	44	9	0.8	0.450
Australia	77-06	17	8	0.9	0.146
UK	86-05	81	15	1.0	0.615
India	91-05	32	5	1.1	0.737
World	92-06	26	4	0.9	0.775

a. Using yield predicted for 2007 by linear trend.

In dry areas, wheat yield is proportional to the crop water use. Extracting more water from the subsoil in those situations where it is present would boost yield in most cases (and lessen the buildup of dryland salinity), and is receiving major attention across the nation lately. So far we have not devised economic agronomic ways of ameliorating those unfavourable subsoils (prospects here look better on the breeding front). Storing more water in the soil ahead of cropping can probably be further improved with better attention to weed control and stubble retention, often implying further engineering modifications to drilling machinery for direct seeding. Precision guidance and controlled traffic can offer some gains here also. Part of the water storage issue is improving the chances of having topsoil moisture for crop planting and germination during the optimum sowing window.

Alternatively, dry sowing at the beginning of the window would guarantee germination on the next significant rain and thus in some years, especially dry ones, secure a more favourable germination date than would waiting for that first rain before beginning to seed. Several things are preventing more widespread dry sowing, in particular concern over weed control. Wheat resistant to knock-down herbicide would eliminate this concern, and becomes an innovation in breeding plus agronomy that could give yield gains also. Another concern is that dry sowing prevents the farmer adjusting the maturity class of the variety for the actual germination date. Again genetic manipulation of the climatic controls over duration to flowering could conceivably solve this, giving single varieties whose maturity class adjusted automatically to sowing date.

Another area of agronomic research receiving special attention is that of biological soil additives. This is not new, being the favoured territory of organic farmers, and hence is somewhat controversial. Some additives are supposed to work as biocontrol agents, protecting wheat roots from soil pathogenic fungii and nematodes. Others appear to have independent growth stimulatory effects. To the extent that wheat yield is still limited by soil pathogens, even with the adoption of improved rotations and of better seed fungicides, the former biocontrol agents could help to boost yields, especially for example where the early vigour of wheat suffers in direct drilled seed beds. We shouldn't forget that we know very little about what is going on under the ground: the spectacular gains with root disease control with for example better crop rotation in the 1980s was a revelation, there could be more. The independent growth stimulatory effect of some biological agents is even less well understood, and deserves further investigation, but it is hard to see more than minor yield gains in this area.

Another "new" area in agronomy for yield gain and to which I want to refer is that of seasonal climate forecasting (SCF) and risk management. If we had perfect seasonal forecasts, variety, sowing time and fertilizer inputs could be tailored to give maximum profit awhile minimizing risk to the farmer. Thus the better the SCF skill the closer we approach this ideal, and assuming farmers normally hold back on inputs, even tactical ones, because of risk aversion, the higher the average yield would be, noting that in years with very bad climatic outlooks farmers may choose not to sow at all. Where does current seasonal forecasting skill sit with respect to perfect forecasts?

SCF skill is far from perfect but several papers using historic records and simulation modeling show how the current skill, usually based on the SOI, could have been used over the historic period to increase yield and profits a little (Hammer et al, 1996). These results are quite controversial (Robertson and Butler, 2002), and we really need to boost seasonal forecasting skill to reap even half of the potential benefits. There may be some possibilities in this area, but I cannot help worrying that the statistically-based historic forecast indices we currently use like SOI may not be relevant to a future with climate change. On the other hand better global circulation models could be.

A related area is that of crop simulation modeling designed to facilitate tactical and strategic decision making: the models can readily incorporate SCF if worthwhile. Yield Prophet is the latest and probably best example; its significant uptake by farm advisers is note worthy (over 500 wheat crops are being modeled in 2007; J. Hunt personal comm).

Earlier I suggested that we knew enough now to optimise crop nutrition. I could add that with precision technology and variable rate technology this can now be done at a within paddock scale if worthwhile, but this is a technology that is unlikely to be increase overall yield. I would however like to leave the door open for the possibility that we are not completely on top of crop nutrition, especially the possibility of deficiencies other than ones involving N and P. With continued cropping these must arise, and there are or will be yield losses until they are recognised.

