Wheat physiology: a review of recent developments

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Abstract. This review focuses on recent advances in some key areas of wheat physiology, namely phasic development, determination of potential yield and water-limited potential yield, tolerance to some other abiotic stresses (aluminium, salt, heat shock), and simulation modelling. Applications of the new knowledge to breeding and crop agronomy are emphasized. The linking of relatively simple traits like time to flowering, and aluminium and salt tolerance, in each case to a small number of genes, is being greatly facilitated by the development of molecular gene markers, and there is some progress on the functional basis of these links, and likely application in breeding. However with more complex crop features like potential yield, progress at the gene level is negligible, and even that at the level of the physiology of seemingly important component traits (e.g., grain number, grain weight, soil water extraction, sensitivity to water shortage at meiosis) is patchy and generally slow although a few more heritable traits (e.g. carbon isotope discrimination, coleoptile length) are seeing application. This is despite the advent of smart tools for molecular analysis and for phenotyping, and the move to study genetic variation in soundly-constituted populations. Exploring the functional genomics of traits has a poor record of application; while trait validation in breeding appears underinvested. Simulation modeling is helping to unravel G × E interaction for yield, and is beginning to explore genetic variation in traits in this context, but adequate validation is often lacking. Simulation modelling to project agronomic options over time is, however, more successful, and has become an essential tool, probably because less uncertainty surrounds the influence of variable water and climate on the performance of a given cultivar. It is the ever-increasing complexity we are seeing with genetic variation which remains the greatest challenge for modelling, molecular biology, and indeed physiology, as they all seek to progress yield at a rate greater than empirical breeding is achieving.

Introduction

A review honouring Australia’s first wheat breeder, William Farrer, in a journal titled Crop and Pasture Science cannot avoid considering wheat physiology’s delivery of useful impact at the crop level, even though plant physiology today spans from the molecular level of functional genomics, through individual organ and plant studies, to that of the crop. Increasingly physiologists appear to expect applications from their research, but the path leading to impact on crop productivity is often more difficult than anticipated. Attention to such impact will be a secondary theme of this review.

‘Recent’ is defined here as the last 10 years or so, but a brief excursion into the history of wheat physiology, is warranted. Much of it is to be found in the predecessor to this Journal, namely the Australian Journal of Agricultural Research (1950–2008), and some bias towards the role of Australian research is admitted. Farrer was in fact one of the first to think and write about adaptive traits in wheat (e.g. Farrer 1898). Interest in numerical components of wheat yield blossomed in the 1920s and 1930s in the UK, with work by F. L. Engledow and S. M. Wadham, moving on, in the 1950s, to crop growth analysis under the guidance of D. J. Watson and G. N. Thorne, and in the following decade, to source-sink yield analysis by breeder J. Bingham. In Australia, H. C. Trumble and A. E. V. Richardson did important early work on wheat transpiration, before C. M. Donald put crop physiology definitively on the map (e.g. Donald 1962), pointing out that plant behaviour in the highly competitive crop community is usually quite different to that of plants in isolation. In 1963 the Canberra Phytotron opened, and for the next 30 years the environmental control of

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wheat growth and development was extensively researched therein, especially by L. T. Evans and I. F. Wardlaw. At Wagga Wagga, in New South Wales, A. T. Pugsley was sorting out the major genes behind phasic development, W. V. Single was grappling with wheat, nitrogen (N) and frost, and R. A. Fischer with haying-off; and in 1969 H. A. Nix published the first physiologically based simulation model of grain yield in the wheat crop. From about then onwards, wheat being Australia’s major crop, the funding for wheat physiology research grew notably, as did the published results. At the same time, research on wheat physiology languished somewhat in Europe, only to be picked up elsewhere in the new world, initially Canada and the USA, then Mexico and Argentina, followed lately by a revival of interest in Europe. Much of these developments are captured in the reviews by Evans et al. (1975), Slafer et al. (1999), Passioura (2002), Fischer (2007) and Reynolds et al. (2009).

