



# Prognosis for genetic improvement of yield potential and water-limited yield of major grain crops

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## ABSTRACT

Genetic improvement of crop yields under potential ( $Y_p$ ) and water scarce conditions ( $Y_w$ ) will be an important avenue to improved food security over the next four decades, at the end of which projected demand for food, feed and biofuel feedstock is expected to level out. Current measured *relative* rates of improvement in  $Y_p$  and  $Y_w$  for the three main cereal crops (maize, wheat and rice) in many cropping systems in the world are mostly well below the 1.16–1.31%  $y^{-1}$  rates required to meet projected demand for cereals in 2050. These relative rates can be expected to fall further if the current *absolute* rates of yield improvement continue unchanged and/or the current indications of stagnation in yield improvement for some crops in some regions of the world become widespread. This review assesses the available evidence for unexploited opportunities for enhancing current rates of genetic improvement for  $Y_p$  and  $Y_w$ , and examines some substantive proposals for achieving the same end through genetic engineering of photosynthesis, above-ground ideotype design, and improvement of root capacity for water uptake. Because time is of the essence, special attention is paid to the time scales required to progress potentially useful traits through to proof of concept under field conditions, from there to farmer-ready cultivars, and for widespread adoption by farmers of the improved cultivars. The requirements of breeders for inclusion of potentially important traits into the conventional breeding process are outlined and the value of molecular breeding tools as aids to genetic improvement of simple and complex traits is considered. Intellectual property and regulatory requirements are taken as additional potential drags on the rates of adoption into the breeding process of useful traits and/or to the free flow of information between research teams. Main conclusions are: (a) there are some unexploited opportunities to improve  $Y_p$  or  $Y_w$  in some crops and/or cropping systems; (b) exploitation of these opportunities could be hastened by increasing funding for focussed research and by identifying and eliminating or reducing drags at various stages of the idea to farmer-ready cultivar chain; (c) the time-scales required for major improvements in yield in farmer-ready cultivars through genetic engineering or ideotype realisation are likely to be measured in decades rather than years; (d) current and expected future relative rates of progress in  $Y_p$  and  $Y_w$  are a matter of real concern and are insufficient to meet projected demand for cereals by 2050. Possible step changes in  $Y_p$  or  $Y_w$  powered by genetic improvements such as exploitation of hybrid vigour in rice or hypothetical successes in the genetic engineering of photosynthesis are unlikely to change this outlook. The pessimistic assessments embodied in the last two conclusions should not obscure the fact that without continued investment in the search for sources of genetic improvement and development of aids to breeding, the unmet demands for cereals in 2050 will be even greater.

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**Abbreviations:** ASI, anthesis-silking interval; CID, carbon isotope discrimination; GxExM, genotype by environment by management interaction; GM, genetic modification; HI, harvest index; IP, intellectual property; NPT, new plant type; QTL, quantitative trait loci; RUE, radiation use efficiency; WUE, water use efficiency;  $Y_p$ , potential yield;  $Y_w$ , Water-limited yield.

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## 1. Introduction

### 1.1. Context

Estimates of world population for 2050 are in the order of nine billion people (Lutz and KC, 2010) resulting in an increased demand for food and feed. Additional weighty drivers of demand for food and feed grains over the next four decades include improved standards of living in many developing nations (Koning et al., 2008; Cirera and Masset, 2010), policy initiatives aimed at reducing

current levels of malnourishment (Bruinsma, 2009), and government policies that encourage the use of biofuels derived from grains (Fischer, 2009a). Estimating the impacts of these drivers on demand for grain and food by 2050 is a complex task hemmed in by uncertainties, but detailed analyses suggest that an increase (with respect to 2006 values) of the order of 49% for cereals (Bruinsma, 2009) will be required to meet expected demand. Estimates of use of cereals as feedstock for first generation biofuels are even harder to formulate, but Fischer (2009a) has estimated (for scenarios that appear reasonably likely) that an extra amount (over and above that required for food and feed) of between 163 Mt and 363 Mt  $y^{-1}$  will be needed for 2050, equivalent to an additional increase in global demand for cereal grains of between 9% and 19% at that time. Meeting these demands for cereals would require global harvests to increase at annual compound rates of 1.16%  $y^{-1}$  (lower biofuel requirement estimate) or 1.31%  $y^{-1}$  (upper biofuel requirement estimate) from now until 2050.

There is a developing, albeit broad, consensus within the scientific and policy-making communities that only a small proportion of the required increase in food production can come from expansion of the area that is currently cropped (Koning et al., 2008; Bruinsma, 2009). Limited availability of currently unexploited agriculturally suitable soils (Smith et al., 2010; Fischer, 2009a), a growing appreciation of the magnitude of the release of  $CO_2$  from soil organic matter that inevitably attends the conversion of grassland or forest to cropping (Spink et al., 2009; Searchinger et al., 2008), a strong desire to preserve hitherto untouched portions of important ecosystems such as tropical rainforest, and a realisation of the dangers inherent in expanding agriculture to fragile ecosystems (Cassman et al., 2003) are important elements in this developing consensus. Additionally, it is expected that there will be losses of good quality agricultural soil for urban development and other non-agricultural uses (Satterthwaite et al., 2010; Smith et al., 2010). Finally, there is a growing realisation that opportunities for expanding irrigation (a key factor in the increases in food production over the last 50 years) are limited and that in at least some production systems water currently used for irrigation will have to be reduced to favour other uses such as industrial or urban consumption (Strzepek and Boehlert, 2010). A hard to quantify factor which may impact on food production in the immediate future is the reduction in inputs used by farmers in developed countries, either because of increased relative prices for fertilisers or because of regulatory restrictions aimed at reducing losses of reactive nitrogen from fields into the broader environment. Berry and Spink (2006) have suggested that changes of this nature may be operating in determining an increasing yield gap between farmer and potential yields for oil seed rape in the UK, and Brisson et al. (2010) include this factor as a possible explanation of yield stagnation for wheat in France.

The above analyses lead to the conclusion that most of the increased food production over the next four decades will have to be achieved through increased crop yields on currently exploited agricultural soils. In some developing countries, especially in Africa, there is considerable scope for improving yields through application of well-understood technologies such as fertilisation (Cooper et al., 2008; Tittonell et al., 2008) but effective implementation of this strategy will also require considerable off-farm changes such as infrastructure improvement, increased availability of inputs for agriculture and effective markets for agricultural produce, as well as diffusion of know how and a reduction of risk aversion among farmers. Successful realisation of the “Africa option”, of itself, would not suffice to cover the required increase to 2050 and would, necessarily, take decades to complete.

There has been some considerable debate in the literature as to whether current rates of yield improvement will suffice to meet the increased demand for 2050. This debate has several dimensions, including spatial measurement scale (i.e., global vs. country

vs. region), crop species (e.g., wheat vs. rice vs. maize), and benchmark used (i.e., farmer yields derived from national or regional statistics, historical yield trial data, side-by-side comparisons of cultivars released at different times in the past, and crop simulation modelling) and conclusions reached are strongly dependent on scale, crop species, approach used and country involved. Further important dimensions of this debate are whether yield progress shows signs of plateauing and whether the relative rates of increase observed in crops and regions in which yields are increasing are sufficient to meet the 1.16–1.31%  $y^{-1}$  compound rates needed to satisfy projected demand in cereals for food, feed and biofuels for 2050 (Bruinsma, 2009; Fischer, 2009a). In wheat (Calderini and Slafer, 1998; Acreche et al., 2008; Brisson et al., 2010; Graybosch and Peterson, 2010; Cassman et al., 2010; Mackay et al., 2011) and rice (Peng et al., 1999) or in both crops (Cassman et al., 2010; Fischer and Edmeades, 2010), there is strong evidence that, at least in some countries (regions) of the globe, yield is plateauing and/or relative rates of yield progress are falling below 1.16% and can be expected to fall further if current trends persist. For maize, and particularly in the US, the situation is somewhat less clear. Some analyses (e.g., Phillips, 2010, country wide data; Fischer and Edmeades, 2010, Iowa) suggest continued increases in farmer yield. On the other hand, Grassini et al. (2011), who focus on irrigated high yield environments in Nebraska, present data that indicate farm yields are approaching or have reached their economic upper limit, quite close to simulated potential yield values. It also needs to be noted that Fischer and Edmeades (2010) estimated a relative rate of progress in potential yield for maize in Iowa of 1%  $y^{-1}$  (just outside the range of 0–0.9%  $y^{-1}$  they estimate for wheat and rice), and Cassman et al. (2010) suggest a yield plateau may be developing for irrigated maize in the US. The hard truth emerging from these different approaches, scales and crops is that the vast majority of data indicate relative rates of potential yield progress fall below the necessary exponential rate required to meet projected demand for 2050 and, in a worrying number of countries and regions, that there is strong evidence of yield plateaus. Some authors (e.g., Jaggard et al., 2010; Ewert et al., 2005) have assumed that current relative rates of yield progress, as derived from linear functions fitted to historical yield data and estimated for the end point of their data series, will be maintained in the future. This seems unlikely, even in the absence of insuperable biophysical limitations. A continuation of current linear trends in yield progress are, almost certainly, the best possible outcome, and this implies a continuously decreasing, rather than a constant relative rate of yield progress.

The routes to the achievement of increased and sustainable global food security by 2050 are several (e.g., Godfray et al., 2010a,b suggest five) and include genetic improvement for grain crop yield potential in unstressed environments (Yp) and for water-limited yield potential in dryland (rainfed) environments (Yw). In this paper we attempt to assess the current status, opportunities and requirements for progress and its verification in both Yp and Yw, paying particular attention to likely timescales. We concentrate on the most important cereals (maize, rice, wheat) because of their dominant contribution to current and likely future global food, feed and biofuel requirements.

## 1.2. Genetic improvement of yield

Breeding is at the heart of any process aimed at improving Yp or Yw, and is currently undergoing a rapid expansion of the technical options available to progress any given set of aims, including Yp and Yw. Consequently, we give due consideration to the nature and practical requirements of breeding processes aimed at achieving farmer-ready cultivars with improved Yp or Yw. Genetic improvement may be further enhanced by new or improved traits made available through genetic engineering or the

mining of existing genetic variability. The identification of these traits and the importance of them should be assessed by whether they fit into frameworks that are appropriate to the improvement of either Yp or Yw, so we make some attempt to deal with this issue. With the 2050 deadline and germplasm development and breeding timescales very much in mind, we have used some published estimates of the likely time required to improve, via genetic engineering, the photosynthetic capacity of crops to illustrate this aspect of the road ahead. In a similar vein, we have documented the time required, in the past, to progress some ideas or discoveries of traits related to improved Yw up to the proof of concept or cultivar release stages. Time is also required for improved cultivars to be widely adopted by farmers, and we briefly touch upon this issue.

The range of traits that have been suggested as possible contributors to the improvement of either or both of Yp and Yw is very large, and we make no attempt at comprehensive coverage of these suggestions. Instead, we have used, as examples of the difficulties that must be faced, two particular processes which we believe are potentially very important and, at the same time, constitute very large challenges for progress to improved yields. Firstly, improvement of photosynthetic capacity for both non-stressed and water-limited conditions, and secondly, improvement of root system capacity to capture water in dry environments.

We recognise that the degree of success that might be achieved in Yp and Yw will be affected by climate change, especially via changes in atmospheric CO<sub>2</sub> and O<sub>3</sub> levels, mean temperatures and frequencies of episodes of heat and water stress (Gornall et al., 2010). These features of climate change will impact on issues such as sowing dates and crops best suited to particular environments; and current rates of progress (or lack thereof) estimated for C3 cereal crop yields across the world include some degree of response to changes in temperature and CO<sub>2</sub>. The knowledge base underpinning attempts to predict possible effects of changes in atmospheric CO<sub>2</sub> and O<sub>3</sub> levels on crop productivity (e.g., Fischer, 2009a; Jaggard et al., 2010) is limited (Gornall et al., 2010), as is the case for acute or chronic changes in temperature (cf. Hall and Sadras, 2009). Breeders and farmers have, in the past, been successful in optimising their activities over broad spatially determined ranges in environmental conditions (Cooper et al., 2008). Effects of climate change will develop slowly over time, so business-as-usual genetic improvement and gradual adaptation of farming systems are likely to handle these effects successfully. In this review we do not deal with the possible effects of climate change on genetic improvement for Yp and Yw.

## 2. Genetic improvement of yield potential

### 2.1. Rates of Yp increase: current status

Any assessment of the prospects for genetic improvement needs to consider what are the current rates of increase in Yp. In what follows, we consider this issue in the context of some of the available empirical (i.e., not theoretical) evidence pertaining to crop species as we know them today, that is, without the possible benefits of bio-engineered photosynthesis. Rather than a comprehensive review, we have concentrated on the main cereals but have, on occasion, had recourse to other crops. Available empirical evidence paints different pictures for each of the main cereals and highlights the fact that the quality of the evidence varies between cereals.

Duvick and Cassman (1999) examined evidence from various sources (including side-by-side yield comparisons of maize hybrids released at different times in rainfed trials, trends in average yields for Iowa and Nebraska, irrigated yield contest results in the same states), and came to the conclusion that while there was evidence for continued increases in Yw, there was no substantive indication

of improvement in Yp of maize hybrids used in the region in the 15 years preceding 1999. Cassman et al. (2010) found an incipient plateau in irrigated maize yields for the western Corn Belt and Great Plains states for the 2002–2008 period, and Grassini et al. (2011) report that model simulations for mean yields of current maize hybrids under optimum water and nitrogen availability in Nebraska are of the order of 17.5 t ha<sup>-1</sup> over the 1988–2008 period, not very different to the mean of 18.2 t ha<sup>-1</sup> reported by Duvick and Cassman (1999) for irrigated contest-winning yields in the same state for 1983–1997. Messina et al. (2009) provide data that suggest that under full irrigation the yield of maize in a target population of environments was increasing at 0.79% y<sup>-1</sup> in 2007, although other less optimistic interpretations of their data are also possible. Taken together, this evidence suggests that Yp of maize under intensive irrigated farming in the US has either not changed over the last two decades or is increasing at a rate insufficient to meet expected demand.