The four areas I have just outlined are all current targets for GRDC supported research. However, taken together I find it hard to anticipate attainable yield increases of more that say 25% arising from this research.

4.2 Conventional plant breeding

Just as some argue that agronomy will be the more important way forward, others opt for breeding. We have seen that there has been steady progress over the last 100 years from breeding, mostly empirical but sometimes analytical and physiologically-guided. Firstly let us ask is there any evidence of a slow down in the rate of this progress. From Australia there are unfortunately no recent studies to answer this question; the newest varieties in Table 1 are now more than 25 years old (Table 1). However more recent studies from overseas (France, UK, China, Mexico), admittedly from humid or irrigated environments, points to steady progress at around 1% pa, with some evidence that rates have declined at CIMMYT in Mexico to around 0.5 % p.a. (Fischer 2006). There is no evidence yield progress has ceased, and it must be remembered the attention breeders can give to yield may have been constrained by recent heavy emphasis on breeding for disease resistance and product quality.

One might expect progress with conventional breeding to slow because genetic variation has become exhausted, or alternatively because the fundamental biological limit of yield is being approached. The first argument is not supported by selection studies by geneticists where natural variation for quantitative traits seems endless even in closed gene pools; several breeders have also asserted this to be the case in their yield breeding programs (Rasmussen and Phillips 1997). And of course breeding programs have huge gene pools sitting in the world's gene banks that they can sample if there are concerned about the lack of genetic diversity. Despite urging from some other geneticists, most breeders are reluctant to do so. Still CIMMYT with it new synthetic program is undertaking a very substantial sampling of the gene pool of one ancestor species of wheat, namely Triticum tauschii: it is probably too soon to say whether there benefits for yield itself in this . The second possible constraint on yield progress, that a fundamental biological limit is being reached, is inevitably related to the upper limits to the efficiency with which radiation and/or water can be traded for reduced CO2, and to the upper limit of harvest index, and has been the subject of much discussion by physiologists, but these days it is generally not considered to be imminent; however because of our ignorance about these fundamental biological issues, this possibility should not be ignored entirely.

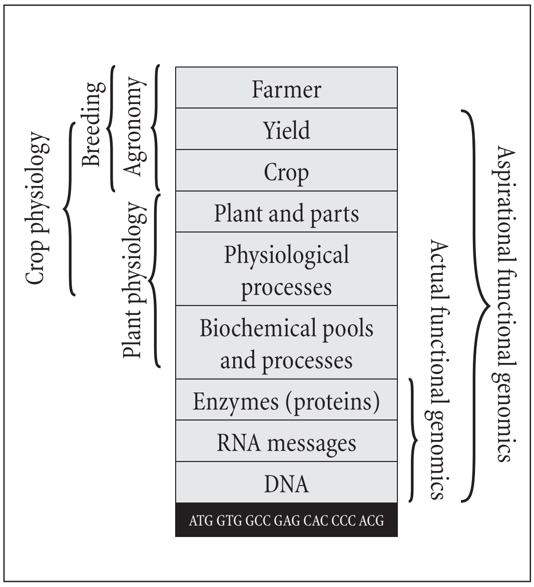
In summary there is a good chance conventional breeding will continue to deliver yield gains at 0.5% pa, or better in wet areas, but we cannot be complacent about the need to encourage more and smarter investment in this effort. Conventional breeding is basically four steps: parent selection, crossing, screening progeny, and yield testing. The last two steps are the expensive ones, and many believe that the cost per unit of genetic progress is steadily increasing. This is occurring despite the huge benefits to breeding from mechanization, robotics, computing, and biometrics that we have seen in the last 40 years. And new tools are arising to help conventional breeding, such as propagation tricks like double haploids, physiologically-based trait postulation and physiological screening tests for yield, simulation modeling to understand G x E, and in particular molecular marker-aided selection (MAS). The last-mentioned technique shows considerable promise, but the effect of MAS on yield progress is likely to be indirect for some time to come, arising from its application to other traits for which it is otherwise difficult to screen, thereby saving resources for yield testing. This is because yield itself has proved a very difficult trait to tag with molecular markers due to its complex determination.

