REVIEW

Prospects of doubling global wheat yields

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Abstract

While an adequate supply of food can be achieved at present for the current global population, sustaining this into the future will be difficult in the face of a steadily increasing population, increased wealth and a diminishing availability of fertile land and water for agriculture. This problem will be compounded by the new uses of agricultural products, for example, as biofuels. Wheat alone provides $\geq 20\%$ of the calories and the protein for the world's population, and the value and need to increase the production is recognized widely. Currently, the world average wheat yield is around 3 t/ha but there is considerable variation between countries, with region-specific factors limiting yield, each requiring individual solutions. Delivering increased yields in any situation is a complex challenge that is unlikely to be solved by single approaches and a multidisciplinary integrated approach to crop improvement is required. There are three specific major challenges: increasing yield potential, protecting yield potential, and increasing resource use efficiency to ensure sustainability. Since the green revolution, yields at the farm gate have stagnated in many countries, or are increasing at less than half the rate required to meet the projected demand. In some countries, large gains can still be achieved by improvements in agronomy, but in many others the yield gains will only be achieved by further genetic improvement. In this overview, the problems and potential solutions for increased wheat yields are discussed, in the context of specific geographic regions, with a particular emphasis on China. The importance and the prospects for improvement of individual traits are presented. It is concluded that there are opportunities for yield increase but a major challenge will be avoiding a simultaneous increase in resource requirements.

The Context

Food Security has risen to the top of the international agenda following recent spikes in the price of food and the perceived growing threat to future supplies (see, e.g., the "G8 Action on Food Security and Nutrition" http://www.state.gov/s/globalfoodsecurity/190282.html). Along with an efficient distribution system and minimizing waste, providing an adequate supply of food is a key contributor to

securing food supply (Parry 2012). Apart from the possibility of famine, a failure in food security inevitably leads to social and political unrest. For example, concerns over food security were a major factor in the overthrow of the Tunisian government in 2011 (http://www.telegraph.co.uk/news/worldnews/africaandindianocean/tunisia/8263177/Is-Tunisia-the-first-domino-to-fall.html; http://voices.washingtonpost.com/political-economy/2011/01/spike_in_global_food_prices_tr.html, 25 May 2012). While providing an

adequate supply of food could be achieved at present for the current global population, sustaining this into the future will be very difficult in the face of a steadily increasing population, increased wealth, and a diminishing availability of fertile land and water for agriculture together with the new uses of agricultural products as biofuels. The challenge is made even more difficult by projected changes to climate, particularly higher temperatures and changes to rainfall distribution and amount (Parry and Hawkesford 2010b; Lobell et al. 2011). Food supply will need to grow by 2–3% each year to meet the projected demand; but in the last decade the yields of the major cereals, rice, maize, and wheat have increased at less than half this rate, with wheat showing the lowest rate of increase (Fig. 1).

Wheat alone provides ≥ 20% of the calories and the protein for the world's population (Braun et al. 2010). The value and need to increase the production of wheat is recognized widely. Currently, the world average wheat yield is around 3 t/ha but there is considerable variation between countries (Table 1). In comparing yields, it is important to also consider cropping systems and in particular whether single or multiple crops are grown in each year. In many countries only spring wheat is grown; but the highest wheat yields of over 15 t/ha that have been achieved are for winter wheat grown with a long growing season at higher latitudes. Even at a single location, in addition to variation due to agronomic and genetic factors, there is often considerable year on year variation reflecting different weather patterns. It is important to recognize that for farmers, maximizing yield is not their sole objective; profitability and managing risk are more important criteria.
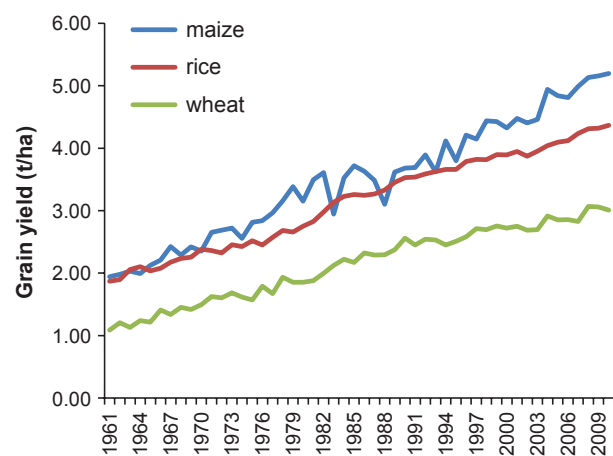
Table 1. Regional variation in wheat production (2010 data from FAOSTAT, http://www.faostat.fao.org, November 2012).

	Area (ha)	Yield (t/ha)	Production (Mt)	% of world
Africa	9,531,013	2.32	22.10	3.38
Argentina	4,373,440	3.41	14.91	2.28
Australia	13,507,000	1.64	22.14	3.39
Canada	8,268,700	2.80	23.17	3.54
China	24,256,086	4.75	115.18	17.62
European Union	26,459,007	5.26	139.07	21.28
France	5,931,000	6.88	40.79	6.24
Germany	3,297,700	7.31	24.11	3.69
India	28,460,000	2.84	80.80	12.36
New Zealand	54,762	8.12	0.44	0.07
Russian Federation	21,639,800	1.92	41.51	6.35
South America	8,133,194	3.17	25.81	3.95
Spain	1,907,300	2.94	5.61	0.86
United Kingdom	1,939,000	7.67	14.88	2.28
United States of America	19,270,900	3.12	60.06	9.19
World	217,219,395	3.01	653.65	100.00

Delivering increased yields is a complex challenge that is unlikely to be solved by a single approach. There are three specific major challenges: increasing yield potential (the maximum yield for a given genotype under optimal conditions), protecting yield potential, and increasing resource use efficiency to ensure sustainability. These challenges are closely related and there is good evidence that increasing yield potential will often also lead to larger yield even under stress conditions. For example, there is a good correlation of yields when crops with a wide variation in yield potential are grown with and without irrigation in the United Kingdom (Fig. 2), although there may

Figure 1. Progress in world average yields for major cereal crop yields. Data from FAOSTAT (the Statistics Division of the Food and Agriculture Organization of the United Nations, http://www.faostat.fao.org).
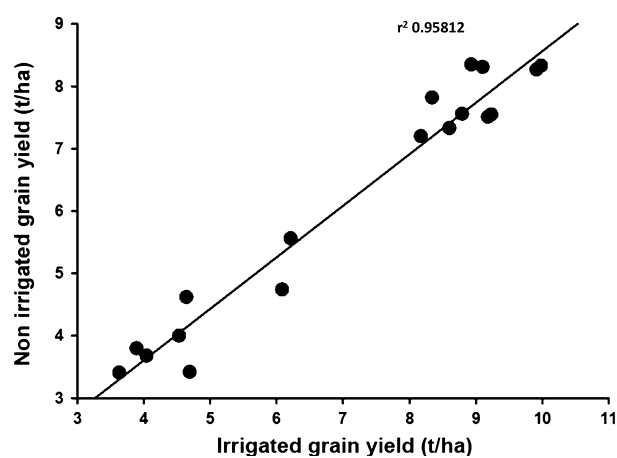

Figure 2. Yields of selected modern wheat genotypes with different dwarfing gene alleles and therefore yield potential grown with and without irrigation on sandy soil in the United Kingdom (M. A. J. Parry, unpubl. data, Woburn farm, Bedfordshire).

be exceptions, for instance some strongly drought resisting genotypes may not have the greatest yield potential.

The strong positive correlation indicates that the yield potential itself is the primary determinant of yield under mild-to-moderate drought stress; however, this relationship may break down under more severe stress (see also Araus et al. 2008). The size of the challenge is such that only an integrated approach can be successful, which will comprise a multidisciplinary approach for the dissection of traits, elucidation of traits and environmental interactions over time and among a range of germplasm, and the application to crop improvement, both with classical and biotechnological methodologies (Parry and Hawkesford 2012).

Grain yield (Y) is a function of the crop biomass (B) multiplied by the harvest index (HI), that is, $Y = HI \times B$. During the green revolution, yields increased dramatically year on year following the introduction of reduced height alleles; these not only increased the HI but also allowed the application of more nitrogen without crop lodging. In the most high-yielding wheat crops, HI already approaches 0.6 (60%) and further improvement is improbable given that leaves and stems are necessary to both produce and support the grain. Further increases in yield potential will therefore require increases in total biomass. Increases in biomass will require improvements in resource use efficiency (Long et al. 2006; Parry and Hawkesford 2010a; Reynolds et al. 2012).