Estimates of yield potential for maize in other regions of the world are hard to come by (cf. Fischer and Edmeades, 2010). However, Luque (2000) compared yields of 7 maize hybrids, released between 1965 and 1997 in Argentina, in side-by-side experiments under irrigation and a range of crop population densities over 2 years. Average yields at crop population densities of 9 pl m<sup>-2</sup> (none of these hybrids exhibited negative yield responses at this population density) increased steadily with year of release from 7.4 to 14.8 t ha<sup>-1</sup>. These increases were associated with longer times to anthesis, greater stay green, greater anthesis RUE, improved partitioning to the ear around flowering, shortened anthesis-silking interval, and better grain set. It may also be important that over the period in which these hybrids were released (almost exclusively for use in rain-fed agriculture) there was a continued process of introgression of US dent germplasm into the flint germplasm that used to characterise Argentine maize and a shift from double hybrids to single hybrids (Luque et al., 2006). Although this result from Argentina is a single example it suggests that, at least in some maize-producing regions of the world, there may be some remaining scope for improving maize Yp.

The standard way of determining relative rates of genetic improvement is to grow historic sets of varieties side by side and to control pests and diseases so as to assess true genetic differences in grain yield, although recent statistical advances in the analysis of unbalanced data sets has also been very important (Smith et al., 2005; de la Vega and Chapman, 2010) and may provide an alternative route that avoids the effects of loss of yield potential of cultivars with time from year of release, as has occurred in rice (see below) and sunflower (de la Vega et al., 2007). Yield potential in irrigated spring wheat, as determined in experiments in the Yaqui Valley in Mexico, was increasing at 0.3% y<sup>-1</sup> in 2005 (Fischer and Edmeades, 2010; Sayre et al., 1997). However, in the warmer environment of Tlatzapán, yields were less than half those of the Yaqui Valley and showed little tendency to increase in cultivars released after 1966 (Reynolds et al., 2000). At both sites there was evidence that higher yields were associated with higher stomatal conductance, lower canopy temperature and greater photosynthesis (Fischer et al., 1998; Reynolds et al., 2000). Historic set studies on irrigated winter wheats from different periods in the main winter wheat regions in China (Zhou et al., 2007; Xiao et al., 2012) have demonstrated mean relative rates of yield increase of 0.68% y<sup>-1</sup> and 0.75% y<sup>-1</sup>, estimated at the year of release of the most recent cultivar.

The most comprehensive data sets for wheat are from the UK where environments are very favourable for temperate species as there is generally adequate rainfall and the season is mild, so that results from rainfed trials may serve, in most years, as an approximation to true yield potential. In the UK national trials are conducted annually contrasting the latest cultivars. These have

complete pest and disease protection and agronomic advances can be separated from improvements due to genetics. Data from rainfed variety trials in the UK and France show consistent upward trends in yields (Spink et al., 2009; Jaggard et al., 2010; Brisson et al., 2010). Mackay et al. (2011) conducted a comprehensive analysis of genetic gain in winter wheat in the UK since 1947 which involved 3590 site-year combinations. They found a linear rate of yield increase of  $69 \text{ kg ha}^{-1} \text{ y}^{-1}$  between 1948 and 2007, a value that translates into a relative rate of  $0.76\% \text{ y}^{-1}$  in 2007. They also found that since 1982 at least 88% of improvement in yields across a range of species could be attributed to genetic improvement. Studies on varieties released in the UK after 1990, which led to an estimated relative rate of genetic gain of  $0.59\% \text{ y}^{-1}$  (Fischer and Edmeades, 2010), showed that the increase in yield has been associated with greater above-ground biomass accumulation, greater pre-anthesis RUE and higher stem water-soluble carbohydrate content at anthesis (Shearman et al., 2005). In spite of the fact that water stress is neither frequent nor intense in the UK, some caution needs to be exercised in assigning the observed yield trends in rain-fed yield trials exclusively to increased yield potential, leaving aside an improved stress tolerance component, as suggested for maize in the US (Duvick and Cassman, 1999) and by Sadras and Lawson (2011) for rainfed wheat in the harsher environment of South Australia. Experiments under irrigation would be helpful in clarifying this uncertainty.

Improvements in yield must come from either increases in crop biomass or harvest index (HI) or from a combination of both of these. Many studies on historic wheat sets up to the 1980s failed to show any increase in crop biomass and the main increases were attributable to an increase in HI (often as a result of earlier flowering). Furthermore, grain number per unit area is the yield component that has been responsible for this increase and there has been little change in kernel weight. However, in the most recent studies on historic data sets in the UK, China, Mexico and Australia (referenced above) there is increasing evidence that increases in crop biomass are beginning to contribute to increased wheat yields.

A careful study aimed at establishing genetic gain in inbred *indica* rice cultivars in the Philippines (Peng et al., 1999, 2000, 2010), using side-by-side trials of cultivars released at different times after 1968, indicates that there has been no progress in potential yield. Rather, breeders efforts have served to maintain a yield potential equivalent to that of the earliest cultivar (IR8, released in 1968, and which currently yields a good deal less than at the time of its release) in the face of some evolving (and, as yet, unidentified) biotic or abiotic challenges. Ideotype-based approaches, backed by evaluation of reputed traits of interest using simulation modelling (e.g., Aggarwal et al., 1997), have been used in attempts to develop new plant type (NPT) inbred cultivars, but there appears to be little, or no, realised gain in potential yield in these NPTs with respect to earlier inbred cultivars (e.g., Yang et al., 2007). Horie et al. (2006) demonstrated that grain yields across a set of nine inbred cultivars over 2 years were associated with canopy conductance, a finding which may point to the existence of some exploitable genetic variability for yield, but this finding has not, to our knowledge, been tested in a breeding program nor linked to genetic gain in rice  $Y_p$ .

The yield advantage of hybrid rice is typically 10–15% more than inbred cultivars (e.g., Peng et al., 1999; Yang et al., 2007; Bueno and Lafarge, 2009; Lafarge and Bueno, 2009; Bueno et al., 2010; Li et al., 2009a). This advantage has been enough to overcome the economic limitations imposed by the greater (with respect to inbreds) annual replacement cost of seed. Hybrid rice now covers close to 60% (mean for 2004–2008) of the area sown to rice in China (Li et al., 2009a), and the area is also expanding, albeit at a slower rate and from a much lower base, in south-east and south Asia (Janaiah and Xie, 2010). Li et al. (2009a) provide data which show that commercial hybrid rice yields have been growing at a steady  $46.4 \text{ kg ha}^{-1} \text{ y}^{-1}$  over the last 25 years (i.e., relative rate of yield advance of  $0.64\% \text{ y}^{-1}$

for 2008). In a comparison involving sets of four hybrids and four inbreds over two seasons, Bueno and Lafarge (2009) found mean hybrid biomass at harvest and mean hybrid HI to be greater than the corresponding values for inbred lines.

Annual replacement cost of seed is especially important in crops such as rice and wheat, which are sown at a much higher crop population density than species such as maize and sunflower in which the introduction of hybrids has been an effective route to increased yield. In contrast to rice there is negligible hybrid wheat grown commercially despite the large private investment in global breeding. In a comparison of hybrid and pureline entries in performance nurseries conducted over 20 years in the southern Great Plains of the US the average yield advantage of the wheat hybrids was about 5% (Koemel et al., 2004). It is likely that the seed production and breeding costs are still not competitive with pureline varieties in wheat.

In summary, empirical evidence for inbred tropical rice and hybrid maize in environments in which intensive agriculture is practiced and important breeding efforts have been made, strongly suggests that there has been little or no change in  $Y_p$  over the last few decades. There may be opportunities to increase maize  $Y_p$  in some regions of the world thanks to introgression of previously unused germplasm, but further research on this issue is required. Genetic improvement of yield potential of inbred tropical rice seems to have plateaued, although hybrids may offer a one-off step-increase. Finally, the difficulties in realising the expected yield advantages of NPT rice may constitute an illustration of the difficulties that must be overcome in ideotype-based approaches to yield improvement. In contrast to maize and rice, there is a fair amount of evidence consistent with a continuing increase in  $Y_p$  in wheat. However, current rates of progress in this crop, measured in a range of environments across the world, are consistently lower than that of the  $1.16\text{--}1.31\% \text{ y}^{-1}$  that would be required to meet projected demands for 2050.

## 2.2. Suggested options for future increases in $Y_p$

Suggested responses to the challenge of increasing yield to meet the 2050 deadline vary considerably in focus and in degree of detail. Some are very generic and, very importantly, often lack time scales for implementation (e.g., Phillips, 2010; Zhang, 2007; Dunwell, 2011) and receive no further attention here.

Other proposals to increase  $Y_p$ , which might be termed top-down or from crop-to-attribute (e.g., Sylvester-Bradley et al., 2005; Berry and Spink, 2006; Spink et al., 2009), are based on current understanding of the ecophysiology of crop radiation capture, the efficiency with which captured radiation is transformed into biomass and the proportion of that biomass converted into grain (i.e., the Monteith (1977) framework), and attempt to design ideotypes that would be able to capture more resources and channel them to yield. Others (bottom-up, or process to crop) focus more narrowly on bio-engineering the photosynthetic process (Murchie et al., 2008; Zhu et al., 2010; Hibberd et al., 2008; Furbank et al., 2009). Still others have a broader remit and seek to cover the full spectrum of the bottom-up and top-down approaches, expanding these to include the use of genetic resources from related and unrelated species (Reynolds et al., 2011; Parry et al., 2011; Foulkes et al., 2011; Spink et al., 2009). Taken together, these proposed frameworks lay out the complexity of the challenges that need to be overcome in order to accumulate the desired traits in elite breeding material that is reasonably free of linkage drag and which might be used to diffuse these traits into locally adapted cultivars fairly quickly. Importantly, several of these contributions attempt to establish possible time-frames for achieving their various targets (e.g., Zhu et al., 2010; Spink et al., 2009; Reynolds et al., 2011). Spink et al. (2009) suggest 5- to 15-year periods might be needed



to improve such traits as delayed canopy senescence, early canopy closure and earlier stem extension in wheat; and bioengineering of photosynthesis might take between 5 and 30 years (see Section 2.3).

We believe that some degree of caution is warranted with respect to the possible time frames referenced above. Reasons for caution include limited success and slow rates of progress in past attempts to improve crops for some physiological traits (e.g., Richards, 2006). Slow rates are mainly attributed to the time required to develop fast and effective selection methods, develop appropriate breeding germplasm and then produce sufficient seed of contrasting lines to obtain proof of concept in the field. Further development will then be dependent on plant breeders having the resources, time and commitment to integrate the physiological trait into genetic backgrounds that are likely to be adopted by industry. During this time breeders will need to deal with possible trade-offs between traits and matching trait to specific environments (i.e., managing genotype by environment interactions). All of these reasons point to longer terms for the achievement of some useful improvement in farmer-ready cultivars with greater  $Y_p$ .

### 2.3. Photosynthesis: the big bazooka in the $Y_p$ game?

Here we consider the prospects and likely time scales for improving yield potential via bioengineering of photosynthesis in C3 crops and/or exploitation of currently available sources of genetic variation for photosynthetic traits. Photosynthesis is the obvious process to consider given that any improvement in it could translate to other crops and to most if not all environments. Improvements in photosynthesis have the potential to translate to higher yields under favourable conditions through improved RUE and also under water-limited conditions through improved water-use efficiency (WUE). Despite breeding efforts world-wide to improve grain yield of all our crops there is only limited evidence to suggest that breeding has increased photosynthesis. Most increases in yield of our main crops achieved by breeding since around 1900 have been due to increases in HI (Fischer and Edmeades, 2010). Maize may be an exception here as the increase in maize yield in southern Canada between 1959 and 1988 was due to greater biomass and an extended period of photosynthesis after flowering (Tollenaar, 1991). Although clearly photosynthesis has increased over time, mainly as a result of improved or extended seasonal radiation capture; increased amounts of nitrogen fertiliser applied to crops has greatly contributed to this as well.

Other factors contributing to the importance of improving photosynthesis include: (a) the likelihood that fertiliser use in high production systems has already been optimised, and (b) that CO<sub>2</sub> enrichment experiments in the field demonstrate that increasing photosynthesis translates to higher grain yields (Long et al., 2006). Several recent papers (Parry et al., 2011; Zhu et al., 2010; Murchie et al., 2008) have comprehensively reviewed the prospects of improving photosynthesis or have focused on the subplot of conversion of the photosynthetic carbon fixation process from its C<sub>3</sub> to its C<sub>4</sub> variant (Hibberd et al., 2008; Furbank et al., 2009). Collectively, they lay out a very broad range of approaches of varying complexity aimed at increasing crop biomass production (and hence yield) that span the mining of existing germplasm for traits such as staygreen and spike photosynthesis through to very complex bioengineering of both the biochemical and photochemical phases of photosynthesis and of its associated processes (e.g., photorespiration).