In reviewing recent research, it is impossible to ignore the boom in molecular biology and functional genomics research. Much adopts a bottom-up or reverse genetics approach, working from the gene level upwards towards function, typically starting with change in gene expression. It is not surprising that it is proving very difficult to reach an understanding of function at higher levels of organisation, especially that of plant phenotypes and crop performance in the field, through this route. However, the alternative, top-down forward genetics approach, starting with observable genetic variation at higher levels of organisation, is bringing some progress at the level of genetic control. Thus, some attention will be given to the latter approach, where relevant, in this review of the physiology of the wheat plant and crop. This will follow under the headings of phenology, potential yield (PY), water-limited PY, effects of some other abiotic stresses (aluminium, salinity, heat shock), advances in simulation modelling, and concluding remarks. Attention will focus on common or hexaploid wheat (*Triticum aestivum* L.) unless otherwise stated.

**Wheat phenology**

**Days to anthesis**

Genetic variation in flowering (anthesis) date and crop duration are primary considerations in adaptation (Evans 1993); these are part of the crop’s physiology or phasic development which describes the occurrence of key growth and development events. Date of anthesis (AN) is the first appearance of dehisced anthers (if a crop, in 50% of spike-producing culms); time to AN is more accurately described as degree-days above a temperature base, usually of 0°C. Duration is under strong genetic control from a few alleles of a relatively limited number of genes affecting sensitivity to photoperiod (*Ppd*), to vernalising cold (*Vrn*), and to earliness *per se* (*Eps*). For these reasons, it has been the favourite subject of geneticists and physiologists for almost 100 years. The classic work on wheat genes by Pugsley (1968, 1972), and on cultivar responsiveness and environmental control by his colleague, Syme (1968), set the scene for a flood of physiological genetic research on the subject (see reviews by Slafer and Rawson 1994 and Slafer et al. 2009). Thus, it is not surprising that molecular biology has had an impact in this area of wheat physiology. Initially isolines and chromosome substitution lines developed laboriously by geneticists and cytogeneticists provided the material for quantification of genetic effects (e.g. Pugsley 1972; Worland 1996; Stelmakh 1998). However, in the last 20 years or so, quantitative trait loci (QTL) analyses has contributed to gene localisation, and in the last decade, perfect molecular markers for several key photoperiod and vernalisation alleles have greatly assisted isolate development and/or characterisation of cultivars. At the same time, the actual biochemistry of gene action in wheat has yielded somewhat to the powerful tools of functional genomics (e.g. Dwivedi et al. 2008; Trevaskis 2010).

González et al. (2005a) usefully summarised early work with *Ppd*-1 and *Ppd*-D1 iso- and chromosome substitution lines: the sensitive alleles delayed anthesis/heading in long days at high latitudes around 2.5 days (*Ppd*-B1) or 5 days (*Ppd*-D1), but in short days at low latitudes, as much as 13 days (*Ppd*-B1)2 Worland (1996) had previously shown that the *Ppd*-D1-sensitive allele delayed heading too much for the adaptation of winter wheats in southern Europe, but that the smaller delays in the UK were inconsequential for performance. Immediately preceding the arrival of accurate molecular markers, Dyck et al. (2004) revealed in spring wheat isolines sown across latitudes 40–58°N in North America that the *Ppd*-D1-sensitive allele, to be found in most spring-planted spring wheats at high latitude, delayed heading on average 3 days. van Beem et al. (2005) determined by test crossing to known sources the sensitive/insensitive alleles at the four *Vrn* loci across 51 cultivars largely from CIMMYT, but did not quantify effects. However, they did measure genetic differences in *Eps* and responsiveness to temperature, using fully vernalised seed, grown under 24-h photoperiod: at 16/6 or 23/12°C, days to anthesis ranged from 59 to 74, and 45 to 63 days, respectively. Recently the first gene for *Eps* appears to have been located on chromosome A1 in *Triticum monococcum* L. (*Eps*-A1), with evidence that a similar gene may be present in hexaploid wheat (Lewis et al. 2008). In one of the earliest studies on *Vrn* alleles with molecular markers (and chromosome substitution lines), Iqbal et al. (2007a, 2007b) quantified the delaying effect on AN of the vernalisation-sensitive alleles at each of the three homeologous loci (*Vrn*-A1, *Vrn*-B1, *Vrn*-D1) across Canadian spring cultivars grown at 54°N. Effects were additive, but also interactive, with the allele at *Vrn*-A1 the strongest; having all sensitive alleles give a winter wheat which was usually far too late, while the genotype with all insensitive alleles was too early and only suited to the most northern short season locations.