Since the green revolution, yields at the farm gate have stagnated in many countries, or are increasing at less than half the rate required to meet the projected demand (Figs. 1 and 3). In some countries, large gains can still be achieved by improvements in agronomy, but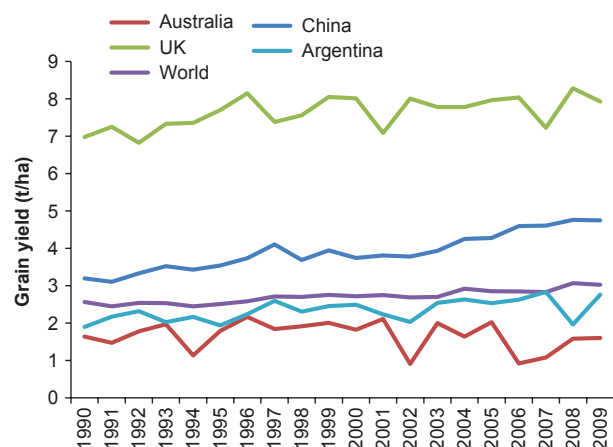 in many others and increasingly the yield gains can only be achieved by further genetic improvement. For example, in the United Kingdom, recent yield increases have been due to genetic improvement but have been less than 0.1 t/ha per year. In contrast, in China between 1990 and 2009, yields have risen from 3.19 to 4.75 t/ha, a 49% increase. From 1998 to 2008, wheat yields in Australia have oscillated and may have stagnated (Ogbonaya et al. 2008) (see Fig. 3).

In response to this lack of progress, several national and international programs are being developed with the aim to dramatically increase the yield of rice (C_4 rice consortium, Hibberd et al. 2008) and wheat (G20-led Wheat Initiative: http://urgi.versailles.inra.fr/Species/Wheat/Projects2/Wheat-Initiative; the Wheat Yield consortium: http://www.cimmyt.org/en/newsletter/38-2009/461-wheat-warriors-the-struggle-to-break-the-yield-barrier, Reynolds et al. 2011; 20:20 Wheat®: http://www.rothamsted.ac.uk/Content.php?Section=Research&Page=Wheat). In this review, we evaluate the prospects for doubling wheat yields to meet projected global demand.

The regional context

In regions with high production, albeit low productivity, for example, the United States of America, China, or India (yields of between 2.84 and 4.75 t/ha, see Table 1), doubling of or even small gains in yield would have a substantial impact on world food production. Improvements on these figures should be achievable, and in China and India in particular, improved crop management practices will undoubtedly increase yield in the future. In the United States of America, crop genetic improvement is more likely to be required for improved yield. The considerable target of doubling wheat yields in Europe, where yields are already 5.26 t/ha on average, represents a massive challenge to breeders to improve intrinsic genetic productivity. China has seen a steady increase in productivity over the past 20 years (Fig. 3) and this is considered in the next section.

What is the basis for genetic improvement of grain yield in China?

Agriculture in China feeds some 22% of the global population with only 7% of the world's arable lands (Piao et al. 2010). In recent years, agricultural growth in China has accelerated remarkably, but most of this growth has been driven by increased yield per unit area rather than by expansion of the cultivated area (Fan et al. 2012). To continue this trend, the fastest and most practical routes to increase yield are to improve agronomy (i.e., soil and crop management practices), in conjunction with continuing genetic improvement. Nevertheless, in the short term

Figure 3. World trends in wheat production (selected representative countries). Data from FAOSTAT (http://www.faostat.fao.org).

the biggest gains will come from combinations of improved crops and improved agronomical practices (Fan et al. 2012).

Knowledge of changes associated with advances in crop productivity is essential in understanding yield limiting factors and developing strategies for future genetic improvement. The most common approach has involved retrospective studies consisting of a direct comparison of old and modern varieties grown simultaneously in dedicated trials.

Zhou et al. (2007) studied the genetic gain for grain yield and associated traits in the Northern China Winter Wheat Region (NCWWR) by comparing cultivars released during the last four decades of the last century. Average annual genetic gains (the improvement in yield as a result of the introduction of new germplasm) in grain yield ranged from 32.07 to 72.11 kg/ha per year in different provinces, with the most significant increase taking place in the early 1980s, largely because of the utilization of dwarfing genes and the 1BL/1RS translocation. The genetic improvement in grain yield was primarily attributed to increased grain weight per spike, reduced plant height, and increased HI. Nevertheless the wide range of values recorded across provinces, together with the lack of a clear pattern of changes in some key yield components, such as spikes/m^2, kernels per spike, thousand grain weight (TGW), or biomass (Zhou et al. 2007), suggest that different breeding strategies have taken place across China. Two recent studies have analyzed the agronomical and physiological basis of the increase in yield potential during the past decades in Henan and Shandong, the two main Chinese provinces in terms of wheat production. Henan Province, located in the southern part of the Yellow and Huai Valleys Facultative Wheat Zone, is the largest wheat producing province in China with a production of 31 million tons harvested from an area of 5.3 million hectares in 2009 (He et al. 2010). Zheng et al. (2011) studying breeding advances during the last three decades showed that the average annual genetic gain in grain yield was 51.30 kg/ha per year, and the significant genetic improvement in grain yield was directly attributed to increased TGW, which also contributed to the significant increase in harvest index. These increases in grain yield were positively correlated with flag leaf photosynthetic rate during grain filling with the most recent cultivars exhibiting higher photosynthesis together with higher stomatal conductance and transpiration rates. In fact previous reports from CIMMYT (International Maize and Wheat Improvement Center) indicated that increases in the yield potential of spring wheat from 1962 to 1988 were positively related with increases in rate of photosynthesis associated with a higher stomatal conductance (Fischer et al. 1998). How-

ever, values of net photosynthesis in the study of Zheng et al. (2011) have to be taken with reservation, since the mean for rates reported 10 days after anthesis was 41.47 μmol/m^2 per second, well above the rates widely reported for wheat (e.g., Fischer et al. 1998; Reynolds et al. 2000), while the values of stomatal conductance were rather modest (with most of genotypes exhibiting values below 100 mmol/m^2 per second (and some even near 30 mmol/m^2 per second). In fact the information provided in the study about the photosynthetic methods used was incorrect; it was indicated in the article that "net photosynthetic rate, transpiration rate, stomatal conductance, and flag leaf temperatures were measured using a Sunfleck Ceptometer (Delta-T Devices, Burwell, Cambridge, U.K.)"; however, a ceptometer is not a device designed for that purpose.

Xiao et al. (2012) studied physiological traits associated with genetic gains in grain yield of winter wheat in Shandong province over the past four decades. Shandong, located in the northern part of the Yellow and Huai Valleys Winter Wheat Zone (YHVWWZ), is the predominant wheat producing region in YHVWWZ, and is the second largest wheat producing province in China with a planting area of around 3.7 million hectares and a production of about 20 million tons (He et al. 2010). The genetic gain in grain yield in Shandong was 62 kg/ha per year, largely associated with increased kernels/m^2 and biomass together with increased HI and reduced plant height. Significant genetic changes were also observed for apparent leaf area index (total leaf area/ground area), chlorophyll content and stem water-soluble carbohydrate (WSC) content at anthesis and photosynthesis rate during grain filling. These authors suggested that genetic gains in grain yield, mainly contributed by increases in kernels/m^2 and biomass, were achieved through improving crop photosynthesis at and after heading, and the source for grain filling may have benefited from increased stem WSC in stems at anthesis. However, again, these results have to be taken with caution as the rates of photosynthesis reported for mature nonsenescent leaves ranged from around 15–16 μmol/m^2 per second, which are clearly below the values beyond 20 μmol/m^2 per second expected for mature nonsenescent leaves. Although there is the possibility that these low rates of photosynthesis were caused by some degree of water stress, values of stomatal conductance were not provided, which also prevents any comparison with the previous study on genetic gains in yield potential of CIMMYT wheats.

Apart from some reservations on the physiological traits as indicated above, these two studies illustrate the concept that genetic gains in yield potential may be achieved through diverse agronomical and physiological mechanisms.

Specific Traits

Trait stability

In many regions, year to year variability in yields can be significant. Generally, farmers prefer guaranteed minimum productivity rather than a gamble on high yields with the alternative being very poor yields. Stability of production and the consequent influence on markets is also to be preferred on a global scale. Therefore, a prerequisite for high-yielding varieties is trait stability, particularly yield but also quality attributes. Traits need to be robust on a year to year basis and across a range of environments.

Canopy architecture and function

The key to increased production is the establishment of a photosynthetically active canopy, optimized for the production of photoassimilate that determines the final grain yield. Approaches to increasing carbon fixation are optimizing canopy architecture and light capture efficiency (targeting complete canopy closure or maximizing leaf angle for light interception), modification of intrinsic photosynthetic efficiency and extension of the grain filling period. Clearly, architecture needs to be optimized for maximum light capture but also traits to avoid disease spread and lodging need to be considered. A secondary but important role of the canopy is N-assimilation and N-storage (as protein), and the subsequent effective remobilization of this N to the grain during crop maturation.