Transgenic approaches aimed at C<sub>3</sub> to C<sub>4</sub> conversion at biochemical and anatomical levels and changes in Rubisco properties are obviously the most difficult to achieve. Here, we do not go over this ground again, but focus on the complexities associated with the various approaches, as perceived by these authors, and the

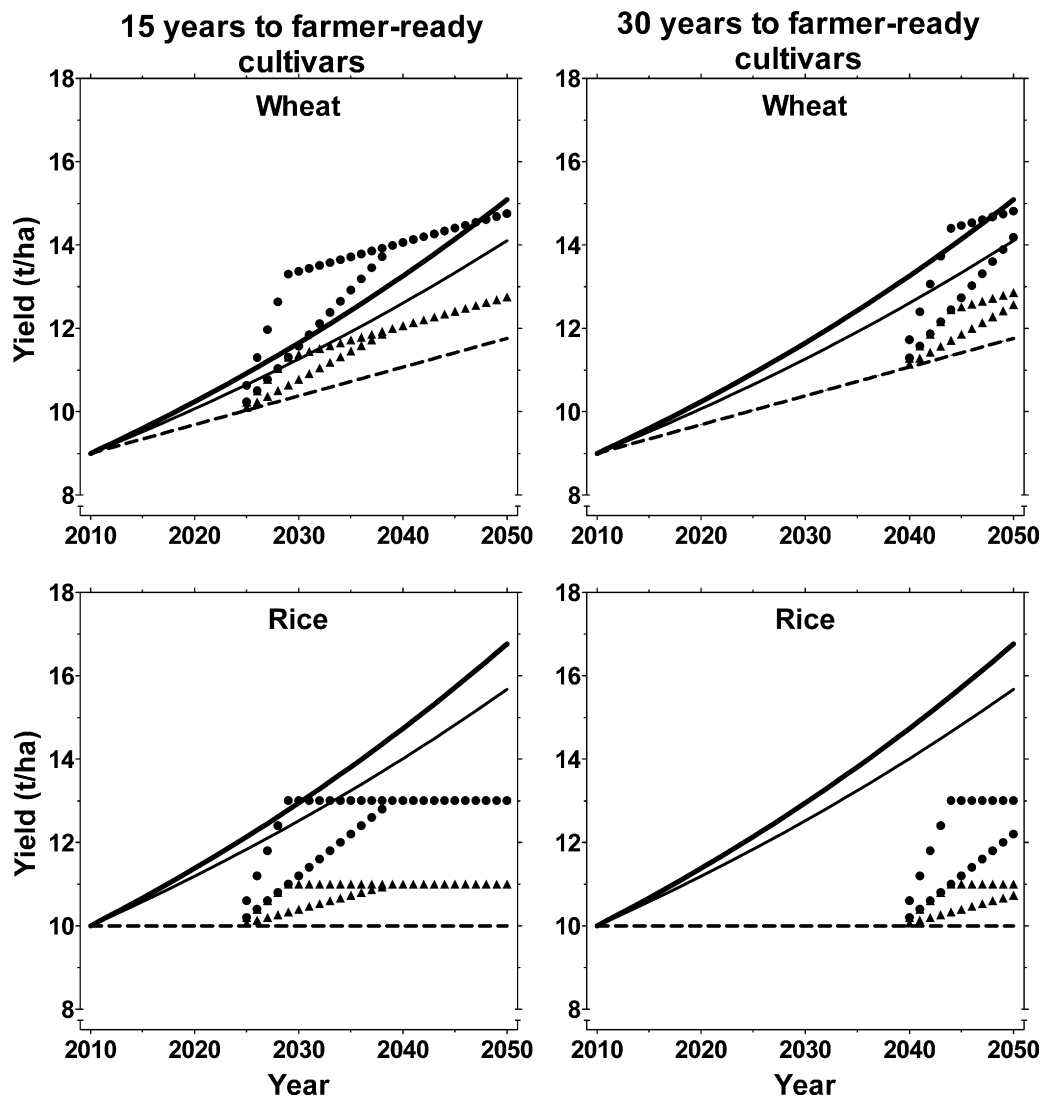
timescales which have been suggested for achieving the various goals (e.g., Table 1 in Murchie et al., 2008, Table 2 in Zhu et al., 2010; and Table 2 in Parry et al., 2011). Perhaps the first thing that needs to be said is that the attempts made in these papers to categorise the proposed approaches according to their degree of complexity and possible impact and, in two of them, to suggest time scales for realisation of the various goals is a very welcome change from generic calls to action to bioengineer photosynthesis or naive claims of the potential importance for global food security of the elucidation of one piece of the photosynthetic process jigsaw puzzle.

In the context of this review, it is important to highlight the fact that estimates of the predicted impact of the various proposed changes in the photosynthetic processes on crop carbon assimilation are mostly in the 5–30% range and time required to achieve success in these assorted objectives from 5 to 20 years. Not surprisingly, there are some differences in forecasts between authors. Thus Zhu et al. (2010) predicts the impact of Rubisco with low or nil oxygenase activity and the C<sub>3</sub> to C<sub>4</sub> conversion in the order of 30% while Parry et al. (2011) suggest 100% for the first and 50% for the second, and increased mesophyll conductance is suggested to require 20 y with high investment by Zhu et al. (2010) but only 5 y by Parry et al. (2011). Zhu et al. (2010) caution that 10–20 additional years may be needed to incorporate any successful changes into farmer-ready cultivars; but Parry et al. (2011) suggest that 5 y might be needed to mine existing germplasm for useful traits and introgress them into wheat lines available for first crosses in breeding programs. These timescales would seem very optimistic for food crops even for relatively simple traits (see, this section and Section 3.4).

The whole issue of strategies for improving photosynthetic performance of crops through bioengineering of the basic processes of carbon fixation is, of necessity, rather speculative. However, the complexity of the challenge is clearly very great and the time needed to achieve progress (in the form of farmer-ready cultivars) will likely be in the order of 20–30 y for changes that could signify improvements in photosynthetic performance of C3 crops of 15–30%, always providing that realisation of these bioengineering goals does not bring into play unconsidered trade-offs that often complicate the transition in scales from process to crop (Sinclair et al., 2004; Passioura, 2010).

A further, often unconsidered, dimension of the challenge to improving grain yields through improved crop photosynthetic performance is the time required for new cultivars to be widely adopted. These intervals can vary considerably with crop and context. Glyphosate-resistant soybean covered practically the whole of the production area of this crop in Argentina in 5 years (Vara, 2004); reaching the current ca. 60% coverage of the rice production area in China with hybrid rice took 15 years (Li et al., 2009a); and spread of GM corn in the US from 1994 onwards took place at a linear rate of 5.8% of sown area per year (Phillips, 2010).

To highlight the magnitude of the challenges that need to be overcome in order to raise  $Y_p$  to the levels required to meet demand expected for 2050, we performed a simple exercise involving wheat and rice, C3 species which might be expected to respond positively to successful bioengineering of the photosynthetic process. The assumptions underlying these projections are outlined in the legend of Fig. 1. Unsurprisingly, projected yields of the two crops, at current linear rates of yield increase, lag further and further behind demand as time from 2010 increases, the lag for rice being much worse than wheat (Fig. 1). By contrast, the sobering conclusion of these back-of-an-envelope speculations about the possible impact of improvements in photosynthesis, is that for rice, even the combination of a 30% step change in yield, with a 15 y delay in producing a farmer-ready cultivar, and full adoption in 5 y would only serve to meet projected maximum (i.e., at 1.31%y<sup>-1</sup> rate of increase) demand between 2028 and 2030 (Fig. 1). All other combinations,



**Fig. 1.** Possible 2010–2050  $Y_p$  trajectories for wheat and rice in relation to projected demand. Curves in each panel show required  $Y_p$  assuming required compound rates of yield increase of  $1.31\%y^{-1}$  (upper curve) and  $1.16\%y^{-1}$  (lower curve) (cf. text Section 1). Continuous dashed line in each panel shows expected yield trajectory assuming current linear rates of yield increase ( $68\text{ kg ha}^{-1}y^{-1}$  for wheat [Mackay et al., 2011],  $0\text{ kg ha}^{-1}y^{-1}$  for rice [Peng et al., 2010]) and initial (2010) values of  $9\text{ t ha}^{-1}y^{-1}$  for wheat (Mackay et al., 2011) and  $10\text{ t ha}^{-1}y^{-1}$  for rice (Bueno and Lafarge, 2009; Peng et al., 2010). Superimposed on the above three lines are estimated trajectories resulting from introduction of farmer-ready cultivars incorporating large (30%, full circles) and moderate (10%, full triangles) increases in crop photosynthetic capacity (Zhu et al., 2010) after delays with respect to 2010 from idea to farmer-ready cultivars of 15-y (left-hand panels) or 30-y (right-hand panels). For each of the two step changes in crop photosynthetic capacity, two linear rates of adoption by farmers are considered: 100% adoption in 5 y (line closer to the y-axis) and 100% adoption in 15 y (line furthest from the y-axis). After complete adoption, current linear rates of yield progress are assumed to continue unchanged.

although leading to improved yield over time, would be insufficient to meet projected demand at any time from now to 2050. For wheat, and with one exception, the only combinations of factors leading to satisfaction of projected maximum demand over two or more decades were a 30% step change in yield and a 15 y delay in obtaining farmer-ready cultivars (Fig. 1). The exception was that a 30% step change after 30 y, combined with full adoption in 5 y is projected to meet demand between 2043 and 2048.

### 3. Genetic improvement of water-limited yield potential

#### 3.1. Rates of improvement in $Y_w$ : current status

The question of whether there has been genetic improvement in  $Y_w$  can be viewed from at least two different viewpoints. Firstly, from sustained increases in yields over time, demonstrated either in side-by-side rainfed trials under standard management or in

rainfed yield contests (e.g., Duvick and Cassman, 1999; Shearman et al., 2005; Sadras and Lawson, 2011), and secondly from variety trials conducted under rainfed conditions over extended periods of time (e.g., Spink et al., 2009; Jaggard et al., 2010; Brisson et al., 2010; Mackay et al., 2011). Fischer and Edmeades (2010) suggest that breeders have been successful in raising  $Y_w$  for both maize in Iowa and wheat in France, the UK and Australia, but the same appears not to apply to rainfed wheat in the Great Plains of North America (Graybosch and Peterson, 2010) or in Spain (Acreche et al., 2008). Estimates of recent rates of progress in  $Y_w$  for wheat in areas for which improvement has been demonstrated are close to  $0.54\%y^{-1}$  (compilation of side-by-side trial data for Australia by R. Fischer, 2009b),  $0.87\%y^{-1}$  in France (variety trial data, Brisson et al., 2010) and  $0.50\%y^{-1}$  (side-by-side trial data for South Australia, Sadras and Lawson, 2011). Duvick and Cassman (1999) provide data which suggests that improvement of  $Y_w$  in rain-fed side-by-side comparisons for maize at optimum densities (i.e., those appropriate to the year of release of the hybrids) of  $0.68\%y^{-1}$  (1992) and  $0.81\%y^{-1}$

(1989) for maize in Iowa. Messina et al. (2009) provide data suggesting Yw for maize in a rain-fed target population of environments in the US was improving at  $0.61\%y^{-1}$  in 2007.

A second and complementary approach to the achievements described above using conventional breeding revolves around conscious attempts to improve Yw using physiological or molecular traits. A large number of putative physiological traits or black-box transgenes that might contribute to improved Yw have been proposed, and a very few of these have actually been demonstrated to be effective in the field for wheat (Richards, 2006 and refs. cited therein) and maize (Campos et al., 2004; Chimenti et al., 2002; Castiglioni et al., 2008; Bänziger et al., 2006). Passioura (1977, 2006) proposed that crop performance under water scarcity could be usefully examined within a framework that envisaged yield as the product of crop seasonal water use (WU), seasonal water use efficiency (WUE) and HI. He further argued that acceptance of putative traits that might contribute to greater yield under water scarcity should be conditional on the experimental demonstration that the trait or gene construct in question operated through alterations in one or more of WU, WUE and HI. Importantly, it has sometimes been possible to link the effects of some of these physiological traits to improvements in one or more of the elements of the Passioura identity, thus allowing a better appreciation of the mode of action of a given trait and its likely appropriateness to specific seasonal patterns of water availability and potential negative trade-offs. Thus, in maize, selection using anthesis-silking interval (ASI) and other traits improved HI (Edmeades et al., 1999, see Section 3.4), and higher osmotic adjustment led to greater WU and HI (Chimenti et al., 2002). In wheat, HI was improved by selection for narrow xylem vessels, WUE and HI were improved by selection using carbon isotope discrimination (CID) (Richards, 2006, see Section 3.4), and higher osmotic adjustment led to improved WU, WUE and HI (Morgan and Condon, 1986).

Yield loss mitigation under water-scarce conditions in rice (especially important for upland, rain-fed, rice) has received less attention in recent years than in wheat and maize. Nevertheless, a project involving a large number of diverse lines grown under managed stress environments has served to demonstrate the existence of significant genetic variability for yield loss mitigation under drought (e.g., Lafitte et al., 2006, 2007), a fact which encourages further research on this issue. A large-effect QTL for yield under drought during the reproductive stage in rice has been reported in a study using a large number of  $F_3$ -derived lines originating in a cross between reportedly sensitive and tolerant lines (Bernier et al., 2007), but the significance of this is hard to discern because of the confounding associations between this QTL and time to flowering and, hence, the congruence between the timings of stress and flowering (cf. Reynolds et al., 2009).

Overall, important messages emerging from the work described above are that opportunities, both past and future, have existed or exist to increase Yw in wheat, maize and rice. In the past, these have been realised through selection for yield in rainfed multi-environment trials conducted within specific target environments (e.g., Duveck and Cassman, 1999; Shearman et al., 2005; Spink et al., 2009; Jaggard et al., 2010; Brisson et al., 2010; Sadras and Lawson, 2011). Selecting for specific traits and yield in managed selection environments designed to mimic the main features of seasonal water availability has also served to effectively advance Yw (Campos et al., 2004) or to demonstrate the existence of exploitable genetic variability for water-scarce yield potential (Lafitte et al., 2006, 2007). Managed stress environments also allow genetic advance for Yw to be quantified (e.g., Campos et al., 2004), serve to demonstrate the usefulness of particular traits (e.g., Campos et al., 2004; Chimenti et al., 2002; Bänziger et al., 2006) and often facilitate the measurement of the three elements of the Passioura identity. Testing of germplasm bearing possible advantageous traits

across a range of naturally occurring water-scarcity levels against check cultivars or sets of cultivars, as exemplified in Richards et al. (2007), also serves to demonstrate the usefulness of reputed traits.