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1This review assumes a specific gene occupies a given position or locus on one of the wheat homeologous chromosomes and codes for a protein; different alleles of the gene produce slightly different proteins or different amounts of a given protein leading to measurable phenotypic changes. Specific known genes are named, abbreviated, and italicised according to standard nomenclature, beginning with capitals, but dominance or recessiveness are not symbolised in any way.

2Since earliness seems to be a more stable state, as seen with photoperiod and vernalisation-insensitive cultivars in warm natural environments, responses to development alleles seem more sensibly expressed relative to the early phenotype, thus as delays in development; an approach adopted here.
Table 1. Alleles of the photoperiod sensitivity gene (Ppd-D1) and the vernalisation genes (Vrn-A1, Vrn-B1, Vrn-D1) in key Australian cultivars (Eagles et al. 2010), as they relate to adaptation to Australia in general, and to Western Australia in particular (Anderson et al. 1996), and to the Triple Dirk isolines (Pugsley 1968, 1972)

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>Genes and alleles</th>
<th>Classification</th>
<th>Sowing date</th>
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<tr>
<td></td>
<td>Ppd-D1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Vrn-A1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Vrn-B1&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>Purple Straw (19th C)</td>
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<td>Federation (1901)</td>
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<td>WW15 (1969)</td>
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<td>Osprey</td>
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<td>Halberd, Spear</td>
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<td>Eradu, Aroona</td>
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<td>Kulin, Gutha</td>
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<td>Triple Dirk</td>
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<td>Triple Dirk B</td>
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<td>Triple Dirk E</td>
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<td>Triple Dirk C</td>
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<sup>a</sup>v is dominant-insensitive allele, b recessive sensitive; Triple Dirk data from H. Eagles (pers. comm.).

<sup>b</sup>a and b are dominant-insensitive alleles, v is recessive sensitive.

Molecular markers permitted Eagles et al. (2009) to identify alleles at four key loci in around 120 Australian cultivars from the 19th Century up until 2007 and in 18 CIMMYT cultivars. This review will adopt their allele nomenclature for the photoperiod gene Ppd-D1 (insensitive allele a, or sensitive allele b), and the vernalisation genes Vrn-A1, Vrn-B1 and Vrn-D1 (all having dominant-insensitive allele a, or sensitive allele v; Vrn-A1 has a second dominant-insensitive allele, b). The classification often corresponded quite well to field performance, for example, of the maturity classes of varieties in Western Australia in the mid 1990s (Table 1). These classes govern the recommended optimal sowing date, such that varieties all reach flowering in a common optimum period in September (Anderson et al. 1996). Table 1 adds the Triple Dirk isolines, developed originally by Pugsley (1968, 1972) and widely used in research globally ever since. Not shown is his Triple Dirk F, which Yoshida et al. (2010) showed to have an insensitive allele at Vrn-D4 (at which gene all other isolines are vernalisation sensitive); these authors also confirmed that in the presence of the weaker insensitive a alleles (Vrn-B1, Vrn-D1, Vrn-D4) there remains a small residual vernalisation response.

More recently, Eagles et al. (2010) have related days to heading to the allelic composition (for Ppd-D1 and Vrn-A1, Vrn-B1 and Vrn-D1 only) of 1085 genotypes across 128 late April to early July sowings at many sites in south-eastern Australia (latitude 34–37°S). There were 8524 observations in this unbalanced dataset, from which allelic effects on days to heading were estimated for an early June sowing. Effects were estimated with considerable accuracy (s.e.d. <0.7 days).