Manipulating photosynthesis

The cumulative photosynthesis of the growing season is the primary determinant of crop biomass. Provided that other constraints do not become limiting, increasing photosynthesis, for example, by increasing the substrate CO_2, as in free air CO_2 enrichment experiments, has been clearly demonstrated to increase yields (Ainsworth and Long 2005). The cumulative photosynthesis can be increased by increasing photosynthetic rate, light interception, or its duration. In some regions, it may be possible to increase the duration of photosynthesis but the growing season is most often constrained either by environmental factors (low/high temperatures and water availability) or by the cropping system. However, there are still opportunities to increase photosynthesis by improving early vigor and by manipulating senescence to delay its onset. Despite the fact that there is considerable variation in the structure of modern wheat canopies (e.g., flag leaf size and leaf angle) light interception is very

efficient (Horton 2000). While further improvements in canopy architecture may be possible, potential increases in photosynthesis are small (Murchie et al. 2009; Reynolds et al. 2012). The biggest potential gains in cumulated photosynthesis would be achieved by increasing the photosynthetic rate. In wheat, only 4.6% of the intercepted radiation is converted to photosynthate, and there is clearly a good deal of room for improvement (Zhu et al. 2010). Numerous potential ways to increase photosynthetic rate have been identified (Parry et al. 2011). Many of these focus on increasing the concentration of CO_2 within the leaf. Simply increasing stomatal and mesophyll conductance will increase photosynthetic rate and yield (Fischer et al. 1998) but may decrease water use efficiency. Internal CO_2 concentrations could be increased by introducing a variety of CO_2 concentrating mechanisms. Each, although worthwhile, requires a number of technological hurdles to be overcome (Hibberd et al. 2008; Zarzycki et al. 2012; Price et al. 2013). An alternative and perhaps simpler approach is to replace the CO_2-fixing enzyme, Rubisco, with one that would deliver higher photosynthetic rates. There is variation in the kinetic properties of Rubisco isolated from different species (Parry et al. 1989; Delgado et al. 1995; Galmés et al. 2005) that is sufficient to at least in theory confer superior characteristics to photosynthesis in wheat (Zhu et al. 2010; Parry et al. 2011) However, it is not currently possible to do this in wheat (Parry et al. 2013).

An alternative approach would be to have an extended grain filling period, for example, an optimized canopy might include complete and early canopy closure together with early flowering. Similarly, an extended grain filling period as a consequence of delayed senescence may be beneficial. Extending the grain filling period is, however, fraught with difficulties and may expose sensitive tissues to late frosts or extremes of temperature or nonoptimal water supply. Even in temperate regions, excess cool and damp conditions during crop maturation, while positively impacting on yield may substantially compromise quality. Delaying senescence may increase carbon fixation but may limit N-remobilization to grain tissues, impact on quality or even sink capacity for carbon assimilation (Derkx et al. 2012).

Phenology

For years, breeders have adapted the length of the crop cycle to each particular environment to avoid climatic restrictions such as frost during flowering and high temperatures during the grain filling period, which could cause irreversible damage to crop yield. Thus, the length of the total cycle is generally well adjusted for a particular environment (Isidro et al. 2011). Although yield

components are built throughout the phases of the crop cycle, some phases are more critical, in terms of grain yield definition, than others. In this context, in wheat and barley, the environmental conditions during the period immediately preflowering is crucial for yield determination, as the most important yield components are defined in that period. The number of tillers per unit area and grains per spike, which are the main components of grains per unit area, are established in the period between 30 days before and 10 days after flowering (Fischer 1984). In fact, that period was named the "critical period" for yield determination. Additionally during the critical period, the number of fertile florets, the main component of grains per spike, is defined. As floret initiation is not the bottleneck determining the final number of grains per spike, as more than 10 floret primordia are initiated into the spikelets, the target is to promote floret survival (Miralles et al. 1998). Stem and spike compete for assimilates during the critical period, thus, the higher the assimilate partitioned to the spikes, the larger the number of fertile florets at flowering and thereby the final number of grains are increased (Fischer 1984). Other studies proposed an extension of the critical period, without changing the length of the cycle, as a strategy to reduce the stem-spike competition and promote floret survival due to heavier spikes at flowering (Halloran and Pennell 1982; Slafer et al. 1996). Studies carried out under controlled (Miralles et al. 2000) and field (Gonzalez et al. 2005a) conditions confirmed that an extension of the period from terminal spikelet formation to the onset of flowering promoted spike fertility, increasing the number of grains per unit area. The ecophysiological basis of the increase in spike fertility due to an elongation of the critical phase is associated with (i) less competition between stem and spike determining heavier spikes at flowering, (ii) a delay of the beginning of spike growth when floret primordia start to die, and (iii) allowing a sustained floret development, due to a reduced inter floret competition within the spikelets allowing more floret primordia to reach the fertile floret stage (Gonzalez et al. 2011). Those observations demonstrated that as floret death and survival were linked to preanthesis spike growth, the strategy of focusing on traits associated with preanthesis spike growth when breeding to increase wheat yield potential further is valuable. To generate the optimum combination of the duration of the preflowering phase, it is necessary to identify the genetic basis by which the stem-elongation phase (or spike development within it) may be extended without changing the total cycle length. There is a link between photoperiod sensitivity, the duration of spike development, and spike fertility (Miralles and Slafer 2007). Thus, the duration of the spike growth period could be manipulated by photoperiod sensitivity genes,

and/or earliness genes per se (Gonzalez et al. 2005b). The last point that should be considered is related to the heritability of this trait. García et al. (2011) showed that selection response to longer critical period in lines with similar cycle to flowering could not be found, possibly as the result of a high environmental influence on this attribute. The phenotypic variability observed in this attribute was not clearly associated with major adaptation genes evaluated (i.e., *Ppd* [photoperiod] and/or *Vrn* [vernalization] genes), suggesting that other minor genes could be associated.

Partitioning

The green revolution was based on plant height reduction to avoid lodging, especially under high yield potential conditions, and allowing higher inputs to be applied to the crop (e.g., fertilizers) to increase yield (Fischer and Stockman 1986). However, the most revolutionary impact of the green revolution was a clear and consistent improvement in the internal partitioning of the plants promoting increases in spike weight due to a reduced competition for carbohydrates between spike and stem. In fact, the spike:stem ratio was increased sharply in new cultivars released after the green revolution compared with older cultivars (Calderini et al. 1997). Plant height reduction increased the HI (i.e., the biomass partitioning to the reproductive organs, the grains). The HI of modern wheat genotypes, as reported for U.K. cultivars, is 55% (Foulkes et al. 2009b). This value is close to the theoretical upper limit of 62% calculated by Austin et al. (1980). Therefore, little opportunities are envisaged to continue increasing grain yield by higher partitioning in this country. On the contrary, the reported values of HI reached by modern Chinese wheat cultivars are between 42% (Xiao et al. 2012) and 46% (Zhou et al. 2007), although values of 49% have been recorded in Hebei Province (Zhou et al. 2007). Clearly there is an opportunity to improve this trait. However, as the relationship between yield and plant height has an optimum (Richards 1992; Miralles and Slafer 1995), further reduction in plant height is unlikely to be a useful strategy for breeders in the future. In fact, plant heights below 0.70 m or above 1 m result in a lower biomass production and lower partitioning to reproductive organs, respectively. Most of modern wheats in Northern China are already within the range of the optimum response of grain yield to plant height, that is, 0.7–0.9 m (Zhou et al. 2007; Zheng et al. 2011). Likewise, the strategies of focusing on increasing yield components per se (grain number mentioned above or grain weight in the following section), in addition to biomass production (see above), could be more helpful for improving yield

potential than attempting plant height and biomass partitioning as in the past.

Grain weight and trade-off between the two main yield components

During the 20th Century, wheat breeding improved grain yield potential by increasing grain number per area in many different countries (Slafer et al. 1994; Calderini et al. 1999; Foulkes et al. 2009b). The enlargement of grain number achieved by breeders coincides with the higher sensitivity of this main yield component to environmental conditions. Grain number has also been recognized as the central reproductive strategy of wheat plants from an evolutionary perspective (Sadras 2007). Therefore, to continue increasing grain yield by augmenting this trait seems to be the way forward. On the contrary, average grain weight is a more conservative attribute than grain number (Fischer 1985; Savin and Slafer 1991; Sadras and Slafer 2012). Grain weight has not been markedly modified by wheat breeding during the past century (Austin et al. 1980; Waddington et al. 1986), some results even showed that individual grain weight was reduced by genetic improvement (Loss et al. 1989; Slafer and Andrade 1989). For a long time, the importance of grain weight was supported only by quality considerations, especially in wheat breeding programs. However, if plant breeders continue to strive for increased wheat yields by selecting for grains set in distal positions of the spike, the inherently less grain weight potential at these distal positions could limit advances in grain yield, in addition to the negative effect on grain element concentration (Calderini and Ortiz-Monasterio 2003). The importance of the trade-off between the two main yield components is not purely speculative because it has been found in cultivars released in Australia between 1958 and 2007 (Sadras and Lawson 2011), and evidence of partial compensation between grain yield and grain number has been reported recently (Calderini et al. 2012; Bustos et al. 2013). The need to increase grain weight and avoid effects on grain number is, therefore, a priority for breeding.