The experience of inferred past gains in Yw through selection for yield in appropriate water-scarce environments, through exploitation of genetic variability generated by appropriate crossing programs, or via attempts to exploit physiological traits discovered through serendipity (e.g., anthesis-silking interval in maize, Campos et al., 2004) or following physiological reasoning (e.g., improved transpiration efficiency, TE, in wheat, Richards, 2006) all point to the fact gains are often fairly small in absolute terms (except under extreme drought) and relative rates of advance are not likely to be high. The yield gain, for example, from improved TE varied from 0% in the most favourable environment to 11% in the driest environment when contrasts were made in the same genetic backgrounds (Rebetzke et al., 2002), although when the contrast was made between high TE cv. Drysdale and low TE cv. Diamondbird yield gains varied from 0 to 35% in wet and dry environments respectively (Richards, 2006). For xylem vessel diameter the yield increased by around 7% in the driest environment and was neutral in the wettest environment (Richards, 2006). The *CsbP* transgene in maize (Castiglioni et al., 2008) provided a 33% increase in yield in the most stressful environment, tapering away toward neutrality in the better ones. These numbers also serve to show that gains will be strongly dependent on the intensity, duration and timing of the exposure to stress (see below). Another important lesson that has come out of all of these studies is that flowering time has a profound influence on yield under drought in all species and that when germplasm is being contrasted then flowering time of each line tested must be quantified so that its influence can be determined.

A great deal has been written about the use of transgenes or over-expressed native genomic regions as tools to improve Yw, but there are few examples in the literature (e.g., Castiglioni et al., 2008) in which adequate field proof has been provided. Even in this case, and given the often unique fit between the mode of action of an effective trait and nature of the target water availability regime, we still need to know how the trait works and what its effects on the elements of the Passioura identity are (Salekdeh et al., 2009).

### 3.2. Frameworks and tools for increasing water-limited potential yield

In water-limited environments, the problem of increasing Yw is even more complex than that of increasing Yp in unstressed environments. Seasonal patterns of crop-available water vary between environments and especially between years within environments (e.g., Chapman, 2008). Understanding the resulting genotype by environment interactions is essential to both the design of effective selection strategies for genetic improvement of yield and for correct interpretation of results obtained in multi-environment trials. A further dimension to this issue is that not all attributes that might contribute to yield loss mitigation under water scarcity are equally useful in all water-scarce environments (e.g., Richards, 2006). Additionally, the genetic architecture of the crop may condition the selection strategy that could lead to the optimum combination of genes or traits for a given environment (e.g., Hammer et al., 2009; Messina et al., 2009; Chenu et al., 2009; Messina et al., 2011). And last, but unfortunately not least, the disconnect between many attempts to isolate genes or genomic regions that might be of interest as sources of yield loss mitigation under water scarcity and the realities of crops growing in water-scarce fields has led, in too many cases, to a focus on plant survival rather than on crop yield loss mitigation (e.g., Sinclair et al., 2004; Passioura, 2010) as an indicator of tolerance to water scarcity.

The Passioura framework has gained a great deal of acceptance among breeders and crop ecophysiologicalists working in water-scarce environments (Richards, 2006) and, more recently, has been recommended in the context of molecular breeding (Salekdeh et al., 2009). Crop simulation models, combined with soil specifications and extended climatic records (e.g., Chapman, 2008) can provide a robust quantitative biophysical diagnosis that will, in combination with the Passioura framework, contribute to the understanding of crop responses to water-scarcity and help in the design of breeding strategies (including the use of managed water supply regimes, Campos et al., 2004) appropriate to given target environments. It seems highly probable that progress in Yw can be achieved using these tools and framework, but the necessary investment in time, experimentation and research facilities for full implementation of this strategy should not be underestimated.

In the context of opportunities and limitations for genetic improvement of Yw, a set of recent papers (Hammer et al., 2005; Messina et al., 2009, 2011; Chenu et al., 2009), based on the combined use of process and genetic/breeding models, deserve special mention. They aim to show how the combination of these two types of models, given information about QTLs or genes linked to potentially interesting traits, can help breeders navigate complex yield-trait performance landscapes, break away from the one-trait-at-a-time approach, and mitigate uncertainties linked to GxExM interactions when using markers for multiple traits. The likely impact of this strategy on the rate of improvement in Yw is hard to assess at this time, either because some details of the work remain confidential (Messina et al., 2011), because the authors have had to use some plausible, but as yet unproven, relationships between processes such as silk extension and its genetic control (Chenu et al., 2009), or because the information requirements (especially, phenotyping) are high. In spite of these restrictions, these papers serve to illustrate the complexity (and likely slowness) of the way forward under water-limited conditions. Importantly, they also serve as a reality check for proposals aimed at increasing Yp (Spink et al., 2009) through breeding aimed at improving crop radiation capture, radiation use efficiency and HI.

Some private sector seed companies have relied on the use of transcription factors or chaperones (isolated from the crop species in question or originating in other species) to improve Yw (e.g., Nelson et al., 2007; Castiglioni et al., 2008; Edgerton, 2009). Research reported in this latter group of papers highlights the potentially important issue that the physiological mode of action of these transcription factors is not reported, something which seriously hinders an appreciation of the water-stress regime for which they might prove effective (cf. Hammer et al., 2005). More informative as to physiological mode of action, but further away from testing in crop species, is the work on transgenes (e.g., Rivero et al., 2007) and transcription factors (e.g., Kasuga et al., 1999) that show some promise as sources of drought tolerance.

In summary, there are indications that genetic improvements in Yw have been achieved in some (albeit not in all) systems by selection in multi-environment rainfed trials or managed stress environments, and that there is or may be potential for further improvement. There have been limited demonstrated incremental gains in Yw using physiological traits and at least one transgenic approach seems to improve Yw in maize. The Passioura framework has been shown to be a useful tool in assessing the mode of action of some physiological traits, and crop simulation models (in combination with long-term climatic records and soil information) can provide very important insights to guide the selection process. New tools, such as the combined use of crop process and genetic models show promise as aids to the improvement process but, at the same time, signal the need for moderating expectations given the complex interactions between specific traits, a highly variable seasonal water supply, and the genetic architecture of the crop. Based

on limited evidence, transgenes may provide a further avenue for improvement of Yw, but there needs to be a fundamental re-think of this issue in order to focus research on yield loss mitigation rather than plant survival or responses to unrealistic rates of stress development when searching for potentially useful genes.

The universe of suggested sources of genes/traits/genomic regions that might contribute to improved Yw is very large and impossible to encompass in this review. We have therefore decided to evaluate root system capacity to capture water as a very important trait (with relative impacts on Yw potentially as great as those of bioengineered photosynthesis on Yp) that merits further assessment (see Section 3.3). In addition, and because time (to 2050) is of the essence, we review the history of past successes in using physiological traits to improve Yw to provide some feeling for the time needed between the identification of a potentially useful trait and its possible release in farmer-ready cultivars (see Section 3.4).

### 3.3. Root system capacity for water uptake: a major target for Yw improvement?

It is recognised that below-ground processes have largely been neglected when considering ways to increase yield. This raises the important requirement to better understand root systems and what genetic opportunities may be available to breeding programs to overcome the various constraints. When soil constraints are remedied by management practices the root systems respond dramatically resulting in improved yields and this suggests that there are good prospects for directed genetic manipulation of root systems resulting in higher yields. The best examples are the application of both major and minor nutrients, seed dressings, rotations, liming and the success of these are widely known. In addition, changed management practices such as earlier sowing can also dramatically improve root system function for nutrient and water capture as the residency time for root systems is extended (Batten et al., 1999; Lilley and Kirkegaard, 2011).

Almost all our crops are likely to be grown in soils which have some constraint. These may be soils which are too hard, too dry, too saline, too acid, limited by nutrients or have soil-borne diseases. Our knowledge of root system function and morphology in soils is still in its infancy and so targets for genetic modification are not always clear. Once identified it is expected that the development of effective selection methods will be challenging. There are of course exceptions to this and there have been some notable success stories. In wheat, for example, tolerance to acid soils is enhanced by a gene responsible for the release of malate from the roots (Delhaize and Ryan, 1995), for salinity the presence of sodium exclusion genes in the roots (Dvořák et al., 1994; Munns et al., 2012) and genes for boron tolerance (Jefferies et al., 2000). Several genes have been identified for tolerance to root cereal cyst nematode (Ogbonnaya et al., 2001) and root lesion nematode (Williams et al., 2002). For all of these examples molecular markers have been identified to improve selection in large breeding populations. Each of these examples is expected to increase nutrient and water uptake as a major limitation to these processes has been removed, and thereby improve both the yield of biomass and of grain.

The above examples are all associated with single identifiable genes that affect a specific root system characteristic. Most root system traits that affect root architecture and root function are likely to be multigenic and hence much more difficult to select for and less amenable to marker assisted selection. A good example of this is xylem vessel diameter in the seminal roots of wheat referred to above. Although this trait has a moderate heritability and can be selected for it is controlled by multiple genes each with a small effect. Lynch and colleagues (Lynch, 2007) have successfully selected for root traits that are multigenic to increase phosphorus acquisition. Evidence for other root system traits that are expected



to increase yield are hard to find. Modelling suggests that deeper roots and more effective root systems have contributed to increased corn yields at higher planting densities in Iowa (Hammer et al., 2009), but Sinclair et al. (2010) found little indication of an equivalent advantage in the case of soybean, underlining the fact that traits need to be assessed in the context of species and cropping system. Lilley and Kirkegaard (2011) also show by modelling that breeding wheat with deeper roots in south-eastern Australia should increase water uptake and yield, but only in more favourable years. Manschadi et al. (2008) provide evidence that root angle of the seminal axes of successful wheat varieties in Australia is associated with the pattern of rainfall. They found that varieties with a higher angle of the seminal axis (less gravitropic) are more common in regions expected to receive their most important rainfall during the vegetative period whereas varieties with a narrow angle (more gravitropic), are likely to be adapted to regions that are reliant on deep water stored in the soil during grain filling. This also appears to be the case for nodal roots in sorghum (Mace et al., 2012) and rice (Kato et al., 2006).

The difficulties associated with measuring root systems in the field means that surrogate shoot traits which may reflect what is happening below-ground or are correlated with root growth can be invaluable. A novel example of this is placing a herbicide deep in the soil so as to select the genotypes which first show herbicide damage as these must have an ability to grow roots deep into the soil faster (Robertson et al., 1985). Other examples are shoot vigour which is correlated with root vigour and root length density (Liao et al., 2004; Richards et al., 2007), reduced tillering in wheat – which is associated with more carbon allocation to roots (Duggan et al., 2005; Richards et al., 2007), and a suite of above-ground traits may reflect the ability to capture deep water in the soil and so any one could be used for selection. The suites of traits are: canopy temperature, stomatal conductance, green leaf area or carbon isotope discrimination (Lopes and Reynolds, 2010; Wasson et al., 2012). The use of surrogate above-ground traits is not, of course, free of risks. For example, higher canopy temperatures might be taken as an indication of a poor root water uptake capacity, but lower stomatal conductance would produce a similar signal but help spread crop water consumption across the season, ensuring enough water for grain filling (Richards, 2006; Zaman-Allah et al., 2011). Whether the hidden half of crops will provide significant opportunities for improvement in the future is correct or not it would be perilous to neglect them at a time when the availability and cost-effectiveness of water and nutrients for crop production is coming under increased scrutiny.

#### 3.4. Time from idea to farmer-ready cultivars. Some case histories

As with Yp (see Section 2.3), an issue that is often ignored in the debate about how and how fast genetic improvement might raise Yw, is the time required to progress from a putatively interesting idea or a discovery to farmer-ready cultivars (i.e., ones that meet all other requirements in terms of yield, product quality and disease resistance) that incorporate the trait of interest. Here, we make a first approximation to the issue by examining some past case histories (as distinct from the prospective analysis presented in Section 2.3) for the use of physiological traits for improved Yw but also to extend this by looking at the time required to incorporate semidwarf genes into wheat for favourable environments resulting in the Green Revolution and to incorporate herbicide and disease resistance in sunflower using molecular tools.

A great many physiological and molecular traits have been proposed as a means to improve water-limited potential yield, and only a few of these (Richards, 2006) have actually progressed to the proof-of-concept stage (defined here as a convincing demonstration of yield loss mitigation under field conditions representative of

the water availability pattern that is being targeted), and even fewer have been incorporated into farmer-ready cultivars. Depending on the source of the trait of interest, the idea-to-proof-of-concept stage in this process can include identification of donors of the trait (or mutagenesis and screening), development of an understanding of the mode of inheritance, development of an effective selection method, and introgression of the trait into suitable test-bed lines using backcrosses and recurrent selection aided by physiological or molecular markers. Time required to complete this stage is a function of trait complexity, inheritance mode, screen simplicity, linkage drag, and money and efforts invested (serendipity has also been known to come into the equation).

One of the first conscious (as distinct from unconscious accumulation of favourable traits through selection for yield in rainfed environments) attempts to improve water-limited yield potential revolved around the rationing, by the plants, of the available soil water during the growing season in order to ensure sufficient residual water to support grain-filling (Passioura, 1972). Initially tested in large pots by restricting water uptake to a single seminal root, this idea evolved into the use of genetic variability in root xylem vessel diameter as a choke-point for water uptake. Variability for this trait and its heritability were explored by Richards and Passioura (1981a,b); and the results of field proof-of-concept experiments (yield contrasts between two cultivars and their recurrently selected narrow-xylem-vessel backcrosses across a range of water availabilities) were published by Richards and Passioura (1989). In this example, time from idea to proof-of-concept was 17 years.

Sinclair et al. (1987) discovered that di-nitrogen fixation in soybean was particularly sensitive to drought, a finding which led to screening soybean lines for variability in sensitivity (Sall and Sinclair, 1991; Sinclair et al., 2000), and the demonstration that yield under water scarcity improved in less-sensitive lines (Purcell and King, 1996). This was followed by a breeding program involving crosses between a low-sensitivity-to-drought donor and a high yielding soybean line and selection of two crosses which yielded better than the high yielding parent under water-scarce conditions (Sinclair et al., 2007) and the release of germplasm bearing the trait (Chen et al., 2007). Simulation modelling (Sinclair et al., 2010) suggests that this trait would produce yield benefits in more than 85% of year by region combinations in the US soybean-growing area. In this case, the time from the initial discovery to proof of concept in the field was 20 years.