5. Functional genomics in future wheat yield progress

5.1 Wheat biotechnology and the big issues with functional genomics

This brings us to the last section of the talk. The need for further yield increases, for greater input use efficiency, and the possible declining efficiency of conventional breeding for yield, plus the apparent promise of new science, have come together to drive substantial research investment in functional genomics, a recent branch of plant molecular biology. This is truly new science, belonging to the last 20 years or so, and well beyond anyone's dreams 50 years ago, at the beginning of my research career. Functional genomics can be defined as the functioning of plants at the gene molecular and enzymatic level of organization, aspiring of course, to manipulate function through this knowledge in order to influence performance at the highest level, namely crop yield and utility (Figure 6). It is part of the molecular biological revolution, the stuff of DNA and RNA function, but for purposes of clarification, it is distinguished here from MAS mentioned above (although there is potential overlap with functional genomics). I separate functional genomics not because it can only deliver yield improvements through genetic engineering otherwise known as transgenics (I have no argument against this technology for improving wheat), but because it has been making too many implausible claims about improving yield. This is not to deny that functional genomics in general is at the cutting edge of biological science, full of excitement, offering solutions to many problems in human health, and even overturning early molecular models of gene action. The question for me is can it help us to improve wheat yield, and how much emphasis does it deserve in wheat research funding?

Figure 6
Hierarchy of levels of organization in the crop



Functional genomics has already delivered crop science and farmers some spectacular new products: I refer to GM (transgenic) crops, built to resist insects, herbicides and viruses: the area planted to such crops globally in 2006 reached 102 million hectares (although there are no GM wheats commercialized yet, such herbicide resistant wheat has been successfully tested in USA (Zhou et al., 2003)). And FG is close to delivering engineered grains of superior nutritional quality, such as rice high in vitamin A precursor (Golden rice) or wheat high in "good starch", namely amylose. But these molecular manipulations, elegant though they are, involve relatively simple metabolic changes within the plant. They comprise a few new foreign plant genes, functioning as expected despite their insertion into the genome of the host crop plant in a shot-gun random manner, a process with the potential to cause other changes to the genome, changes which are inevitably negative for performance. (Although transgenic herbicide and insect resistance doesn't directly target yield, and is seen primarily as cost reducing, experience shows that there have been small positive yield effects presumably as a result of better weed and insect control, and the better agronomy allowed; Canadian canola growers claim 10% yield gains with GM canola (Brown et al 2007)).

It is much more difficult to envisage engineering which can improve a complex trait like yield under well watered conditions (yield potential) or yield under inadequate water (popularly known as drought resistance, better known as water productivity).

My doubts about genetic engineering improving yield are several fold:

(1) Natural evolution, then the helping hand of the early farmers and finally the breeders, have unwittingly refined the genetic make up of our major crop plants such that simple genetic changes for better performance have all likely been exploited, and negative ones discarded. In the past changes in agronomy created new environments which in turn offered opportunities for genetic gain (eg higher soil fertility through fertilizer demanded short wheats, better weed control permitted more erect canopies). Currently the knock down herbicide, glyphosate, has led to herbicide- resistant crops, at least saving costs if not delivering yield increases. Agronomic changes in the future could create new opportunities for breeding and transgenics alike, but they are hard to anticipate.

(2) The number of genes involved in these traits and the levels of complexity in the control of their function is large, and is making progress very difficult, and more difficult the more complex or, in genetic terms the more quantitative, is the trait. Recent excitement about the newly discovered role of micro RNAs in the regulation of gene function, while as scientifically significant as to suggest a paradigm shift in biology akin to that which arose when DNA was first elucidated, simply makes purposeful engineering of complex traits even less plausible (for an update on this complexity see Gerstein et al 2007).

(3) An added constraint is that even if likely candidate genes and regulators are inserted, consequences for the targeted traits cannot be screened in the laboratory or even glasshouse, requiring exposure to real field environments and crop communities for proper assessment. Mn tolerance involves an Mn transporter shunting toxic Mn into the vacuole and this can be assessed in single cells, but salt (NaCl) resistance could be resistance to Na uptake in roots, sequestration of Na within the plant, and/or tolerance to elevated Na levels in the protoplast (Munns et al, 2006), all of which need whole plant studies. Assessment of putative modifications for greater yield obviously requires plots in real field environments, and all the complexities of G x E that this brings, something still quite removed from our new widely touted phenomics facitities.