Very few studies showed a positive impact of wheat breeding on grain weight during the 20th Century (Cox et al. 1988) or part of it (Calderini et al. 1995). More recently, the contribution of grain weight to the improvement of grain yield has been reported in Australia after a negative trend till to the 1980s (Sadras and Lawson 2011). Apparently, a break point in grain weight at the 1980s was also the cause of grain yield increase found in Henan Province, China (Zheng et al. 2011). However, most of the grain weight increase seems to be more evident since 2000 taking into account that a previous study evaluating wheat cultivars released in Henan between 1960 and 2000

did not shown clear trends for this and other traits (see Fig. 2 in Zheng et al. 2011 and Zhou et al. 2007). Contrasting results were found in Shandong Province, the second largest wheat producer of China. In this study, the driver of the yield increase was grain number per unit area, while no effect of wheat breeding was found for averaged grain weight (Xiao et al. 2012). Although no direct comparisons could be made between the studies, it is interesting to point out that the highest grain number and weight reported for Shandong (22461 grains/m^2 and 51.6 g, averaged across experiments) were similar to that of Henan (20335 grains/m^2 and 51.0 g), but interestingly a higher trade-off between these yield components is apparent in Shandong (Fig. 4). Speculatively, and considering the Australia and Henan cases, it is likely that wheat breeding in Shandong has to start increasing grain weight.

The increase in grain weight in breeding programs by the simple choice of lines carrying heavier grain has been little effective as shown by Wiersma et al. (2001), where a complete compensation between grain number and grain weight was reported after eight cycles of selecting heavier grain lines without any improvement of grain yield. Therefore, this highlights the need of identifying mechanisms to improve the two main yield components simultaneously. A promising strategy to increase yield potential by combining both yield components has been proposed in Bustos et al. (2013) through crossing genotypes with high grain number with others with a high TGW (and similar yield), particularly if the chance to put together both yield components in the same genotype could be facilitated by increasing the number of possible outcomes through a doubled haploid (DH) population. Additionally, it would be interesting to assess whether the changes
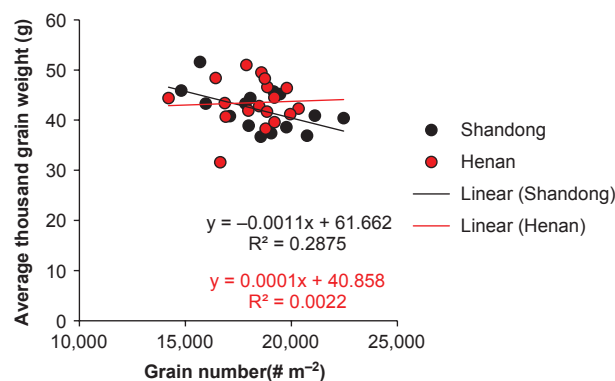

Figure 4. Relationship between grain weight (TGW) and grain number of wheat cultivars released at different areas in Shandong and Henan Provinces. Source: Zheng et al. (2011) and Xiao et al. (2012).

that occurred in TGW could also be achieved at specific positions due to its beneficial impact on quality traits (Calderini and Ortiz-Monasterio 2003) and milling efficiency (Marshall et al. 1986). Similarly, the identification of physiological bases driving grain weight would be worthwhile when considering that grain weight is scarcely source limited during grain filling under both at potential and in Mediterranean stress (Cartelle et al. 2006) conditions. Accordingly, the relationships between grain weight and ovary weight (Hasan et al. 2011), and the similarity between grain size dynamics and expansins (proteins which loosen cell walls) expression (Lizana et al. 2010) may be exploited to develop tools for wheat breeding programs aimed at increasing grain yield.

Roots

Root systems have an important role to play in contributing to crop performance. Wheat roots extend more than 1 m in depth (Thorup-Kristensen et al. 2009), although root density is highest in the top few centimeters and optimal for interception of applied nutrients and rainfall. Increased yields will lead to increased demand for water and nutrients that must be captured from the soil via the roots. In many environments, a more extensive root system or deeper rooting might be advantageous, especially at lower plant densities. As plant density reaches a maximum in the highest yielding environments, there is probably no advantage to increasing root density and rather it would be advantageous not to over invest biomass in surplus roots.

Breeding for root characteristics has been seldom considered, principally because of the difficulties of scoring phenotypes directly and the absence of suitable proxy measurements. Laboratory screens have focused mainly on seedlings, with traits correlating to field performance in only some cases (Wojciechowski et al. 2009; Bai et al. 2013). Nitrogen supply directly influences root proliferation (Zhang and Forde 1998) indicating a highly developed and efficient capture system at least in some species. Further improvements on root architecture may focus on root proliferation at depth (Foulkes et al. 2009a).

How much fertilizer?

Nitrogen is required for wheat production, initially to establish an adequate photosynthetically active canopy; the target is full closure and efficient light interception. Second, nitrogen is required for grain production and much of this requirement is met by remobilization from leaf and stem tissues during senescence and crop maturation.

Increasing N-supply initially results in increased yield as a greater canopy may be generated, in the absence of other abiotic or biotic limitations. Once a closed canopy is achieved, further N-supply can at best only result in "excess" vegetative development, which is not able to increase photosynthetic capacity, and hence no increase in yield is seen. N-uptake by the crop will continue to increase and much of this will result in a higher grain protein. Proportionally however, the larger N-inputs are not matched proportionally by increase grain N, resulting in a lower overall nitrogen use efficiency (Barraclough et al. 2010).

In a simple calculation, doubling wheat yields might be expected to require double the nitrogen; this only holds true if grain protein content is to be maintained (see below). In fact if increased yields are derived from increased carbon fixation and a lower protein content is acceptable, the projected increase in demand for nitrogen may be much less. It may also be anticipated that a higher crop density will result in greater capture efficiency, particularly if root densities are increased (see above).

Quality considerations

At present the requirement for grain protein is as a result of demand for dietary protein and for commercial requirements for baking. Wheat has multiple end uses from feed to pasta to bread making, each end use having differing requirements for protein and fulfilled by specific wheat types. With increased yield either increased N will need to be applied to maintain grain N or lower protein content will have to be accepted. As bread-making quality is dependent on protein composition rather than quantity (see, e.g., Tronsmo et al. 2003; Shewry 2009), there is the potential to reduce total protein content, by selecting for specific protein compositions. Alternatively the development of baking processes requiring lower protein contents will reduce N-demands of wheat crops. If, however, wheat is a critical dietary source of protein such a reduction is not desirable.

Within the United Kingdom modern wheats, the range of grain N varied from 1.1% to 2.8% N (equating to around 6.3–16% protein) among multiple genotypes grown at a range of nitrogen inputs, from extremely deficient to luxury supply (Barraclough et al. 2010). There is clearly a great plasticity in the ability to tolerate a wide range of grain protein concentrations; however, equally important is the protein composition. Protein composition also varies greatly between varieties and in response to nitrogen (Wan et al. 2013, indicating a clear opportunity to select for "better" protein types.

Protecting Yield Potential

Abiotic stress: what is threatening yield potential, insufficient genetic advances or climate change?

Stagnation in yield for bread wheat and other cereals has occurred during the last decades in most European countries (Peltonen-Sainio et al. 2009; Brisson et al. 2010; Olesen et al. 2011), as well as in China (You et al. 2009; Piao et al. 2010) and also in other parts of the world (Calderini and Slafer 1998; Ladha et al. 2003).

The case of France illustrates how even the highly advanced agriculture of a developed country is being challenged by climate change. Thus, a stagnation of potential bread wheat yield has been observed in France since the middle of the 1990s, and the possibility of a decline in breeding progress has been suggested (Brisson et al. 2010). However, a recent study has shown that since the end of the 1980s, genetic progress has been partly or totally counterbalanced by the adverse effects of climate change (Oury et al. 2012). Therefore, yield potential trials may be affected in some degree by adverse climatic conditions, the main factor being climate warming (Oury et al. 2012).

Thus, it may be that genetic progress has not experienced any weakening during the last decades, and may be considered as continuous (Oury et al. 2012). This linear trend, with no perceptible limitation to genetic progress in recent years, has also been found in Finland, in the study of Peltonen-Sainio et al. (2009).