Farquhar et al. (1982) demonstrated that discrimination against  $C^{13}$  (carbon isotope discrimination, CID) was associated with low transpiration efficiency (TE) of wheat, raising the possibility that CID could be used to distinguish between varieties for TE, as well as a trait which might be useful in mitigating early exhaustion of soil moisture reserves in environments subjected to late-season (for wheat) drought. Farquhar and Richards (1984) confirmed this linkage between CID and TE, leading to a breeding program that demonstrated that the trait had good heritability and that lines from backcrosses to existing commercial varieties had better yields under drought in field tests (Rebetzke et al., 2002). The first commercial variety bearing this trait was released in 2002 (Drysdale), with subsequent releases from 2004 onwards (Rees, Scout, and Envoy) (Richards, 2006). In this case, time from the idea to the first farmer-ready variety took 20 years.

Maize breeders and physiologists had long recognised that under drought conditions a delay in silking (i.e., the time between pollen shedding by the tassel and silk emergence on the spike) or anthesis-silking interval (ASI) was negatively associated with yield (e.g., DuPlessis and Dijkhuis, 1967; Jensen, 1971) and there are indications that this trait was one of several used in private sector breeding for stress tolerance in the 1970s (G.O. Edmeades, personal communication). However, the first openly documented

attempt to use ASI, combined with other traits such as leaf elongation, stay green and yield potential to form an explicit selection index, in a selection program conducted in managed drought stress environments is probably the one for tropical maize initiated in 1975 at CIMMYT by Ken Fischer and colleagues. This led to the first published results by Fischer et al. (1989) (i.e., an idea to proof of concept interval of 14 years), later expanded and confirmed on the basis of further work by Bolaños and Edmeades (1993, 1996). Although CIMMYT made improved tropical maize germplasm emerging from this selection process available, there does not appear to have been any documented cultivar releases. However, Bänziger and colleagues initiated a successful selection program for drought and N-stress tolerance in Zimbabwe in 1996 based on the CIMMYT-Mexico experience (reviewed in Bänziger et al., 2006). This program led to the release, in 2000 (i.e., a proof-of-concept to farmer-ready cultivar interval of 11 years) of Zm521, which was rapidly adopted in the region. This release has been followed by other drought-tolerant OPV's and hybrids which have had an important regional acceptance.

The above examples of the time required to progress from an idea or discovery to farmer useable cultivars might overestimate these intervals because the research was not conducted on a full time basis. Nevertheless, each of the above traits are complex and controlled by many genes and this will almost certainly extend the time from discovery to adoption. It is likely that complex traits will be the norm for physiological traits that will improve Yw or Yp. It is therefore of interest to investigate the time taken to introduce a simply inherited trait into wheat that improves Yp for favourable growing conditions and the release of new varieties in south Asia. The best example is the introduction of dwarfing genes into wheat which, together with better rust resistance, has become known as the Green Revolution. Plant height has always been of major importance to wheat and rice breeders in favourable environments as it is the main way to reduce lodging. Until about the 1950s height had generally been considered a trait that is controlled by many genes each with a small effect. To manipulate it in breeding programs requires large populations compared to a trait that is controlled by a single gene that is easy to observe. Single genes responsible for plant height were not well documented in wheat in the 1950s. However, breeders in Japan were using single genes to reduce plant height in the 1800s without knowing it. The discovery of important wheat germplasm for height and its use in breeding outside Japan, and also the meteoric rise in adoption of semi-dwarf wheats has been documented by Dalrymple (1978). Briefly, Dr S.C. Salmon collected seed from a range of short wheats in Japan in 1946 and distributed them to seven breeding programs in the US. They were directly used in breeding by Dr Orville Vogel in Washington State University who was looking for ways to reduce straw length because of the increased use of artificial fertilisers and problems with lodging. Dr Norman Borlaug at the Rockefeller's International Wheat Improvement Project in Mexico had exhausted sources of dwarfness in breeding wheat and received seeds from Vogel in 1953. The first semi-dwarf variety was released in the US in 1961 and in Mexico in 1962 where a shuttle breeding program was used with 2 generations of selection each year. Seed of the first Mexican wheat arrived in India in 1962 and more in 1963 and the best of these were released as varieties in 1965. Thus, even for a simply inherited and easily selected trait, recognised as having very high value under favourable conditions, it took 15 years from germplasm identification to a new variety in the US and 12 years using a shuttle breeding program for new varieties in India.

We draw on two further examples, neither of which relate directly to cereals or Yw, but which may serve as minimum estimates of the idea-to-cultivar release intervals. Both relate to sunflower, a species for which current breeding technology allows 3–4 generations a year using embryo-rescue, and both relate to

fairly simple traits amenable to marker-assisted selection for the trait in a context of genome-wide selection that ensures high value agronomic traits are maintained in selected material after the introgression of the trait of interest. In addition, in both cases proof of concept is fairly simple (i.e., yes or no) under glasshouse or small field plot conditions, thus avoiding the need for testing over several years and/or locations in the field to ensure adequate exploration of a range of environmental conditions. The first example relates to obtaining a herbicide-resistant mutant through mutagenesis (screening is performed by spraying mutagenised seedlings with herbicide) followed by development of a molecular marker and introgression of the trait into elite parental lines (Sala and Bulos, *in press*; Sala, personal communication). Time from formulation of the initial development protocol to successful isolation of a resistant mutant, determination of trait heritability and development of a marker was 5 years, and another 4 years passed before the first hybrids bearing the trait were released to farmers. The second example involves the introgression of resistance to verticillium wilt (caused by *V. dahliae*), an important biotic challenge for sunflower breeders (Creus et al., 2007). New resistance genes were identified using inoculations under controlled conditions, and molecular markers for these genes identified (Galella et al., 2012) and later used in the introgression process. The time required to progress from screening for sources of resistance to this and to other diseases of sunflower through to the development of markers and introgression of resistance traits into parental lines and release of new, resistant hybrids has taken between 8 and 14 years, depending on the complexity of the traits involved (Zambelli, personal communication).

Taken together, these case histories highlight the need to assign adequate weighting to the time required to progress traits of interest through development and testing and on to their incorporation into farmer-ready cultivars. We recognise that progress in the first three cases (narrow xylem vessels, drought tolerant di-nitrogen fixation, and CID) might have been faster if the research required had been the exclusive focus of the researchers involved and possibly if good molecular tools had been available to hasten introgression and production of converted cultivars. We also recognise that future developments in the techniques of molecular breeding and gene-to-phenotype models may help shorten times to commercial availability of new cultivars carrying the traits of interest. Nevertheless, the two sunflower cases, in which molecular tools were deployed and the number of generations per year that can be achieved is high, suggest that, even under these conditions, the process of trait identification, development and testing may still require a number of years.

## 4. Current and future breeding and the breeders' toolbox

### 4.1. Requirements for successful breeding

It is pertinent to consider what the nature of plant breeding is expected to be like in the future and whether the rate of breeding progress for Yp and Yw is likely to be enhanced as new enabling technologies become available and more widespread. This is important as the time involved from initial cross to varietal release in the majority of breeding programs where improved combinations of existing variation are being sought is often about 10 years. Conventional breeding will remain the mainstay of genetic advances in crops in the next decades. Thus, the fundamental principles and processes used today in breeding will almost certainly remain. However, actual breeding methodologies will continue to evolve and improve as they have over the last two decades and new technologies to enhance breeding processes will be implemented. Recent advances have centred on methodologies to

improve selection efficiency and speed to market and they include the implementation of molecular markers for simply inherited traits, more efficient experimental designs and statistical data processing and more efficient data capture among other things (Knapp, 1998; Smith et al., 2005; Kuchel et al., 2007). In addition, new thinking on gene to phenotype models for complex traits linked to a target population of environments (Hammer et al., 2005) and to yield-trait performance landscapes for agricultural environments (Messina et al., 2011) is also emerging which integrates the various – omics with information management and crop growth models. Genetic engineering, where new genes are introduced using transformation methods, will continue to develop as new genes and gene combinations of value are identified. However, these genes/traits will be integrated into, and be dependent upon, a conventional breeding program. In other words they will form part of the tool box of conventional breeders. Likewise it is expected that hybrid technologies will become more widespread in other crops as it has for rice in the last decade leading to further advances (Yang et al., 2007). The breeding of parent lines for hybrid production will also be dependent on a conventional breeding program.

The reason conventional breeding methods will remain the cornerstone of crop improvement is that they effectively and efficiently combine multiple traits together into a single new variety. Many traits contribute to yield and adaptation and these are most effectively selected in the target field environment where large populations can be grown. Selection for highly heritable traits critical for yield and adaptation such as height and flowering time can be made in early generations and many other traits can also be visually selected quickly and moderately effectively in the target environment. Such traits may be leaf development, vigour, maintenance of green leaves, canopy characteristics, synchronous reproductive development, size of reproductive organs, grain retention, lodging, pollen development, kernel size, colour, etc. Most of these are controlled by numerous genes most of which are unknown. Molecular methods have been of little value in these early segregating stages when very large populations are grown. In addition to selecting for these traits which may be required for yield and yield stability is the selection for resistance/tolerance to as many pests, diseases and soil constraints as possible. Selection for many of these can also be made visually in the target field environment although specialised environments for selection may sometimes be more effective. If they are simply inherited then molecular markers may be important for hard to measure traits (Kuchel et al., 2007) in specific populations. Grain characteristics for some crops are vital for consumer acceptance and also for the industrial processes used to manufacture acceptable food products, and these may also need to be selected. These are also complex genetically and where they are important they will inevitably slow breeding progress for yield. In wheat, for example, to be suitable to manufacturers of bread or noodles, the grain must give a high flour yield, and have desirable properties associated with water absorption, colour, colour stability, mixing time, extensibility, etc. as well as another suite of characters that measure end product features. Many genes, each of small effect, are associated with each of these characteristics (Li et al., 2009b).

It is in this overall breeding process that GM technologies are integrated so as to introduce new genes/traits into either hybrids or inbred lines for commercial release. Thus, to be competitive and to be accepted in the market place GM traits must be introduced into parent lines that are derived from conventional breeding programs and these then become integrated into a standard breeding program. Likewise, trait based breeding programs (e.g., Richards et al., 2010) where a trait responsible for improved yield, or provides tolerance to biotic or abiotic stress, or results in a more desirable end quality, will also need to be tested in conventional breeding programs to assess their competitiveness and potential in the market place.

The major technology changes heralded as revolutionary for crop breeding in the last 3 decades have been the use of marker assisted selection (MAS) and transformation technologies resulting in GM crops. Although MAS has been important for some simply inherited traits it has failed to be effective in breeding for complex traits associated with yield, tolerance to abiotic and biotic factors and grain quality (Bernardo, 2008; Xu and Crouch, 2008). For complex traits multiple quantitative trait loci (QTL) each having a small effect are usually identified which makes MAS for complex traits almost impossible, particularly in variable environments, although gene-to-phenotype modelling (Hammer et al., 2005) may help to mitigate this problem. Also, populations used for QTL identification are often not representative of breeding populations and so marker implementation for complex traits may not be effective.

Dramatic changes in recent years in the cost of DNA sequence information, along with improved bioinformatic tools to interrogate the sequence information, promises to further drive and modify conventional breeding practices in the future. These changes will inevitably expand our molecular horizons beyond the use of single markers for genes with a large effect to complex traits which are affected by many genes each with a small effect. Genomic selection (GS) has been used very effectively in animal breeding (Hayes et al., 2009) and has considerable potential in crops (Zhong et al., 2009; Jannink et al., 2010). SNP chips for the main crops are now available, the smallest being wheat with about 100,000 SNPs, and direct sequencing of germplasm is becoming widespread. These provide the opportunity to use all the polymorphic markers to predict crop performance and crop characteristics and this should enhance selection efficiencies. Genomic selection requires a training sub-population upon which accurate phenotypic data on yield and any other complex trait such as grain quality is obtained. Genomic estimated breeding values can be determined from the training population which is representative of the larger breeding population and these breeding values are then applied to the breeding population prior to any phenotypic evaluation (Zhong et al., 2009). It is emphasised that phenotypic data that is both accurate and repeatable will be critical so that the genomic information can be utilised effectively.

Underpinning the value of all molecular information for use in breeding is the importance and availability of fast and accurate phenotyping (Hammer et al., 2005; Finkel, 2009; Richards et al., 2010). The phenotyping component is the bottleneck to further crop improvement as it is often difficult, expensive, time consuming, laborious and technically difficult and it is often destructive. In addition, in contrast to the genotype, the expression of the phenotype is subject to environmental and seasonal fluctuations and to genotype  $\times$  environment interactions leading to a low repeatability and heritability. This is not unique to plants as the same problem limits progress in human medicine as well (Venter, 2011). An important key to successful phenotyping is to correctly design the screen used for phenotyping so that it mimics the target environment. Application of crop simulation models to the correct characterisation of stress regimes can be a powerful aid (e.g., Chapman, 2008), and the use of carefully defined managed stress environments played an important part in the success of the selection index for ASI, stay green and other traits in improving tropical maize Yw in Mexico and Zimbabwe (Fischer et al., 1989; Bänziger et al., 2006).

Non-invasive technologies that measure plant form, function, aspects of metabolism and content, often called phenomics, has been touted as a way to overcome this bottleneck as measurements are often fast, repeatable and accurate and can be automated (Furbank and Tester, 2011). Nevertheless, a problem with much of the phenomics activities so far is the emphasis on controlled environments which, for most traits, rarely have relevance to the real environments in the field when the application is for breeding.

However it is not unrealistic to think that non-invasive measurement of crop biomass, grain yield, grain nitrogen and grain moisture of an entire breeding trial should soon be possible, thereby improving the efficiency of the selection process.

GM crops that have been commercialised have been remarkably successful (James, 2011). Their success centres around the introduction of genes controlling the biochemistry of the plant to synthesise new chemical compounds (primarily Bt insect toxin) or to make the plants tolerate applied alien compounds (glyphosate tolerance). These alterations allow multiple crop species to be defended against a broad spectrum of insect pests and competition by weed species. There is a tendency to believe that these remarkable successes in GM technology will continue and will readily translate to new genes/traits which alter physiological or biochemical processes that influence yield or tolerance to abiotic stress. However, this translation is unlikely. Most traits we may wish to alter to increase yield or tolerance to abiotic stress are complex and it is unlikely that single genes will be important over a range of species and environmental conditions as we scale up from single plants to crop canopies and beyond where seasonal conditions are variable and unpredictable. The underlying gene networks and pathways are likely to dampen effects of single processes. Thus although GM technology will continue to be effective in altering end product quality and tolerance/resistance to biotic factors it is very unlikely these technologies will result in significant and widespread yield improvements directly as a result of a changed biochemistry. It is noteworthy that of the 39 commercial releases of GM traits in 2008 none directly targeted yield or abiotic stress; rather traits are for pest resistance/tolerance or product quality (Stein and Rodriguez-Cerezo, 2010).