These reasons were valid at the outset of transgenic research say 20 years ago and they are still valid, even more so in the case of the complexity question. Nevertheless, I have searched hard for exceptions to this gloomy prognosis on yield advance via trangenics. There are only two published papers with field plot results involving wheat engineered for higher yield, one of which I shall cite later. I have noted the often optimistic statements coming from the large life science companies, and appreciate that they are investing huge amounts in this challenge (shareholders or farmers funds depending on your point of view). Noting that the private sector isn't going to readily publish scientifically anything exciting on yield, I have looked at the data bases on patents and field tests with transgenics. But reading patents is enough to drive you to despair, and there doesn't seem to be much in the USDA field test pipeline (Table3), although I do note an increase in the % of current maize and cotton tests which mention the phenotypic property "drought". What's disappointing is that few of the test descriptions give any clue as to the plausibility of what transgenes are being tested (the descriptor mostly states CBI (confidential business information) from the private sector).

So I doubt there is anything which will reach farmers anytime soon. I hope I am proved wrong, the world needs these breakthroughs, not skeptical old scientists. Whether this is a smart way for the world to go about FG is another question, but since I believe it is shareholder funds and not thus competitive with the public sector, I guess this risk taking should be applauded. But a great deal of prebreeding research of relevance to yield transgenics is taking place on crops of interest to the private sector (see below); how this interfaces and complements the private sector investment is not at all clear. As well many crops and environments are not being targeted by the life science companies, and this is a particular problem for the developing world and Australia.

Table 3

Field test release permits for transgenic crops considered by USDA, all phenotypes and phenotypes which mention either yield or drought, for the whole period 1997 to now, and for permits which are current at 1 August 2007.

	Field Test Release Permits					
Crop	All permits since 1997			Permits which are current		
	All phenotypes	Phenotype "yield"	Phenotype "drought"	All phenotypes	Phenotype "yield"	Phenotype "drought"
Wheat	429	29 (7%)	12 (3%)	15	0	1 (0.7%)
Maize	6258	298 (5%)	200 (3%)	482	23 (5%)	64 (13%)
Soybean	1291	81 (6%)	9 (0.7%)	185	14 (8%)	1 (0.5%)
Cotton	868	15 (2%)	21 (2%)	65	0	11 (17%)

5.2 A way forward for transgenics and yield improvements

I would like to finish with a more optimistic view of the yield problem than suggested in the previous section, for indeed science is "the art of the soluble", and I am sure Farrer would not have given up so soon on FG. Let's consider the best that we have in the public sector, for at least that is published. Most projects have taken the approach that there could still be single processes which are acting as bottle necks in yield formation, thus becoming major determinants of yield.

Such a process, by being simpler, might be both more amenable to favourable transgenic modification and to easier evaluation, not always needing field plantings. (Incidentally identifying such processes is precisely the business of crop physiology, a point to which I shall return).

This approach has targeted yield bottlenecks in favourable or optimal environments, but more commonly, has arisen where the target field environment has a major stress, resistance to the particular stress becoming the obvious yield bottleneck and a clearer target for genetic engineering. Several examples of each type follow:

(1) Under favourable conditions, yield in all crops is about maximizing the use of solar radiation to convert CO2 to sugar in the photosynthesis process (and distributing that sugar maximally to grains). There is now growing evidence that increased photosynthetic activity at the leaf level at key stages of development is linked to genetic improvement of yield in wheat (and other cereals). Transgenics with a more efficient photosynthetic system at the leaf level would therefore be a likely way to increase yield.

One approach, especially for C3 plants like wheat (and rice and soybeans), lies with the key CO2 capturing enzyme, rubisco, which is apparently inefficient as enzymes go, ironically so as it is the most the abundant enzyme in the world. Rejiggering this enzyme has been the "holy grail" of much photosynthesis research for some time, with little success so far (Parry et al 2007). This is no surprise: the enzyme is huge, is coded both in the nucleus and the chloroplast making engineering especially difficult, seems to trade off specificity for CO2 against rate of turnover, and has been subject to evolutionary forces since almost the beginning of life on earth. Still there are glimmers of hope, and new tools, so the search will not be abandoned just yet. After all the potential impact, not just for wheat, is huge: it could be the smartest new technology for sequestering more CO2.