Apart from the direct effects of a higher temperature increasing photorespiration and dark respiration losses or shortening the crop cycle, an increase in mean temperature may negatively affect yield physiology at other levels. For example, it may have an (either direct or indirect) effect increasing frequencies for winter and spring droughts (Brisson et al. 2010). More precisely, drought during stem elongation leads to a decrease in vegetative dry matter, with a concomitant reduction in number of grains per unit area (Sinclair and Jamieson 2006); and drought and/or high temperatures during grain filling lead to reduced grain weight (Gooding et al. 2003). Whatever the mechanism, estimated decreases in productivity per 1°C increase in temperature during the growing season may reach easily 5% (or more) of actual yields (Kalra et al. 2008; You et al. 2009; Gallais et al. 2010).

The adverse effect of global warming on crop productivity has already been demonstrated in other parts of the world: for example, the increase in night temperatures has been related to the stagnation or the decrease in rice yields in Asia (Ladha et al. 2003; Peng et al. 2004);

similarly, the harmful effects of high temperatures were identified for maize and soybean yields in the United States of America (Lobell and Asner 2003), and for wheat yield in China (You et al. 2009) and India (Kalra et al. 2008). Moreover, some of the above studies (Kalra et al. 2008; Oury et al. 2012) underline the fragility of intensive agriculture, which appears all the more sensitive to climate when yields are high.

In the case of China, for example, current knowledge does not allow a clear assessment of the impact of anthropogenic climate change on China's water resources and agriculture. Future study must improve regional climate simulations, especially of precipitation, and develop a better understanding of the managed and unmanaged responses of crops to changes in climate, diseases, pests, and atmospheric constituents (Piao et al. 2010). Moreover, it is expected that increasing social concerns in China about pollution and environmental sustainability of agriculture will further trigger the research interest for a higher efficiency in the use of resources by crops (Fan et al. 2012).

For China, countrywide, a 4.5% reduction in wheat yields is attributed to rising temperatures over the period 1979–2000 (You et al. 2009). Warmer daytime temperatures are likely to have decreased wheat yields over a wide range, from 6% to 20% per °C (Tao et al. 2008) which stresses the need for regional and crop-specific studies. Therefore, increasing the genetic gains beyond the current values is a requirement if we aim to cope with the reductions in crop yield caused by climate change.

Biotic assaults

Pathogens (viruses, bacteria, fungi, oomycetes, and nematodes) are among the major biotic stresses affecting plants, impacting on crop production principally by reducing yield and quality. Conservative estimates of global losses to plant pathogens across all plant industries are in the order of 10% (Strange and Scott 2005).

Estimating the overall global impact of diseases in wheat production is difficult. Many published accounts exist of the impact of individual diseases on yield of a susceptible genotype, and of the impact on production of regional epidemics of a single disease. For example, stripe rust of wheat can cause yield losses in excess of 70% in susceptible cultivars. Sporadic epidemics of the disease have caused substantial losses in most wheat growing regions of the world. In 1993, stripe rust epidemics in selections from the CIMMYT-generated wheat line, Veery, caused significant yield losses in Yemen, Ethiopia, and Iran (McIntosh et al. 1995). Winter wheat production in China is also affected by recurring epidemics of stripe rust (Stubbs 1985), with epidemics in 1950, 1964, and 1990

estimated to have caused losses of 6, 3, and 2.5 million tons, respectively (Wan et al. 2007).

In Australia, where wheat yields are relatively low (see Fig. 3), principally due to a lack of water, a recent analysis of the impact of diseases in wheat production by Murray and Brennan (2009) estimated that they cause a current average annual loss of AUD$913 million, or $76.64 per hectare, to the Australian wheat industry. The estimated losses equated to about 19.5% of the average annual value of the wheat crop over the past decade, with five diseases accounting for about 65% of the overall loss: yellow spot (23% of overall loss; caused by *Pyrenophora tritici-repentis*), stripe rust (14%; *Puccinia striiformis* f. sp. *tritici*), *Septoria nodorum* blotch (12%), crown rot (8%; caused by *Fusarium*), and root lesion nematode (8%; *Pratylenchus neglectus*).

Another combined example from China is regarding the yield losses due to *Fusarium* head blight (FHB). FHB is a major disease of wheat production affecting the Southern winter wheat and Northeast spring wheat growing areas in China, which are the largest wheat producing areas in China (Lu and Chen 2012). Global warming is causing the early onset of the rainy season, and combined with changes in farming systems, especially with increasing corn stubble residues, resulted in a heavy epidemic of FHB in 2012, and consequently serious yield losses in these regions (Zhang et al. 2012). In this case, lack of both FHB resistance cultivars and FHB-resistant resources adapted to the winter wheat growing region in these areas are the main limitations of protecting yield potential.

Clearly, protecting future production from losses of the magnitude estimated in the study by Murray and Brennan (2009) will be critical if world wheat production is to double. Chemical control is now used in many parts of the world for disease control in broadacre cropping including wheat. For example, about $280 million has been spent on fungicides in eastern Australia to control stripe rust in wheat following a single incursion of the wheat stripe rust pathogen from North America in 2002 (Wellings 2007). Concerns over the use of chemicals in food production will, however, increase the role of genetics in disease control.

The application of knowledge of the genetics of resistance in plant breeding has made a major contribution to reducing yield losses caused by pathogens. The study by Murray and Brennan (2009) also estimated the magnitude of losses in wheat to diseases in Australia if current control measures were not in place. They estimated that already, resistance breeding contributes $869 million annually to the control of stem rust and stripe rust alone.

Genetic approaches to control diseases in wheat are increasingly emphasizing the concept of durable resistance, first defined by Johnson (1978) as resistance that remains effective when a cultivar is grown widely in environments favoring disease development. The concept of durable resistance acknowledges the diversity of resistance to disease in plants and the dangers of making generalizations. To understand the underlying mechanisms and genetics of durable resistances, it is necessary to consider each case independently. Durable resistance is an important component of durable disease control. Most strategies to control pathogens in crops involve the integrated use of agronomic practices and genetic resistance (Park et al. 2009). The need for genetic resistance is likely to be less if agronomic practices provide long-term sustained control. Outbreaks of pathogens with limited dispersal ability (e.g., many soil-borne pathogens) typically have little effect beyond the farm on which they occur and control at the level of the individual paddock by practices such as rotation and fallow can be effective, reducing the need for genetically resistant cultivars. In contrast, outbreaks of pathogens with high dispersal ability (e.g., many air-borne pathogens such as rusts) can require regional, national, and in some cases international coordination to achieve effective and sustained control because of their particularly high epidemic and pandemic potentials (McIntosh et al. 1995). While genetic resistance is a desirable component of control strategies in these cases, its use depends on the availability of resistance in adapted germplasm, the genetic complexity of available resistance, and ease of phenotypic selection of resistance.

One of the greatest challenges in protecting crops from pathogens has come from exotic pathogen incursions, and significant crop losses have occurred as a result of accidental intercontinental movements of plant pathogens (Finckh 2008). It is quite feasible that in future, such long distance movements of plant pathogens may become more frequent due to changes in climate and increased international movement of people and goods, necessitating even greater coordination in the control of plant diseases at the continental or even global levels. Scherm and Coakley (2003) noted that the rate of exotic pathogen invasion in the United States of America had increased from about five instances per decade from 1940 to 1970, to more than three times this during the 1990s. A similar situation has been observed in Australia with incursions of exotic wheat rust isolates, four instances of which were detected in the 45 years from 1925 to 1970, four over the 30 years from 1970 to 2000, and three over the past 7 years (Park et al. 2011). While the increases noted by Scherm and Coakley (2003) were attributed to increased global trade in plant produce, a trend that may continue with global climate change, in Australia, the increased frequency of wheat rust incursions is likely associated with increased international travel and contaminated clothing (e.g., Wellings 2007). Changes in concentration of key

atmospheric gases and global warming may also affect disease incidence. Retrospective studies of the annual incidences of the two wheat pathogens *Phaeosphaeria nodorum* and *Mycosphaerella graminicola* in grain since 1843 at Rothamsted U.K. established that they were positively and negatively associated with atmospheric concentration of SO_2 (Shaw et al. 2007). While the concentration of SO_2 has declined in Europe and North America over the past 20 years, these results nonetheless illustrate a potential cause and effect connection between atmospheric gas concentration and pathogen incidence. According to Coakley et al. (1999), predicted increases in CO_2 concentration could either favor or hinder plant pathogens, making precise predictions difficult.