#### 4.2. Hindrances to progress

The Green Revolution which commenced in the 1960s occurred at a time when most agricultural research was undertaken by publicly funded research organisations and germplasm and technology was freely exchanged between research partners and countries. During this time Intellectual Property (IP) was not a strong consideration in agricultural innovation. However, IP is now of considerable importance to both public and private research agencies to protect innovations required to increase food production and to transfer technologies and germplasm to collaborators and between countries. IP protection has become important in conventionally bred germplasm but its importance is exacerbated where GM technologies are involved. As IP has become more prominent in cultivar development there has been a corresponding decline in public investment in plant breeding but an increased private sector investment particularly in the developed countries. Thus, for the adoption of new varieties farmers in all countries need to adjust to the reality of the private sector having more control over seed distribution. Although this is unlikely to be an impediment in developed countries where hopefully it will speed up genetic progress, it could be an impediment in developing countries (Lea, 2008). Nevertheless, where multiple technologies owned by several agencies are used for cultivar development, as is likely for most traits/genes in GM technologies, then delays in cultivar release are likely because of regulatory issues. An example of this is the release of Golden Rice, which used GM technology to synthesise beta-carotene, a pre-cursor of vitamin A in the rice endosperm, which is expected to be of widespread health importance in rice dependent poor populations. Research on golden rice commenced in 1992 with the first field trials in 2004 and the expected release of cultivars to farmers in 2013 (Al-Babili and Beyer, 2005; Potrykus, 2010). It is estimated that overcoming the regulatory hurdles related to GM as well as the many patents and organisations involved has delayed the release of the first cultivars

by at least 10 years (Potrykus, 2010). The stringent regulatory requirements for the release of GM varieties is very costly and this is also expected to be a major impediment to, or in many cases prevent, the release of GM varieties. It is also likely to sideline public agencies as they will be unable to meet these costs on their own.

The time taken for the development and incorporation of new traits for yield or abiotic stress into cultivars by conventional breeders is also very slow as we outlined in Sections 2.3 and 3.4. In the overall research and development required for cultivar release it is likely that insufficient attention or funding is provided for the appropriate field evaluation of traits and the development of suitable germplasm for breeders. This is a major impediment to the adoption of a trait by breeders and hence delays or prevents cultivar release to farmers. For breeders to select for another trait in their breeding program they will first want proof of concept that the incorporation of the trait will result in an improvement in yield. This usually requires demonstration that in germplasm appropriate to their breeding programs (near-isogenic lines or large populations) there is an advantage when the trait is present. Once proven breeders will also want a fast and effective selection method to select for the trait and this may be either molecular markers or a fool-proof phenotyping method. Both of these can take time to develop and usually requires specialist skills (Richards et al., 2010). In the public sector proof of concept and germplasm development are often neglected, or do not happen as the required expertise for this is not available or there is the belief that the breeders should be responsible for it and so uptake of research results does not happen. Furthermore, funding agencies often do not appreciate the complexities and expertise required for adoption by breeders. This disconnect between pre-breeding and breeding may significantly delay or prevent uptake of new traits/technologies by breeders.

An often neglected factor that will be pivotal to achieving our food production targets is the availability of new cohorts of agricultural scientists trained in plant breeding, genetics, biotechnology, crop physiology and agronomy. Decreased government investment and support for agricultural sciences in our higher education systems have led to reductions in crop research and shortages of trained staff in agribusiness, consulting, natural resource management and biosecurity. It is hoped that the global concern over food security and the efficient and equitable production and distribution of food, together with concerns over the maintenance of important ecosystems and natural resources, all of which are expressed in both the popular and scientific media, will inspire a new generation of young scientists.

## 5. Conclusions

Genetic variation in each of our major food crops has been successfully recombined by plant breeders over the last 100 years to make consistent yield gains. Genetic improvement together with better crop management resulted in the Green Revolution in the 1960s leading to dramatic improvements in yield, particularly under irrigation in developing countries, and in turn to food surpluses and to cheaper food in the developed world. However, in recent years there has been a frightening decline in global grain stocks and, together with adverse weather conditions in some regions, resulted in spikes in food prices (Koning et al., 2008) and social unrest in some countries. This as well as a sharp increase in fertiliser price and the concern over declining water resources available to agriculture provided the wake-up call required for society to realise that we may not be able to meet the global demand for food and feed grain by the middle of this century. To meet the demand for our major cereals, maize, wheat and rice, without increasing food prices then global harvests have to increase at an annual compound rate of between 1.16 and 1.31% $y^{-1}$ .



In examining results from long term studies that have evaluated elite genetic material and the best released varieties of maize, wheat and rice in well managed trials of historic sets of the best varieties or hybrids in both water unlimited and water-scarce environments we could find no examples that show *current* rates of increase of Yp or Yw that are close to the  $1.16\text{--}1.31\%y^{-1}$  required to satisfy projected demand for cereals in 2050. In fact a worrying number of cases of nil rates of increase of Yp or Yw were identified or suggested in various crop/environment combinations. These findings are broadly consistent with what has been found by others (e.g., Cassman et al., 2010) using subnational or national statistical records, but the management factor adds some uncertainty to the true significance of these observations.

Thus, in the challenge to progress Yp and Yw enough to meet projected demand for cereals by 2050, the timescales that have emerged are not a good basis for optimism. On the other hand, the revolution in biotechnology, primarily the low cost of DNA sequence information and advances in recombinant DNA technologies, together with fast and non-destructive phenotyping and computational wizardry, have provided some optimism (Phillips, 2010; Dunwell, 2011; Furbank and Tester, 2011). However, whilst we can gain some useful insights thanks to these new tools, their impacts in terms of future yield gains and acceleration of the breeding process are still uncertain. There also remain unexploited opportunities for increasing Yp or Yw through targeted genetic improvement of the most important traits thought to limit yield. In addition, the processes to identify important traits for different regions have been improved by new tools to analyse seasonal variability and trait impact and these will provide a better focus. There are several routes to improve Yp or Yw and a number of candidate traits and genes are available. Here we identify photosynthetic capacity and root system function as two which we believe offers most promise in the future. A major consideration is that most of the important traits are genetically complex creating an added challenge. In addition, there prevails an unrealistic view of the time taken to incorporate new traits into varieties for farmers. In the case histories we considered of successful examples of trait integration into breeding the timescale from initial research to the release of new cultivars to farmers or to proof-of-concept in elite germplasm was around 20 years. Even in those cases in which introgression of fairly simple traits, governed by one or few genes, was backed by the full strength of current molecular breeding tools, this time span was of the order of 10 years. Variety adoption by farmers then occurs and this may be rapid in the case of blockbuster GM traits such as glyphosate resistance and pest resistance (Bt) or dwarfing genes in rice and wheat during the 1970s, but then longer for hybrid rice in China today. Times are expected to be much more gradual for other traits. Regulatory requirements and IP considerations are likely to add an extra level of uncertainty to the delivery time in the future.

Given the above, it is extremely hard to be optimistic that the current compound rates of progress in Yp and Yw will increase very much, if at all, in the near term even with the best methodologies and breeding programs. While this is obviously speculative, then so too is the optimistic (naïve) alternative. Also, the uncertainty and doubt over whether transgenic approaches will be effective (apart maybe from bioengineering photosynthesis) and the very long gestation period from the development of a new or existing trait to delivery in the form of new cultivars, leaves us with a very pessimistic view.

Whilst it is important to say that increased investment in research is going to be crucial just to maintain current rates of improvement, there is also an urgent need to focus on structural issues in the research, development and cultivar delivery chain, as well as on training a new generation of agricultural scientists. There remains a large gap between scientists close to the molecular level

of organisation and the realities that breeders, agronomists and farmers have to face. Passioura (2010) strongly argues the need to change the way that research is generally organised and the important need to facilitate a culture of dialogue between scientists of different disciplines. This in turn is likely to focus attention on the most important and feasible approaches to crop genetic improvement and in turn redirect some research activity into more productive avenues. It should also enable a speedier transfer of traits to breeders. An increasing amount of cultivar development and delivery is through private companies and so private-public partnerships will be increasingly important to coordinate and to agree on mutually acceptable terms of engagement. The need for increased research investment and for structural/sociological change is clearly urgent if we are to meet the projected demand for food.

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### References

- Acreche, M.M., Briceño-Félix, G., Martín Sánchez, J.A., Slafer, G.A., 2008. Physiological bases of genetic gains in Mediterranean bread wheat yield in Spain. *Eur. J. Agric.* 28, 162–170.
- Aggarwal, P.K., Kropff, M.J., Cassman, K.G., ten Berge, H.F.M., 1997. Simulating genotypic strategies for increasing rice yield potential in irrigated, tropical environments. *Field Crops Res.* 51, 5–17.
- Al-Babili, S., Beyer, P., 2005. Golden rice: five years on the road—five years to go? *Trends Plant Sci.* 10, 565–573.
- Bänziger, M., Setimela, P.S., Hodson, D., Vivek, B., 2006. Breeding for improved drought tolerance in maize adapted to southern Africa. *Agric. Water Manage.* 80, 212–224.
- Batten, G.D., Fettel, N.A., Mead, J.A., Khan, M.A., 1999. Effect of sowing date on the uptake and utilization of phosphorus by wheat (cv. Osprey) grown in central New South Wales. *Aust. J. Exp. Agric.* 39, 161–170.
- Bernardo, R., 2008. Molecular markers and selection for complex traits in plants: learning from the last 20 years. *Crop Sci.* 48, 1649–1664.
- Bernier, J., Kumar, A., Ramaiah, V., Spaner, D., Atlin, G., 2007. A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. *Crop Sci.* 47, 507–518.
- Berry, P.M., Spink, J.H., 2006. A physiological analysis of oilseed rape yields: past and future. *J. Agric. Sci. (Camb.)* 144, 381–392.
- Bolaños, J., Edmeades, G.O., 1993. Eight cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. *Field Crops Res.* 31, 253–268.
- Bolaños, J., Edmeades, G.O., 1996. The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. *Field Crops Res.* 48, 65–80.
- Brisson, N., Gate, P., Gouache, D., Charmet, G., Oury, F.-X., Huard, F., 2010. Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. *Field Crops Res.* 119, 201–212.
- Bruinsma, J., 2009. The resource outlook to 2050. By how much do land, water use and crop yields need to increase by 2050? In: Proc. FAO Expert Meeting on How to Feed the World in 2050, 24–26 June 2009. FAO, Rome (available at <http://www.fao.org/wsfs/forum2050/background-documents/expert-papers/en/>).
- Bueno, C.S., Lafarge, T., 2009. Higher crop performance of rice hybrids than elite inbreds in the tropics. 1. Hybrids accumulate more biomass during each phenological phase. *Field Crops Res.* 112, 229–237.
- Bueno, C.S., Pasquin, E., Tubaña, B., Lafarge, T., 2010. Improving sink regulation, and searching for promising traits associated with hybrids, as a key avenue to