In photoperiod-insensitive genotypes (Ppd-D1 a), a single vernalisation sensitive v allele delayed heading on average 2.3 days, but the Vrn-D1 allele was the most powerful (3.1 days) and the Vrn-B1 allele the least (1.6 days). Furthermore, effects were not exactly additive (i.e. epistasis) such that substituting a single insensitive a allele hastened heading most (4.1 days) when compared to the winter type (vvv), and hardly at all (0.4 days) when it gave rise to a totally spring genotype (aaa). The analysis also indicated the effects of v alleles were greater when the post-sowing environment was warmer (despite the fact that all vernalisation requirements would have been satisfied naturally within 48 days of sowing even at the warmest site-years), notably so when comparing the winter type with those with only one a allele (i.e. avv, var, vva). This explained the greater delay in flowering with winter wheats (vvv) the warmer the site. Finally the photoperiod-sensitive allele (Ppd-D1 b) was estimated to delay heading on average 7 days compared to the insensitive one (Ppd-D1 a), an effect which was greatest in fully vernalisation-insensitive genotypes (aaa, 11.8 days).

Eagles et al. (2010) has been highlighted because it shows the way forward: the value of more exactly identifying key alleles, and the power of modern statistics for deducing patterns from complex unbalanced data. But the identified alleles explained only 45% of the genetic variance in days to heading (main effect of genotypes), while there was also a genotype × sowing-site variance component equal to 20% of the main effect. Probably other major genes are involved (e.g. Ppd-B1, Vrn-D4), and even unknown major genes and alleles<sup>3</sup>, such as those controlling Eps. In addition the dataset covered a relatively narrow range of latitude and sowing dates. Taking a wider dataset of 24 winter wheat and five spring wheat cultivars grown across 12 years and 82 global locations ranging from latitude 19 to 61° in the International Winter Wheat Performance Nursery, White et al. (2008) had earlier considered the allelic classification at Ppd-D1.

<sup>3</sup>There can be significant sequence variation beyond the region of any allele targeted by a given molecular marker.
Vrn-A1, Vrn-B1, and Vrn-D1 in an effort to predict days to flowering in the set. Using the simulation model CERES version 4.0.2.0, cultivar parameters for photoperiod sensitivity (P1D) and vernalisation sensitivity (P1V) were fitted across 105 site-years, following which P1D parameter values were fitted to the known photoperiod alleles, and P1V to the vernalisation ones, to give relationships which could be used in CERES as an allele-based algorithm. Validation across 257 additional sowings (at separate sites), showed that using the original parameters explained only 27% of the genetic variation, compared to even less (17%) with the allele-based approach. In conclusion, using molecular markers to identify the major development alleles and thus to predict AN, has progressed rapidly recently, and obviously will be an exciting area for the near future. The challenge will be to improve predictive accuracy, for breeders usually target environments where only a few days difference in AN can be significant for performance, and yet they have handled the issue empirically with relative ease since William Farrer himself.

Beyond degree-days to anthesis

A new challenge would be to develop cultivars for which date of AN was the same (or at least always optimal) regardless of sowing date. Given the uncertainty surrounding sowing (germination) date in dryland cropping at intermediate latitudes with autumn and winter planting, this would mean farmers need not hold a suite date. Given the uncertainty surrounding sowing (germination) AN was the same (or at least always optimal) regardless of sowing. A new challenge would be to develop cultivars for which date of AN can be significant for performance, and yet they have handled the issue empirically with relative ease since William Farrer himself.

Potential yield

PY is defined as the yield achieved by an adapted cultivar in the absence of manageable biotic and abiotic stresses, in particular lack of water, and in the presence of a given representative natural resource base of climate and soil. In many situations around the...
Flowering date and crop duration