While a great deal of knowledge now exists from how individual host and pathogen genes interact and how resistance genes function in plants, to ecologically based studies of host:pathogen interactions, much remains to be learnt at the interface of the genetics of resistance and crop physiology. The cloning of resistance genes and corresponding avirulence genes have indicated considerable complexity not only in structure but also in the way in which gene products interact and trigger resistance. At the crop level and beyond, few large-scale studies have addressed in detail the effects of genetic diversity in crops in reducing disease incidence. In one such study, in which the control of *Magnaporthe grisea* was examined in 3342 ha of rice crops in China, the benefits of genetic diversity were very clear, with varietal mixtures resulting in an 89% yield increase in susceptible varieties (Zhu et al. 2000). Clearly, genetic diversity is important in sustained control of plant diseases, and it has been argued that even in cases where specific or major resistance genes are used, genetic diversity can be used as insurance against lack of durability and hence as a means of reducing genetic vulnerability (McIntosh 1988). The durability of some single gene resistances, despite extensive use, and the preferential survival of some pathogen genotypes in the absence of no obvious advantage in terms of virulence that has been well documented with wheat rust pathogens in Australia, indicates that the interaction of hosts and pathogens is indeed complex.

Creating and Exploiting New Diversity

One key feature of conventional breeding is the identification and exploitation of genetic diversity for the kinds of key traits described above. A major issue for cereal breeding programs is that the variation in such key traits has progressively become more limited, at least among elite breeding germplasm for maize. Additional variation in such traits has been generated, for example, by the recreation of synthetic wheat and by wide crossing (Mujeeb-Kazi et al. 2008). Several commercial cultivars with desirable yield potential and FHB resistance have been reported in Henan Province, China (Yang et al. 2009; Zhang et al. 2012). These have been derived from common wheat, its wild relatives, and some of their bridge materials, such as triticale, perennial *Elytrigia elongate*, perennial *Elytrigia intermedia*, and *Leymus*, etc., by multi-step conventional wide crossing assisted by tissue culture techniques. This shows the potential significance of creating and exploiting new diversity through wide crossing to expand the common wheat gene pool for doubling wheat yield in the future. Mutagenesis can also be used to generate additional variation, and globally more than 1000 wheat cultivars derived from mutagenesis have been commercially released (Parry et al. 2009). Additional variation is also being produced by genetic transformation but although lines with interesting traits (e.g., pest resistance, drought tolerance, quality) have been evaluated, few have yet been commercialized.

Conclusions and Sustainability Issues

There is a clear need to increase productivity, and optimistically there is great potential for both genetic and agronomic routes to yield improvement. Greater yields with germplasm improvements, increasing intrinsic photosynthetic mechanisms, fine tuning partitioning, and increasing resistance to stresses are all viable approaches, particularly when combined with optimized use of water and fertilizer; there is every prospect of doubling world wheat yields. Increased yields will, however, come at a cost and greater inputs are inevitable. Huge increases in water consumption, increased nitrogen fertilizer use with associated environmental impacts, and requirements for nonrenewable mineral resources such as potassium and phosphorus are to be expected. It is essential, that in parallel with efforts to increase productivity, optimum resource use efficiency is also considered. Without efficiency, increased wheat production will not be sustainable.

Conflict of Interest

None declared.

References

Ainsworth, E. A., and S. P. Long. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol. 165:351–371.

Araus, J. L., G. A. Slafer, C. Royo, and M. D. Serret. 2008. Breeding for yield potential and stress adaptation in cereals. Crit. Rev. Plant Sci. 27:1–36.

Austin, R. B., J. Bingham, R. D. Blackwell, L. T. Evans, M. A. Ford, C. L. Morgan, et al. 1980. Genetic improvement in winter wheat yield since 1900 and associated physiological changes. J. Agric. Sci. 94:675–689.

Bai, C., Y. Liang, and M. J. Hawkesford. 2013. Identification of QTL associated with seedling root traits and their correlation with mature plant height in wheat. J. Exp. Bot. In press.

Barraclough, P. B., J. R. Howarth, J. Jones, R. Lopez-Bellido, S. Parmar, C. E. Shepherd, et al. 2010. Nitrogen efficiency of wheat: genotypic and environmental variation and prospects for improvement. Eur. J. Agron. 33:1–11.

Braun, H. J., G. Atlin, and T. Payne. 2010. Multi-location testing as a tool to identify plant response to global climate change. Pp. 115–138 in M. P. Reynolds, ed. Climate change and crop production. CABI Climate Change Series, U.K.

Brisson, N., P. Gate, D. Gouache, G. Charmet, F.-X. Oury, and F. Huard. 2010. Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. Field Crops Res. 119:201–212.

Bustos, D. V., A. K. Hasan, M. P. Reynolds, and D. F. Calderini. 2013. Combining high grain number and weight through a DH-population to improve grain yield potential of wheat in high-yielding environments. Field Crops Res. In press.

Calderini, D. F., and I. Ortiz-Monasterio. 2003. Grain position affects grain macronutrient and micronutrient concentrations in wheat. Crop Sci. 43:141–151.

Calderini, D. F., and G. A. Slafer. 1998. Changes in yield and yield stability in wheat during the 20th century. Field Crops Res. 57:335–347.

Calderini, D. F., M. F. Dreccer, and G. A. Slafer. 1995. Genetic improvement in wheat yield and associated traits. A re-examination of previous results and the latest trends. Plant Breeding 114:108–112.

Calderini, D. F., M. F. Dreccer, and G. A. Slafer. 1997. Consequences of breeding on biomass, radiation interception and radiation-use efficiency in wheat. Field Crops Res. 52:271–281.

Calderini, D. F., M. Reynolds, and G. A. Slafer. 1999. Genetic gains in wheat yield and associated physiological changes during the twentieth century. Pp. 351–377 in E. H. Satorre and G. A. Slafer, eds. Wheat: ecology and physiology of yield determination. Food Product Press, The Haworth Press, New York.

Calderini, D. F., A. Quintero, J. Le Gouis, S. Mouzeyar, P. R. Shewry, and S. McQueen-Mason. 2012. Improving grain filling and potential grain size. Pp. 24–29 in M. P. Reynolds, H. J. Braun, and E. Quilligan, eds. 2nd International Workshop of the Wheat Yield Consortium, CENEB, CIMMYT. Cd. Obregón, Sonora, México.

Cartelle, J., A. Pedro, R. Savin, and G. A. Slafer. 2006. Grain weight responses to post-anthesis spikelet-trimming in an old and a modern wheat under Mediterranean conditions. Eur. J. Agron. 25:365–371.

Coakley, S. M., H. Scherm, and S. Chakraborty. 1999. Climate change and plant disease management. Annu. Rev. Phytopathol. 37:399–426.

Cox, T. S., R. J. Shroyer, L. Ben-Hui, R. G. Sears, and T. J. Martin. 1988. Genetic improvement in agronomic traits of hard red winter wheat cultivars from 1919 to 1987. Crop Sci. 28:756–760.

Delgado, E., H. Medrano, A. J. Keys, and M. A. J. Parry. 1995. Species variation in Rubisco specificity factor. J. Exp. Bot. 46:1775–1777.

Derkx, A., S. Orford, S. Griffith, J. Foulkes, and M. J. Hawkesford. 2012. Identification of differentially senescing mutants of wheat and impacts on yield, biomass and nitrogen partitioning. J. Integr. Plant Biol. 54:555–566.

Fan, M., J. Shen, L. Yuan, R. Jiang, X. Chen, W. J. Davies, et al. 2012. Food security. Improving crop productivity and resource efficiency to ensure food security and environmental quality in China. J. Exp. Bot. 63:13–24.

Finckh, M. R. 2008. Integration of breeding and technology into diversification strategies for disease control in modern agriculture. Eur. J. Plant Pathol. 121:399–409.

Fischer, R. A. 1984. Wheat. Pp. 129–153 in W. H. Smith and S. J. Banta, eds. Symposium on Potential Productivity of Field Crops Under Different Environments. IRRI, Los Baños, Philippines.

Fischer, R. A. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. J. Agric. Sci. 105:447.

Fischer, R. A., and Y. M. Stockman. 1986. Increased kernel number in Norin 10 derived dwarf wheat: evaluation of a cause. Aust. J. Plant Physiol. 12:767–784.

Fischer, R. A., D. Rees, K. D. Sayre, Z. M. Lu, A. G. Condon, and A. L. Saavedra. 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. Crop Sci. 38:1467–1475.

Foulkes, M. J., M. J. Hawkesford, P. B. Barraclough, M. J. Holdsworth, S. Kerr, S. Kightley, et al. 2009a. Identifying traits to improve the nitrogen economy of wheat. Recent advances and future prospects. Field Crops Res. 114:329–342.

Foulkes, M. J., M. P. Reynolds, and R. Sylvester-Bradley. 2009b. Genetic improvement of grain crops. Pp. 355–385 *in* V. O. Sadras and D. F. Calderini, eds. Crop physiology: applications for genetic improvement and agronomy. Academic Press, Elsevier, Amsterdam.

Gallais, A., F.-X. Oury, and P. Gate. 2010. P. 15 *in* Evolution des rendements de plusieurs plantes de grande culture. Une réaction différente au réchauffement climatique selon les espèces. Compte-rendu de la séance du 5 mai 2010 de l'Académie d'Agriculture de France.