- increase yield potential of the rice crop in the tropics. *Field Crops Res.* 118, 199–207.
- Calderini, D.F., Slafer, G.A., 1998. Changes in yield and yield stability in wheat during the 20th century. *Field Crops Res.* 57, 335–347.
- Campos, H., Cooper, M., Habben, J.E., Edmeades, G.O., Schussler, J.R., 2004. Improving drought tolerance in maize: a view from industry. *Field Crops Res.* 90, 19–34.
- Cassman, K.G., Dobermann, A., Walters, D.T., Yang, H., 2003. Meeting cereal demand while protecting natural resources and improving environmental quality. *Annu. Rev. Environ. Resour.* 28, 315–358.
- Cassman, K.G., Grassini, P., van Wart, J., 2010. Crop yield potential, yield trends and global food security in a changing climate. In: Illel, D., Rosenzweig, C. (Eds.), *Handbook of Climate Change and Agroecosystems: Impacts, Adaptation, and Mitigation*. World Scientific, pp. 37–51.
- Castiglioni, P., Warner, D., Bensen, R.J., Anstrom, D.C., Harrison, J., Stoecker, M., Kumar, G., Salvador, S., D'Ordine, R., Navarro, S., Back, S., Fernandes, M., Targolli, J., Dasgupta, S., Bonin, C., Luethy, M.H., Heard, J.E., 2008. Bacterial RNA Chaperones confer abiotic stress tolerance in plants and improved grain yield in maize under water-limited conditions. *Plant Physiol.* 147, 446–455.
- Chapman, S.C., 2008. Use of crop models to understand genotype by environment interactions for drought in real-world and simulated plant breeding trials. *Euphytica* 161, 195–208.
- Chen, P., Sneller, C.H., Purcell, L.C., Sinclair, T.R., King, C.A., Ishibashi, T., 2007. Registration of soybean germplasm lines R01-416F and R01-581F for improved yield and nitrogen fixation under drought stress. *J. Plant Growth Regul.* 1, 166–167.
- Chenu, K., Chapman, S.C., Tardieu, F., McLean, G., Welcker, C., Hammer, G.L., 2009. Simulating the yield impacts of organ-level quantitative trait loci associated with drought response in maize: a “gene-to-phenotype” modeling approach. *Genetics* 183, 1507–1523.
- Chimenti, C.A., Marcantonio, M., Hall, A.J., 2002. Divergent selection for osmotic adjustment results in improved drought tolerance in maize (*Zea mays* L.) in both early growth and flowering phases. *Field Crops Res.* 95, 305–315.
- Cirera, X., Masset, E., 2010. Income distribution trends and future food demand. *Philos. Trans. R. Soc. B* 365, 2821–2834.
- Cooper, P.J.M., Dimes, J., Rao, K.P.C., Shapiro, B., Shiferaw, B., Twomlow, S., 2008. Coping better with current climatic variability in the rain-fed farming systems of sub-Saharan Africa: an essential first step in adapting to future climate change? *Agric. Ecosyst. Environ.* 126, 24–35.
- Creus, C., Bazzalo, M.E., Grondona, M., Andrade, F., León, A.J., 2007. Disease expression and ecophysiological yield components in sunflower isohybrids with and without *Verticillium dahliae* resistance. *Crop Sci.* 47, 703–708.
- Dalrymple, D.G., 1978. Development and spread of high-yielding varieties of wheat and rice in the less developed nations. *Foreign Agricultural Economic Report*, USDA, No. 95. Washington DC, 134p.
- Delhaize, E., Ryan, P.R., 1995. Aluminum toxicity and tolerance in plants. *Plant Physiol.* 107, 315–321.
- de la Vega, A.J., Chapman, S.C., 2010. Mega-environment differences affecting genetic progress for yield and relative value of component traits. *Crop Sci.* 50, 574–583.
- de la Vega, A.J., DeLacy, I.H., Chapman, S.C., 2007. Progress over 20 years of sunflower breeding in central Argentina. *Field Crops Res.* 100, 61–72.
- Duggan, B.L., Richards, R.A., van Herwaarden, A.F., 2005. Agronomic evaluation of a tiller inhibition gene (*tin*) in wheat II. Growth and partitioning of assimilate. *Aust. J. Agric. Res.* 56, 179–186.
- Dunwell, J.M., 2011. Crop biotechnology: prospects and opportunities. *J. Agric. Sci. (Camb.)* 149, 17–27.
- DuPlessis, D.P., Dijkhuis, F.J., 1967. The influence of time lag between pollen shedding and silking on the yield of maize. *S. Afr. J. Agric. Sci.* 10, 667–674.
- Duvick, D.N., Cassman, D.N., 1999. Post-Green Revolution trends in yield potential of temperate maize in the North-Central United States. *Crop Sci.* 39, 1622–1630.
- Dvořák, J., Noaman, M.M., Goyal, S., Gorham, J., 1994. Enhancement of the salt tolerance of *Triticum turgidum* L. by the *Kna1* locus transferred from the *Triticum aestivum* L. chromosome 4D by homoeologous recombination. *Theor. App. Genet.* 87, 872–877.
- Edgerton, M.D., 2009. Increasing crop productivity to meet global needs for food, fuel, and fiber. *Plant Physiol.* 149, 7–13.
- Edmeades, G.O., Bolaños, J., Chapman, S.C., Lafitte, H.R., Bänziger, M., 1999. Selection improves drought tolerance in tropical maize populations: I. Gains in biomass, grain yield, and harvest index. *Crop Sci.* 39, 1306–1315.
- Ewert, F., Rounsevell, M.D.A., Reginster, I., Metzger, M.J., Leemans, R., 2005. Future scenarios of European agricultural land use I. Estimating changes in crop productivity. *Agric. Ecosyst. Environ.* 107, 101–116.
- Farquhar, G.D., O'Leary, M.H., Berry, J.A., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* 9, 121–137.
- Farquhar, G.D., Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* 11, 539–552.
- Finkel, E., 2009. With 'Phenomics,' plant scientists hope to shift breeding into overdrive. *Science* 325, 380–381.
- Fischer, G., 2009a. World food and agriculture to 2030/50: how do climate change and bioenergy alter the long-term outlook for food, agriculture and resource availability? In: Proc. FAO Expert Meeting on How to Feed the World in 2050, (available at <http://www.fao.org/wsfs/forum2050/background-documents/expert-papers/en/>).
- Fischer, K.S., Edmeades, G.O., Johnson, E.C., 1989. Selection for the improvement of maize yield under moisture-deficits. *Field Crops Res.* 22, 227–243.
- Fischer, R.A., 2009b. Farming systems of Australia: exploiting the synergy between genetic improvement and agronomy. In: Sadras, V.O., Calderini, D.F. (Eds.), *Crop Physiology: Applications for Genetic Improvement and Agronomy*. Academic Press, San Diego, CA, pp. 23–54.
- Fischer, R.A., Edmeades, G.O., 2010. Breeding and cereal yield progress. *Crop Sci.* 50, S86–S98.
- Fischer, R.A., Rees, D., Sayre, K.D., Lu, Z.-M., Condon, A.G., Larquée-Saavedra, A., 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate and cooler canopies. *Crop Sci.* 38, 1467–1475.
- Foulkes, M.J., Slafer, G.A., Davies, W.J., Berry, P.M., Sylvester-Bradley, R., Martre, P., Calderini, D.F., Giffiths, S., Reynolds, M.P., 2011. Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *J. Exp. Bot.* 62, 469–486.
- Furbank, R.T., von Caemmerer, S., Sheehy, J., Edwards, G., 2009. C<sub>4</sub> rice, a challenge for plant phenomics. *Funct. Plant Biol.* 36, 845–856.
- Furbank, R.T., Tester, M., 2011. Phenomics—technologies to relieve the phenotyping bottleneck. *Trends Plant Sci.* 16, 635–644.
- Galella, M.T., Bazzalo, M.E., Morata, M., Cimmino, C., Kaspar, M., Grondona, M., Reid, R., Zambelli, A., León, A., 2012. Pyramiding QTLs for *Verticillium dahliae* resistance. In: 18th International Sunflower Conf., Mar del Plata, Argentina, 27 February–1 March.
- Grassini, P., Thorburn, J., Burr, C., Cassman, K.G., 2011. High-yield irrigated maize in the Western U.S. Corn Belt: I. On-farm yield, yield potential, and impact of agronomic practices. *Field Crops Res.* 120, 142–150.
- Graybosch, R.A., Peterson, C.J., 2010. Genetic improvement in winter wheat yields in the Great Plains of North America, 1959–2008. *Crop Sci.* 50, 1882–1890.
- Godfray, H.C.J., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Nisbett, N., Pretty, J., Robinson, S., Toulmin, C., Whiteley, R., 2010a. The future of the global food system. *Philos. Trans. R. Soc. B* 365, 2769–2777.
- Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., Whiteley, R., 2010b. Food security: the challenge of feeding 9 billion people. *Science* 327, 812–818.
- Gornall, J., Betts, R., Burke, E., Clark, R., Camp, J., Willett, K., Wiltshire, A., 2010. Implications of climate change for agricultural productivity in the early twenty-first century. *Philos. Trans. R. Soc. B* 365, 2973–2989.
- Hall, A.J., Sadras, V.O., 2009. Whither crop physiology? In: Sadras, V.O., Calderini, D.F. (Eds.), *Crop Physiology: Applications for Genetic Improvement and Agronomy*. Elsevier, Amsterdam, pp. 545–570.
- Hammer, G.L., Chapman, S.C., van Oosterom, V., Podlich, D.W., 2005. Trait physiology and crop modelling as a framework to link phenotypic complexity to underlying genetic systems. *Aust. J. Agric. Res.* 56, 947–960.
- Hammer, G.L., Dong, Z., McLean, G., Doherty, A., Messina, C., Schussler, J., Zinselmeier, C., Paszkiewicz, P., Cooper, M., 2009. Can changes in canopy and/or root system architecture explain historical maize yield trends in the U.S. Corn Belt? *Crop Sci.* 49, 299–312.
- Hayes, B.J., Bowman, P.J., Chamberlain, A.J., Goddard, M.E., 2009. Genomic selection in dairy cattle: progress and challenges. *J. Dairy Sci.* 92, 433–443.
- Hibberd, J.M., Sheehy, J.E., Langdale, J.A., 2008. Using C<sub>4</sub> photosynthesis to increase the yield of rice—rationale and feasibility. *Curr. Opin. Plant Biol.* 11, 228–231.
- Horie, T., Matsuura, S., Takai, T., Kuwasaki, K., Ohsumi, A., Shiraiwa, T., 2006. Genotypic difference in canopy diffusive conductance measured by a new remote-sensing method and its association with the difference in rice yield potential. *Plant Cell Environ.* 29, 653–660.
- Jaggard, K.W., Qi, A., Eric, S., Ober, E.S., 2010. Possible changes to arable crop yields by 2050. *Philos. Trans. R. Soc. B* 365, 2835–2851.
- James, C., 2011. Global Status of Commercialized Biotech/GM Crops: 2010 ISAAA Brief No. 42. ISAAA, Ithaca, NY, ISBN: 978-1-892456-49-4.
- Janaiah, A., Xie, F., 2010. Hybrid rice adoption in India: farm level impacts and challenges. *IRRI Tech. Bull.* no. 14. IRRI, Los Baños, Philippines, 20 p.
- Jannink, J.-L., Lorenz, A.J., Iwata, H., 2010. Genomic selection in plant breeding: from theory to practice. *Brief. Funct. Genomics* 9, 166–177.
- Jefferies, S.P., Pallotta, M.A., Paull, J.G., Karakousis, A., Kretschmer, J.M., Manning, S., Islam, A.K.M.R., Langridge, P., Chalmers, K.J., 2000. Mapping and validation of chromosome regions conferring boron toxicity tolerance in wheat (*Triticum aestivum*). *Theor. App. Gen.* 101, 767–777.
- Jensen, S.D., 1999. Breeding for drought and heat tolerance in corn. In: Sutherland, J.I., Falasca, R.J. (Eds.), *Proc. 26th Annual Corn and Sorghum Res. Conf. Chicago*, December 14–16, 1971. ASTA, Washington, DC, pp. 198–208.
- Kasuga, M., Liu, Q., Miura, S., Yamaguchi-Shinozaki, K., Shinozaki, K., 1999. Improving plant drought, salt, and freezing tolerance by gene transfer of a single stress-inducible transcription factor. *Nat. Biotechnol.* 17, 287–291.
- Kato, Y., Abe, J., Kamoshita, A., Yamagishi, J., 2006. Genotypic variation in root growth angle in rice and its association with deep root development in upland fields with different water regimes. *Plant Soil* 287, 117–129.
- Knapp, S.J., 1998. Marker assisted selection as a strategy for increasing the probability of selecting superior genotypes. *Crop Sci.* 38, 1164–1174.
- Koemel, J.E., Guenzi, A.C., Carver, B.F., Payton, M.E., Morgan, G.H., Smith, E.L., 2004. Hybrid and pureline hard winter wheat yield and stability. *Crop Sci.* 44, 107–113.
- Koning, N.B.J., van Ittersum, M.K., Becx, G.A., van Boekel, M.A.J.S., Brandenburg, W.A., van den Broek, J.A., Goudriaan, J., van Hofwegen, G., Jongeneel, R.A., Schiere, J.B., Smies, M., 2008. Long-term global availability of food: Continued abundance or new scarcity? *Neth. J. Agric. Sci.* 55, 229–292.
- Kuchel, H., Fox, R., Reinheimer, J., Mosionek, L., Willey, N., Bariana, H., Jefferies, S., 2007. The successful application of a marker-assisted wheat breeding strategy. *Mol. Breed.* 20, 295–308.
- Lafarge, T., Bueno, C.S., 2009. Higher crop performance of rice hybrids than elite inbreds in the tropics. 2. Does sink regulation, rather than sink size, play a major role? *Field Crops Res.* 114, 434–440.