(2) In cereals generally it seems that under favourable conditions grain yield after flowering is limited by the sink strength of the grain itself. Since cereal grain is largely starch, it has been proposed that starch synthesis in the grain endosperm is the critical sink process, and that, in turn, the key limitation to this is the activity of the enzyme ADP glucose pyrophosphorylase (AGP), which is involved in the synthesis of all endosperm starch from imported sucrose. The notion of an AGP bottleneck has been around since at least 1992 (Stark et al 1992). Subsequently, elegant molecular biology has engineered a more active gene-enzyme system and put it into wheat (and maize and rice), which boosts AGP activity in the endosperm. This led to a 15 year effort and elegant molecular biology, and ultimately field testing and reporting (Meyer et al 2007), but the results from the 2 years testing are unfortunately disappointing. Five backcross lines with and without the AGP transgene yielded exactly the same as the original spring wheat and had the same seed or kernel weight, despite higher yields being seen in earlier spaced plantings in the growth chamber and later the field. What went wrong?

(3) A good example, admittedly from rice, of a major but intermittent stress in an otherwise favourable cropping environment is that of the damage to pollen formation in temperate paddy rice by chilling (night temperatures < about 13C) during a narrow period just after meiosis. This is a special problem in fact in

Australia, and a substantial effort in elucidating the phenomenon at the molecular level has been made here, and also in Japan. Results suggest that the sensitivity to cold is associated with reduced expression of genes coding an invertase enzyme and a monosaccharide transporter in the tapetum wall of the anther (both involved in getting sugar to the pollen grains, Oliver et al 2007). But this is not the end of the story: the lower gene expression under chilling could be mediated by higher levels of the common plant hormone, ABA, and that the genes synthesizing ABA in rice anthers could be closer to the true receptor of chilling (Oliver et al 2007). Even so, overcoming this "simple" constrain has to date proved beyond the power of transgenics, and the involvement of ABA, and hence probably also related hormones like GA and ethylene, makes the problem more, rather than less, complex; it's like peeling the onion. Again great functional genomics, but practical benefits a dogged by the underlying complexity. I mention it here because a related phenomenon is found in wheat: again around meiosis, male fertility and hence grain set, is very sensitive to moisture stress, and it seems that again reduced activity of cell wall invertase is involved (Koonjul et al 2005), and probably also ABA, the first reference on the latter effect coming from the late physiologist Jim Morgan (Morgan 1980), employed by NSW Agriculture in Tamworth. Another plausible target for a genetic engineering solution with possible implications for yield under drought, but unlikely to be effected any time soon.

(4) Eight years ago, a Farrer orator pointed to the possibility of inserting a gene into wheat for the excretion of an enzyme called phytase by roots in order to improve performance under phosphorus shortage which is a common stress in Australian soils. Certainly a plausible idea. This enzyme can dissolve inositol phosphate (a phytate) which happens to contain much of the organic phosphorus in soils but which is insoluble and apparently poorly available to normal plant roots. Subsequently such research continued here in Canberra, and a fungal phytase gene has been engineered not into wheat but into another useful plant for Australian farmers, subterranean clover, and it appears to lead to excretion of hugely increased amounts of phytase into the rhzosphere. Unfortunately however the transgenic clover plants showed improved phosphorus nutrition in only one soil type, and many complications have been uncovered which impact on the feasibility of the task (George et al, 2005; Richardson et al 2006). Don't get me wrong, this has again been wonderful science, and there are still glimmers of hope for the original notion, but the practical results after almost a decade of solid research are a little disappointing.