Galmés, J., J. Flexas, A. J. Keys, J. Cifre, R. A. C. Mitchell, P. J. Madgwick, et al. 2005. Rubisco specificity factor tends to be larger in plant species from drier habitats and in species with persistent leaves. Plant Cell Environ. 28:571–579.

García, G. A., M. L. Appendino, R. A. Serrago, M. Helguera, L. Vanzetti, L. Lombardo, et al. 2011. Variability of pre-anthesis phases as a strategy for increasing grain number in wheat (*Triticum aestivum* L.). Field Crops Res. 124:408–416.

Gonzalez, F., G. A. Slafer, and D. J. Miralles. 2005a. Floret developmental and survival in wheat plants exposed to contrasting photoperiod and radiation environments during stem elongation. Funct. Plant Biol. 32:189–197.

Gonzalez, F., G. A. Slafer, and D. J. Miralles. 2005b. Pre-anthesis development and number of fertile florets in wheat as affected by photoperiod sensitivity genes *Ppd-D1* and *Ppd-B1*. Euphytica 146:253–269.

Gonzalez, F. G., D. J. Miralles, and G. A. Slafer. 2011. Wheat floret survival as related to pre-anthesis spike growth. J. Exp. Bot. 62:1–13.

Gooding, M. J., R. H. Ellis, P. R. Shewry, and J. D. Schafield. 2003. Effects of restricted water availability and increased temperature on the grain filling, drying and quality of winter wheat. J. Cereal Sci. 37:295–309.

Halloran, G. M., and A. L. Pennell. 1982. Duration and rate of development phases in wheat in two environments. Ann. Bot. 49:115–121.

Hasan, A. K., J. Herrera, C. Lizana, and D. F. Calderini. 2011. Carpel weight, grain length and stabilized grain water content are physiological drivers of grain weight determination of wheat. Field Crops Res. 123:241–247.

He, Z. H., X. C. Xia, and A. P. A. Bonjean. 2010. Wheat improvement in China. Pp. 51–68 *in* Z. H. He and A. P. A. Bonjean, eds. Cereals in China. CIMMYT, Mexico, D.F.

Hibberd, J. M., J. E. Sheehy, and J. A. Langdale. 2008. Using C4 photosynthesis to increase the yield of rice - rationale and feasibility. Curr. Opin. Plant Biol. 11:228–231.

Horton, P. 2000. Prospects for crop improvement through the genetic manipulation of photosynthesis: morphological and biochemical aspects of light capture. J. Exp. Bot. 51:475–485.

Isidro, J., F. Alvaro, C. Royo, D. J. Miralles, and L. F. Garrido. 2011. Changes in apical development of durum wheat caused by breeding during the 20th century: analysis by

phases and its implications for yield formation. Ann. Bot. 107:1355–1366.

Johnson, R. 1978. Practical breeding for durable resistance to rust diseases in self-pollinating cereals. Euphytica 27:529–540.

Kalra, N., D. Chakraborty, A. Sharma, H. K. Rai, M. Jolly, S. Chander, et al. 2008. Effect of increasing temperature on yield of some winter crops in northwest India. Curr. Sci. 94:82–88.

Ladha, J. K., D. Dawe, H. Pathak, A. T. Padre, R. L. Yadav, B. Singh, et al. 2003. How extensive are yield declines in long-term rice-wheat experiments in Asia? Field Crops Res. 81:159–180.

Lizana, X. C., R. Riegel, L. D. Gomez, J. Herrera, A. Isla, S. J. McQueen-Mason, et al. 2010. Expansins expression is associated with grain size dynamics in wheat (*Triticum aestivum* L.). J. Exp. Bot. 61:1147–1157.

Lobell, D. B., and G. P. Asner. 2003. Climate and management contributions to recent trends in US agricultural yields. Science 299:1032.

Lobell, D. B., W. Schlenker, and J. Costa-Roberts. 2011. Climate trends and global crop production since 1980. Science 333:616–620. doi:10.1126/science.1204531.

Long, S. P., X. G. Zhu, S. L. Naidu, and D. R. Ort. 2006. Can improvement in photosynthesis increase crop yields? Plant Cell Environ. 29:315–330.

Loss, S. P., E. J. M. Kirby, K. H. M. Siddique, and M. W. Perry. 1989. Grain growth and development of old and modern Australian wheats. Field Crops Res. 21:131–146.

Lu, W., and P. Chen. 2012. Pp. 1–2 *in* Research progress of wheat scab in China. Proceedings of the 4th International Symposium on Fusarium Head Blight, Nanjing, China, organized by Nanjing Agricultural University, Jiangsu Academy of Agricultural Sciences, Journal of Genetics and Genomics, and Jiangsu Society of Genetics.

Marshall, D. R., D. J. Mares, H. J. Moss, and F. W. Ellison. 1986. Effects of grain shape and size on milling yields in wheat. II. Experimental studies. Aust. J. Agric. Res. 37:331–342.

McIntosh, R. A. 1988. The role of specific genes in breeding for durable stem rust resistance in wheat and triticale. Pp. 1–9 *in* N. W. Simmonds and S. Rajaram, eds. Breeding strategies for resistance to the rusts of wheat. CIMMYT, Mexico.

McIntosh, R. A., C. R. Wellings, and R. F. Park. 1995. P. 200 *in* Wheat rusts. An atlas of resistance genes. CSIRO, Melbourne, Australia.

Miralles, D. J., and G. A. Slafer. 1995. Yield, biomass and yield components in dwarf, semidwarf and tall isogenic lines of spring wheat under recommended and late sowing dates. Plant Breeding 114:392–396.

Miralles, D. J., and G. A. Slafer. 2007. Sink limitations to yield in wheat: how could it be reduced? J. Agric. Sci. 145:139–149.

Miralles, D. J., S. D. Katz, A. Colloca, and G. A. Slafer. 1998. Floret development in near isogenic wheat lines differing in plant height. Field Crops Res. 59:21–30.

Miralles, D. J., R. A. Richards, and G. A. Slafer. 2000. Duration of stem elongation period influences the number of fertile florets in wheat and barley. Aust. J. Plant Physiol. 27:931–940.

Mujeeb-Kazi, A., A. Gul, M. Farooq, S. Rizwan, I. Ahmad. 2008. Rebirth of synthetic hexaploids with global implications for wheat improvement. Aust. J. Agric. Res. 59:391–398.

Murchie, E. H., M. Pinto, and P. Horton. 2009. Agriculture and the new challenges for photosynthesis research. New Phytol. 181:532–552.

Murray, G. M., and J. P. Brennan. 2009. P. 69 *in* The current and potential costs from diseases of wheat in Australia. Grains Research and Development Corporation, Canberra Australia.

Ogbonaya, F. C., M. van Ginkel, and R. Brettell. 2008. Synthetics for wheat improvement – Proceedings of the 1st Synthetic Wheat Symposium, September 2006. Aust. J. Agric. Res. 59:389–390.

Olesen, J. E., M. Trnka, K. C. Kersebaum, A. O. Skjelvag, B. Seguin, P. Peltonen-Sainio, et al. 2011. Impacts and adaptation of European crop production systems to climate change. Eur. J. Agron. 34:96–112.

Oury, F.-X., C. Godin, A. Mailliard, A. Chassin, O. Gardet, A. Giraud, et al. 2012. A study of genetic progress due to selection reveals a negative effect of climate change on bread wheat yield in France. Eur. J. Agron. 40:28–38.

Park, R. F., J. J. Burdon, D. I. Guest, and M. J. Ayliffe. 2009. Dynamics of crop-pathogen interactions: from gene to continental scale. Pp. 423–447 *in* V. O. Sadras and D. F. Calderini, eds. Applied crop physiology: at the boundaries with genetic improvement and agronomy. Elsevier, London, U.K.

Park, R. F., T. Fetch, D. Hodson, Y. Jin, K. Nazari, M. Prashar, et al. 2011. International surveillance of wheat rust pathogens - progress and challenges. Euphytica 179:109–117. doi:10.1007/s10681-011-0375-4.

Parry, M. A. J. 2012. Food and energy security: exploring the challenges of attaining secure and sustainable supplies of food and energy. Food Energy Secur. 1:1–2. doi.org/10.1002/fes3.1.

Parry, M. A. J., and M. J. Hawkesford. 2010a. Food security: increasing yield and improving resource use efficiency. Proc. Nutr. Soc. 69:1–9.

Parry, M. A. J., and M. J. Hawkesford. 2010b. Genetic approaches to reduce greenhouse gas emissions: increasing carbon capture and decreasing environmental impact. Pp. 139–150 *in* M. P. Reynolds, ed. Climate change and crop production. CABI International, Wallingford, U.K.

Parry, M. A. J., and M. J. Hawkesford. 2012. An integrated approach to crop genetic improvement. J. Integr. Plant Biol. 54:250–259.