- Lafitte, H.R., Li, Z.K., Vijayakumar, C.H.M., Gao, Y.M., Shi, Y., Xu, J.L., Fu, B.Y., Yu, S.B., Ali, A.J., Domingo, J., Maghirang, R., Torres, R., Mackill, D., 2006. Improvement of rice drought tolerance through backcross breeding: evaluation of donors and selection in drought nurseries. *Field Crops Res.* 97, 77–86.
- Lafitte, H.R., Yongsheng, G., Yan, S., Li, Z.-K., 2007. Whole plant responses, key processes, and adaptation to drought stress: the case of rice. *J. Exp. Bot.* 58, 169–175.
- Lea, D., 2008. The expansion and restructuring of intellectual property and its implications for the developing world. *Ethical Theor. Moral Pract.* 11, 37–60.
- Li, J., Xin, Y., Yuan, L., 2009. Hybrid rice technology development: ensuring China's food security. IPFRI discussion paper 0918. IPFRI, Washington, DC, 28 p.
- Li, Y., Song, Y., Zhou, R., Branlard, G., Jia, J., 2009b. Detection of QTLs for bread-making quality in wheat using a recombinant inbred line population. *Plant Breed.* 128, 235–243.
- Liao, M., Fillery, I.R.P., Palta, J.A., 2004. Early vigorous growth is a major factor influencing nitrogen uptake in wheat. *Funct. Plant Biol.* 31, 121–129.
- Lilley, J.M., Kirkegaard, J.A., 2011. Benefits of increased soil exploration by wheat roots. *Field Crops Res.* 122, 118–130.
- Long, S.P., Zhu, X.G., Naidu, S.L., Ort, D.R., 2006. Can improvement in photosynthesis increase crop yields? *Plant Cell Environ.* 29, 315–330.
- Lopes, M.S., Reynolds, M.B., 2010. Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. *Funct. Plant Biol.* 37, 147–156.
- Luque, S.L., 2000. Bases ecofisiológicas de la ganancia genética en el rendimiento del maíz en la Argentina en los últimos 30 años. MSc Thesis. University of Buenos Aires, 96 p.
- Luque, S.F., Cirilo, A.G., Otegui, M.E., 2006. Genetic gains in grain yield and related physiological attributes in Argentine maize hybrids. *Field Crops Res.* 96, 383–397.
- Lutz, A.G., KC, S., 2010. Dimensions of global population projections: what do we know about future population trends and structures? *Philos. Trans. R. Soc. B* 365, 2779–2791.
- Lynch, J.P., 2007. Roots of the second green revolution. *Aust. J. Bot.* 55, 493–512.
- Mace, E.S., Singh, V., Van Oosterom, E.J., Hammer, G.L., Hunt, C.H., Jordan, D.R., 2012. QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench) co-locate with QTL for traits associated with drought adaptation. *Theor. Appl. Genet.* 124, 97–109.
- Mackay, I., Horwell, A., Garner, J., White, J., McKee, J., Philpott, H., 2011. Reanalyses of the historic series of UK variety trials to quantify the contributions of genetic and environmental factors to trends and variability in yield over time. *Theor. Appl. Genet.* 22, 225–238.
- Manschadi, A.M., Hammer, G.L., Christopher, J.T., deVoil, P., 2008. Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.). *Plant Soil* 303, 115–129.
- Messina, C.D., Hammer, G., Dong, Z., Podlich, D., Cooper, M., 2009. Modeling crop improvement in a GxExM framework via gene-trait-phenotype relationships. In: Sadras, V.O., Calderini, D.F. (Eds.), *Crop Physiology: Applications for Genetic Improvement and Agronomy*. Elsevier, Amsterdam, pp. 235–265.
- Messina, C.D., Podlich, D., Dong, Z., Samples, M., Cooper, M., 2011. Yield-trait performance landscapes: from theory to application in breeding maize for drought tolerance. *J. Exp. Bot.* 62, 855–868.
- Monteith, J.L., 1977. Climate and efficiency of crop production in Britain. *Philos. Trans. R. Soc. B* 281, 277–294.
- Morgan, J.M., Condon, A.G., 1986. Water use, grain yield, and osmoregulation in wheat. *Aust. J. Plant Physiol.* 13, 523–532.
- Munns, R., James, R.A., Xu, B., Athman, A., Conn, S.J., Jordans, C., Byrt, C.S., Hare, R.A., Tyerman, S.D., Tester, M., Plett, D., Gilliam, M., 2012. Wheat grain yield on saline soils is improved by an ancestral transporter gene. *Nat. Biotechnol.* 30, 360–364.
- Murchie, E.H., Pinto, M., Horton, P., 2008. Agriculture and the new challenges for photosynthesis research. *New Phytol.* 181, 532–552.
- Nelson, D.E., Repetti, P.P., Adams, T.R., Creelmann, R.A., Wu, J., Warner, D.C., Anstrom, D.C., Bensen, R.J., Castiglioni, P.P., Donnarummo, M.G., Hinchey, B.S., Kumimoto, R.W., Maszle, D.R., Canales, R.D., Krolkowski, K.A., Dotson, S.B., Gutterson, N., Ratcliffe, O.J., Heard, J.E., 2007. Plant nuclear factor Y(NFY) B subunits confer drought tolerance and lead to improved corn yields on water-limited acres. *PNAS* 104, 16450–16455.
- Ogbonnaya, F.C., Subrahmanyam, N.C., Moullet, O., Majnik, J.D., Eagles, H.A., Brown, J.S., Eastwood, R.F., Kollmorgen, J., Appels, R., Lagudah, E.S., 2001. Diagnostic DNA markers for cereal cyst nematode resistance in bread wheat. *Aust. J. Agric. Res.* 52, 1367–1374.
- Parry, M.A.J., Reynolds, M., Salvucci, M.E., Raines, C., Andralojc, P.J., Zhu, X.-G., Price, G.D., Condon, A.G., Furbank, R.T., 2011. Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. *J. Exp. Bot.* 62, 453–467.
- Passioura, J.B., 1972. The effect of root geometry on the yield of wheat growing on stored water. *Aust. J. Agric. Res.* 23, 745–752.
- Passioura, J.B., 1977. Grain yield, harvest index, and water use of wheat. *J. Aust. Inst. Agric. Sci.* 43, 117–120.
- Passioura, J.B., 2006. Increasing crop productivity when water is scarce – from breeding to field management. *Agric. Water Manage.* 80, 176–196.
- Passioura, J.B., 2010. Scaling up: the essence of effective agricultural research. *Funct. Plant Biol.* 37, 585–591.
- Peng, S., Cassman, K.G., Virmani, S.S., Sheehy, J., Khush, G.S., 1999. Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. *Crop Sci.* 39, 1552–1559.
- Peng, S., Laza, R.C., Visperas, R.M., Sanico, A.L., Cassman, K.G., Khush, G.S., 2000. Grain yield of rice cultivars and lines developed in the Philippines since 1966. *Crop Sci.* 40, 307–314.
- Peng, S., Huang, J., Cassman, K.G., Laza, R.C., Visperas, R., Khush, G.S., 2010. The importance of maintenance breeding: a case study of the first miracle rice variety-IR8. *Field Crops Res.* 119, 342–347.
- Phillips, R.L., 2010. Mobilizing science to break yield barriers. *Crop Sci.* 50, S99–S108.
- Potrykus, I., 2010. Regulation must be revolutionized. *Nature* 466, 561.
- Purcell, L.C., King, C.A., 1996. Drought and nitrogen source effects on nitrogen nutrition, seed growth, and yield in soybean. *J. Plant Nutr.* 19, 969–993.
- Rebetzke, G.J., Condon, A.G., Richards, R.A., Farquhar, G.D., 2002. Selection for reduced carbon isotope discrimination increases aerial biomass and grain yield of rainfed bread wheat. *Crop Sci.* 42, 739–745.
- Reynolds, M., Manes, Y., Izanloo, A., Langridge, P., 2009. Phenotyping approaches for physiological breeding and gene discovery in wheat. *Ann. Appl. Biol.* 155, 309–320.
- Reynolds, M.P., Delgado B, M.I., Gutiérrez-Rodríguez, M., Larqué-Saavedra, A., 2000. Photosynthesis of wheat in a warm, irrigated environment: I: genetic diversity and crop productivity. *Field Crops Res.* 66, 37–50.
- Reynolds, M., Bonnett, D., Chapman, S.C., Furbank, R.T., Manès, Y., Mather, D.E., Parry, M.A.J., 2011. Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. *J. Exp. Bot.* 62, 439–452.
- Richards, R., 2006. Physiological traits used in the breeding of new cultivars for water scarce environments. *Agric. Water Manage.* 80, 197–211.
- Richards, R.A., Passioura, J.B., 1981a. Seminal root morphology and water use of wheat. I. Environmental effects. *Crop Sci.* 21, 249–252.
- Richards, R.A., Passioura, J.B., 1981b. Seminal root morphology and water use of wheat. II. Genetic variation. *Crop Sci.* 21, 253–255.
- Richards, R.A., Passioura, J.B., 1989. A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. *Aust. J. Agric. Res.* 40, 943–950.
- Richards, R.A., Watt, M., Rebetzke, G.J., 2007. Physiological traits and cereal germplasm for sustainable agricultural systems. *Euphytica* 154, 409–425.
- Richards, R.A., Rebetzke, G.J., Watt, M., Condon, A.G., Spielmeier, W., Dolferus, R., 2010. Breeding for improved water productivity in temperate cereals: phenotyping, quantitative trait loci, markers and the selection environment. *Funct. Plant Biol.* 37, 85–97.
- Rivero, R.M., Kojima, M., Gepstein, A., Sakakibara, H., Mittler, R., Gepstein, S., Blumwald, E., 2007. Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *PNAS* 104, 19631–19636.
- Robertson, B.M., Hall, A.E., Foster, K.W., 1985. A field technique for screening for genotypic differences in root growth. *Crop Sci.* 25, 1084–1090.
- Sadras, V.O., Lawson, C., 2011. Genetic gain in yield and associated changes in phenotype, trait plasticity and competitive ability of South Australian wheat varieties released between 1958 and 2007. *Crop Past. Sci.* 62, 533–549.
- Sala, C.A., Bulos, M. Inheritance and molecular characterization of broad range tolerance to herbicides targeting acetoxyacid synthase in sunflower. *Theor. Appl. Genet.*, in press. <http://dx.doi.org/10.1007/s00122-011-1710-9>.
- Satterthwaite, D., McGranahan, G., Tacoli, C., 2010. Urbanization and its implications for food and farming. *Philos. Trans. R. Soc. B* 365, 2809–2820.
- Salekdeh, G.H., Reynolds, M., Bennett, J., Boyer, J., 2009. Conceptual framework for drought phenotyping during molecular breeding. *Trends Plant Sci.* 14, 488–496.
- Sall, K., Sinclair, T.R., 1991. Soybean genotypic differences in sensitivity of symbiotic nitrogen fixation to soil dehydration. *Plant Soil* 133, 31–37.
- Sayre, K.D., Rajaram, S., Fischer, R.A., 1997. Yield potential progress in short bread wheats in North West Mexico. *Crop Sci.* 37, 36–42.
- Searchinger, T., Heimlich, R., Houghton, R.A., Dong, F., Elobeid, A., Fabiosa, J., Tokgoz, S., Hayes, D., Yu, T.-H., 2008. Use of U.S. croplands for biofuels increases greenhouses gases through emissions from land-use change. *Science* 319, 1238–1240.
- Shearman, V.J., Sylvester-Bradley, R., Scott, R.K., Foulkes, M.J., 2005. Physiological processes associated with wheat yield progress in the UK. *Crop Sci.* 45, 175–185.
- Sinclair, T.R., Muchow, R.C., Bennett, J.M., Hammond, L.C., 1987. Relative sensitivity of nitrogen and biomass accumulation to drought in field-grown soybean. *Agron. J.* 79, 986–991.
- Sinclair, T.R., Purcell, L.C., Vadez, V., Serraj, R., King, C.A., Nelson, R., 2000. Identification of soybean genotypes with N2 fixation tolerance to water deficits. *Crop Sci.* 40, 1803–1809.
- Sinclair, T.R., Purcell, L.C., Sneller, C.H., 2004. Crop transformation and the challenge to increase yield potential. *Trends Plant Sci.* 9, 1360–1385.
- Sinclair, T.R., Purcell, L.C., King, C.A., Sneller, C.H., Chen, P., Vadez, V., 2007. Drought tolerance and yield increase of soybean resulting from improved symbiotic N2 fixation. *Field Crops Res.* 101, 68–71.
- Sinclair, T.R., Messina, C.D., Beatty, A., Samples, M., 2010. Assessment across the United States of the benefits of altered soybean drought traits. *Agron. J.* 102, 475–482.
- Smith, A.B., Cullis, B.R., Thomson, R., 2005. The analysis of crop cultivar breeding and evaluation trials: an overview of current mixed model approaches. *J. Agric. Sci.* 143, 449–462.
- Smith, P., Gregory, P.J., van Vuuren, D., Obersteiner, M., Havlík, P., Rounsevell, M., Woods, J., Stehfest, E., Bellarby, J., 2010. Competition for land. *Philos. Trans. R. Soc. B* 365, 2941–2957.
- Spink, J., Street, P., Sylvester-Bradley, R., Berry, P., 2009. The potential to increase productivity of wheat and oilseed rape in the UK. Report to the Government Chief Scientific Adviser, 126 p. (available at: <http://www.commercialfarmers.co.uk/PotentialProductivity.pdf>).
- Stein, A.J., Rodriguez-Cerezo, E., 2010. International trade and the global pipeline of new GM crops. *Nat. Biotechnol.* 28, 23–25.

- Strzepek, K., Boehlert, B., 2010. Competition for water for the food system. *Philos. Trans. R. Soc. B* 365, 2927–2940.
- Sylvester-Bradley, R., Foulkes, J., Reynolds, M., 2005. Future wheat yields: evidence, theory and conjecture. In: Sylvester-Bradley, R., Wiseman, J. (Eds.), *Yields of Farmed Species*. Nottingham University Press, Nottingham, UK, pp. 233–260.
- Tittonell, P., Shepherd, K.D., Vanlauwe, B., Giller, K.E., 2008. Unravelling the effects of soil and crop management on maize productivity in smallholder agricultural systems of western Kenya—an application of classification and regression tree analysis. *Agric. Ecosyst. Environ.* 123, 137–150.
- Tollenaar, M., 1991. Physiological basis of genetic improvement of maize hybrids in Ontario from 1959 to 1988. *Crop Sci.* 31, 119–124.
- Vara, A.M., 2004. Transgénicos en Argentina: más allá del boom de la soja. *Rev. Iberoam. Ciencia Tecnol. Sociedad* 3, 101–129.
- Venter, J.C., 2011. The human genome at 10: successes and challenges. *Science* 331, 546–547.
- Wasson, A.P., Richards, R.A., Chatrath, R., Misra, S.C., Sai Prasad, S.V., Saxena, D.C., Rebetzke, G.J., Kirkegaard, J.A., Christopher, J., Watt, M., 2012. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *J. Exp. Bot.* 63, 3485–3498.
- Williams, K., Taylor, S., Bogacki, P., Pallotta, M., Bariana, H., Wallwork, H., 2002. Mapping of the root lesion nematode (*Pratylenchus neglectus*) resistance gene *Rlnn1* in wheat. *Theor. Appl. Genet.* 104, 874–879.
- Xiao, Y.G., Qian, Z.G., Wu, K., Liu, J.J., Xia, X.C., Ji, W.Q., He, Z.H., 2012. Genetic gains in grain yield and physiological traits of winter wheat in Shandong Province, China, from 1969 to 2006. *Crop Sci.* 52, 44–56.
- Xu, Y., Crouch, J.H., 2008. Marker-assisted selection in plant breeding: from publications to practice. *Crop Sci.* 48, 391–407.
- Yang, W., Peng, S., Laza, R.C., Visperas, R.M., Dionisio-Sese, M.L., 2007. Grain yield and yield attributes of new plant type and hybrid rice. *Crop Sci.* 47, 1393–1400.
- Zaman-Allah, M., Jenkinson, D.M., Vadez, V., 2011. Chickpea genotypes contrasting for seed yield under terminal drought stress in the field differ for traits related to the control of water use. *Funct. Plant Biol.* 38, 270–281.
- Zhang, Q., 2007. Strategies for developing green super rice. *PNAS* 104, 16402–16409.
- Zhong, S., Dekkers, J.C.M., Fernando, R.L., Jannink, J.-L., 2009. Factors affecting accuracy from genomic selection in populations derived from multiple inbred lines: a barley case study. *Genetics* 182, 355–364.
- Zhou, Y., He, Z.H., Sui, X.X., Xia, X.C., Zhang, X.K., Zhang, G.S., 2007. Genetic improvement of grain yield and associated traits in the northern China winter wheat region from 1960 to 2000. *Crop Sci.* 47, 245–253.
- Zhu, X.-G., Long, S.P., Ort, D.R., 2010. Improving photosynthetic efficiency for greater yield. *Annu. Rev. Plant Biol.* 61, 235–261.