(5) Not wanting to sound totally pessimistic about genetic engineering for yield potential and yield in the face of abiotic stress resistance, I would like to comment briefly on recent work on a submergence tolerance gene (sub1A) in rice (Xu et al 2006). Engineering this allele into submergence susceptible rice did confer submergence tolerance in the transgenic rice. Perhaps it is instructive that the only real world success story I have here comes from a very simple stress (anoxia), a particular stage of development (post germination), and that the transgenics only involved engineering a rice allele back into rice to prove its role, for the allele now has tight molecular markers which can be used to conventionally backcross this effective stress resistance trait into susceptible cultivars.

All the above examples are in fact intimately linked to what wheat (and rice) physiologists/ breeders have striven to do all the time, namely to dissect yield formation, identify limiting physiological processes, seek to identify genetic variation in these processes, and to use this variation to enhance the process, and hence enhance yield. We physiologists have learnt that identifying limiting processes can be tricky for there are many hidden tradeoffs. But there have also been successes. For example theoretical considerations of light penetration in canopy photosynthesis led to proposals to improve canopy photosynthesis under potential conditions by making leaves smaller and more erect, proposals which have been vindicated to a considerable extent if one observes the canopies of modern crop varieties, including modern wheats.

These last observations perhaps suggest a way forward. Several have argued that more progress will be made if yield is only dissected down to the level of key physiological processes which in turn become the target of functional genomics if and when necessary.

This is in essence a top down approach. If we consider how we might improve the performance of a well designed car, it is like looking at the gearing, the fuel delivery, or the electrics of the car, rather than starting with the individual parts, spread in their thousands on the workshop floor. Obviously functional genomics must link to physiology, and I don't think it is doing so well enough. Physiology should dictate areas of focus of functional genomics and hence areas of priority for support, and it should guide the subsequent research. At the moment, questions of excitement, glamour and hyberbole mean that the boot is on the genomics foot. It needs to change if we are to apply functional genomic to purposeful or analytical plant improvement for quantitative traits like yield. Recently a whole book was devoted to this subject (Spiertz et al 2007), in which a lot of attention was given inter alia to the role of simulation models as tools for the necessary linking across levels of organization in plants and crops.

I am not sure I so convinced of that, but I do agree with the overall conclusion that more investment is needed in linking whole-plant (and crop) physiology to molecular biology and genomics (Struik et al, 2007). I felt my argument was vindicated on recently learning that the prestigious Max Plank organization in Germany now has an institute for Molecular Plant Physiology.

6. Concluding remarks

As a crop physiologist, I have been especially talking about analytical plant breeding, but have not ignored empirical plant breeding, namely the mixing genes from many likely sources through hybridization, and screening largely by eye albeit under managed environments, and yield testing widely in order to find the rare improved recombinants. Much breeding progress in the past has been more empirical than analytical, progress coming from breeders playing the numbers game successfully, with little understanding of function at the gene or physiological level, or even despite this perceived understanding. Farrer spent most of his effort breeding for rust resistance and better grain quality, but his great success came from Federation, not noted for either trait, but adapted though earliness, shorter stature, and perhaps lower tillering to drier environments. We don't even understand the basis of hybrid vigour or heterosis more than 70 years after it was first used in maize, yet it is a major means by which higher yields of maize, sorghum, rice and several other crops have been delivered to farmers. Of course empirical breeding is, as mentioned, accessing modern tools all the times, but to a considerable extent it is skipping underlying function. And we shouldn't loose sight of the fact that conventional methods of wheat breeding continues to deliver yield progress of the order of 0.5 to 1% per annum, while attending to disease resistance and quality as well.

Farrer started us on scientific wheat breeding and, with others, foreshadowed improved agronomy, in particular soil management. We have come a long way with breeding and agronomy in the 100 years since Farrer, and we know a lot about how we have achieved this. Yet further progress is essential if we are to keep up with demand, and climate change and arable land pressures. But progress now is becoming more difficult, and will certainly demanding more research investment per unit of progress than before. The exciting new field of molecular science, in particular functional genomics, has yet to have much impact on crop improvement, apart for the 100 m ha of input saving GM crops, yet it seems to be receiving the lion's share of the pre-breeding research dollar. While not suggesting we take funds away from plant functional genomics research, we need to make sure that the glamour and optimism which surrounds this molecular plant science doesn't detract from investment in the other more traditional research areas of breeding and agronomy, and indeed we must make sure these various paths forward become better linked.

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