Parry, M. A. J., A. J. Keys, and S. Gutteridge. 1989. Variation in the specificity factor of C-3 higher-plant Rubisco determined by the total consumption of ribulose-P2. J. Exp. Bot. 40:317–320.

Parry, M. A. J., P. J. Madgwick, C. Bayon, K. Tearall, A. Hernandez-Lopez, M. Baudo, et al. 2009. Mutation discovery for crop improvement. J. Exp. Bot. 60:2817–2825.

Parry, M. A. J., M. Reynolds, M. E. Salvucci, C. Raines, P. J. Andralojc, X.-G. Zhu, et al. 2011. Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. J. Exp. Bot. 62:453–467.

Parry, M. A. J., P. J. Andralojc, J. C. Scales, M. E. Salvucci, H. Alonso, and S. M. Whitney. 2013. Rubisco activity and regulation as targets for crop improvement. J. Exp. Bot. 64:717–730.

Peltonen-Sainio, P., L. Jauhiainen, and I. P. Laurila. 2009. Cereal yield trends in northern European conditions: changes in yield potential and its realisation. Field Crops Res. 110:85–90.

Peng, S., J. Huang, J. E. Sheehy, R. C. Laza, R. M. Visperas, X. Zhong, et al. 2004. Rice yields decline with higher night temperature from global warming. Proc. Natl. Acad. Sci. USA 101:9971–9975.

Piao, S., P. Ciais, Y. Huang, Z. Shen, S. Peng, J. Li, et al. 2010. The impacts of climate change on water resources and agriculture in China. Nature 467:43–51.

Price, G. D., J. L. L. Pengelly, B. Forster, J. Du, S. M. Whitney, S. von Caemmerer, et al. 2013. The cyanobacterial CCM as a source of genes for improving photosynthetic CO_2 fixation in crop species. J. Exp. Bot. 64:753–768.

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

Reynolds, M., D. Bonnett, S. Chapman, R. Furbank, Y. Manes, D. Mather, et al. 2011. Raising yield potential of wheat: (I) Overview of a consortium approach and breeding strategies. J. Exp. Bot. 62:439–452.

Reynolds, M., J. Foulkes, R. Furbank, S. Griffiths, J. King, E. Murchie, et al. 2012. Achieving yield gains in wheat. Plant Cell Environ. 35:1799–1823.

Richards, R. A. 1992. The effects of dwarfing genes in spring wheat in dry environments I. Agronomic characteristics. Aust. J. Agric. Res. 43:517–527.

Sadras, V. O. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. Field Crops Res. 100:125–138.

Sadras, V. O., and C. Lawson. 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 Pasture Sci. 62:533–549.

Sadras, V. O., and G. A. Slafer. 2012. Environmental modulation of yield components in cereals: heritabilities

reveal a hierarchy of phenotypic plasticities. Field Crops Res. 127:215–224.

Savin, R., and G. A. Slafer. 1991. Shading effects on the yield of an Argentinean wheat 655 cultivar. J. Agric. Sci. 116:1–7.

Scherm, H., and S. M. Coakley. 2003. Plant pathogens in a changing world. Australas. Plant Pathol. 32:157–165.

Shaw, M. W., S. J. Bearchell, B. D. L. Fitt, and B. A. Fraaije. 2007. Long-term relationships between environment and abundance in wheat of *Phaeosphaeria nodorum* and *Mycosphaerella graminicola*. New Phytol. 177:229–238.

Shewry, P. R. 2009. Wheat. J. Exp. Bot. 60:1537–1553.

Sinclair, T. R., and P. D. Jamieson. 2006. Grain number, wheat yield, and bottling beer: an analysis. Field Crops Res. 98:60–67.

Slafer, G. A., and F. H. Andrade. 1989. Genetic improvement in bread wheat (*Triticum aestivum*, L.) yield in Argentina. Field Crops Res. 21:289–296.

Slafer, G. A., E. H. Satorre, and F. H. Andrade. 1994. Increases in grain yield in bread wheat from breeding and associated physiological changes. Pp. 1–68 *in* G. A. Slafer, ed. Genetic improvement of field crops. Marcel Dekker, New York.

Slafer, G. A., D. F. Calderini, D. J. Miralles. 1996. Yield components and compensation in wheat: opportunities for further increasing yield potential. Pp. 101–133 *in* M. P. Reynolds, S. Rajaram and A. McNab, eds. Increasing yield potential in wheat: breaking the barriers. CIMMYT, Mexico, DF.

Strange, R. N., and P. R. Scott. 2005. Plant disease: a threat to global food security. Annu. Rev. Phytopathol. 43:83–116.

Stubbs, R. W. 1985. Stripe rust. Pp. 61–101 *in* A. P. Roelfs and W. R. Bushnell, eds. The cereal rusts. Vol. II. Academic Press, Orlando, FL.

Tao, F. L., M. Yokozawa, J. Y. Liu, and Z. Zhang. 2008. Climate-crop yield relationships at provincial scales in China and the impacts of recent climate trends. Clim. Res. 38:83–94.

Thorup-Kristensen, K., M. S. Cortasa, and R. Loges. 2009. Winter wheat roots grow twice as deep as spring wheat roots, is this important for N uptake and N leaching losses? Plant Soil 322:101–114.

Tronsmo, K. M., E. M. Faergestad, J. D. Schofield, and E. M. Magnus. 2003. Wheat protein quality in relation to baking performance evaluated by the Chorleywood bread process and a hearth bread baking test. J. Cereal Sci. 38:205–215.

Waddington, S. R., J. K. Ransom, M. Osmanzai, and D. A. Saunders. 1986. Improvement in the yield potential of bread wheat adapted to northwest Mexico. Crop Sci. 26:698–703.

Wan, A. M., X. M. Chen, and Z. H. He. 2007. Wheat stripe rust in China. Aust. J. Agric. Res. 58:605–619.

Wan, Y., P. R. Shewry, and M. J. Hawkesford. 2013. A novel family of γ-gliadin genes are highly regulated by nitrogen supply in developing wheat grain. J. Exp. Bot. 64:161–168.

Wellings, C. R. 2007. *Puccinia striiformis* in Australia: a review of the incursion, evolution, and adaptation of stripe rust in the period 1979–2006. Aust. J. Agric. Res. 58: 567–575.

Wiersma, J. J., R. H. Busch, G. G. Fulcher, and G. A. Hareland. 2001. Recurrent selection for kernel weight in spring wheat. Crop Sci. 41:999–1005.

Wojciechowski, T., M. J. Gooding, L. Ramsay, and P. J. Gregory. 2009. The effects of dwarfing genes on seedling root growth of wheat. J. Exp. Bot. 60:2565–2573.

Xiao, Y. G., Z. G. Qian, K. Wu, J. J. Liu, X. C. Xia, W. Q. Ji, et al. 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.

Yang, C. L., J. H. Hou, Z. J. Song, X. L. Li, and C. Y. Li. 2009. Pedigree analysis of main wheat varieties and utilization of core germplasms in Henan province. Shandong Agric. Sci. 1:27–31.

You, L., M. W. Rosegrant, S. Wood, and D. Sun. 2009. Impact of growing season temperature on wheat productivity in China. Agric. For. Meteorol. 149:1009–1014.

Zarzycki, J., S. D. Axen, J. N. Kinney, and C. A. Kerfeld. 2012. Cyanobacterial-based approaches to improving photosynthesis in plants. J. Exp. Bot. doi:10.1093/jxb/ers294.

Zhang, H., and B. G. Forde. 1998. An *Arabidopsis* MADS box gene that controls nutrient-induced changes in root architecture. Science 279:407–409.

Zhang, J., M. Luo, and T. Shen. 2012. Pp. 6–7 *in* Identification and screening of resources resistant to Fusarium Head Blight (FHB) in winter wheat region of Northern China. Proceedings of the 4th International Symposium on Fusarium Head Blight, Nanjing, China, organized by Nanjing Agricultural University, Jiangsu Academy of Agricultural Sciences, Journal of Genetics and Genomics, and Jiangsu Society of Genetics.

Zheng, T. C., X. K. Zhang, G. H. Yin, L. N. Wang, Y. L. Han, L. Chen, et al. 2011. Genetic gains in grain yield, net photosynthesis and stomatal conductance achieved in Henan Province of China between 1981 and 2008. Field Crops Res. 122:225–233.

Zhou, Y., Z. H. He, X. X. Sui, X. C. Xia, X. K. Zhang, and G. S. Zhang. 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, Y., H. Chen, J. Fan, Y. Wang, Y. Li, J. Chen, et al. 2000. Genetic diversity and disease control in rice. Nature 406:718–722.

Zhu, X.-G., S. P. Long, and D. R. Ort. 2010. Improving photosynthetic efficiency for greater yield. Annu. Rev. Plant Biol. 61:235–261.