While phasic development provides the temporal framework within which the crop develops, climate and cropping system constraints, along with empirical selection, have generally optimised the dates of sowing, AN and maturity within which PY is realised. Relatively simple considerations of T\text{mean} and solar radiation seem to underpin the flowering date for maximum yield in wheat. At low latitudes (~30°), optimum flowering date is a compromise, following closely upon the early spring maximum in photothermal quotient [PTQ = solar radiation/(T\text{mean} – 4.5°)] for greatest grains/m² (GN), but tempered by the need to maximise weight per grain (GW), which is inversely related to post-flowering temperatures (e.g. Ortiz Monasterio et al. 1994). At intermediate latitudes (~30–40°), with autumn-sown spring wheats, where winters are cold enough to notably slow growth, these relationships still appear to hold (e.g. Stapper and Fischer 1990b). At even higher latitudes, where severe winter cold and winter wheats predominate, at least in humid northern Europe where grain filling is mild, for example in south-east UK, PY appears to be relatively insensitive to variation in date of AN around an optimum of early June (Foulkes et al. 2004). In the UK solar radiation peaks in June, T\text{mean} in July–August, but spring temperatures are too low for the above PTQ to apply; nevertheless, May is probably the month with the best growth per unit of development time. At the highest latitudes for wheat, where spring-sown spring wheats prevail (e.g. Canada), the situation is distinct: sowing as early as soil warming allows and flowering as late as permitted by autumn frost appears to be optimum, because maximising days from sowing to flowering is linked to higher yield in such environments (e.g. Iqbal et al. 2007b).

Extra total duration before flowering is important with high-latitude spring wheats because the time to build leaf area and grain sites is inevitably short. How important it is in the other three situations mentioned is a misunderstood issue. Fischer (1985) working with irrigated spring wheat in Mexico (latitude 27°N) suggested that a longer duration to AN, giving full light interception at earlier stages of development, may increase leaf and tiller production, and total dry matter at flowering, but does...
not increase spike dry weight (SDW). The latter is maximised as long as full light interception is reached before the onset of spike growth (penultimate leaf emergence, see above); with well managed crops, full light interception is easily achieved before this point in the crop’s development (unless extra early cultivars are used). Studies with well watered autumn-sown spring cultivars of differing times to flowering in southern Australia appear to confirm this (e.g. Stapper and Fischer 1990a; Gomez-Macpherson and Richards 1995): the extra early growth with longer cycle wheats is also associated with greater lodging risk and perhaps greater respiratory losses later on, although it does open up the possibility of early grazing without yield loss, and does bring larger root systems, but this may not carry a net benefit under humid conditions. In intermediate winter-cold environments, such as humid south-western Victoria, a more intermediate duration and sowing date combination may be optimum (Rivkin and O’Leary 2010). Finally, where winter growth is severely constrained by low temperatures such as most winter wheat environments, sowing date is more a question of being early enough to guarantee good winter survival; spring growth can still be excessive and N is managed to avoid this. Thus, it appears that, except with high-latitude spring wheats, increased sowing to AN duration and the resultant increased crop biomass at AN may not be critical for maximising yield, with sowing date therefore driven by other considerations.

Grain number

The consideration of grain yield as the product of grains/m^2 (GN) and final GW has become common. It has the advantage of two components separated somewhat temporally and easy to determine, although care needs to be taken regarding the fate of small grains in mechanical threshing. In many cases yield variation and yield progress is associated with GN changes which, more recently, have been linked to dry weight accumulation in spikes (g/m^2) at flowering. This framework, which actually traces back to Bingham (1969), was further developed by Fischer (1984), has been adopted in recent reviews (Fischer 2007; Miralles and Slafker 2007; Reynolds et al. 2009), and will be used here. This strong emphasis therein on dry matter accumulation and partitioning up to flowering was challenged recently by Sinclair and Jamieson (2006) who saw the crops’ acquisition of reduced N as equally or more fundamental to yield determination, than that of assimilate from photosynthesis driving GN. However, under potential conditions, where, by definition yield is relatively unresponsive to N, there is no evidence to support this notion, and even under conditions of N stress, GN at least is more directly related to SDW than to spike N (see rebuttal in Fischer 2008). Thus:

\[
\text{SDW}_a = D_s \times \text{CGR} \times F_s
\]

where SDW_a is the dry weight of spikes at anthesis (per unit area basis), D_s is the duration of spike growth, and CGR and F_s are, respectively, the rate of crop dry accumulation and the fraction of this dry matter growth partitioned to the spike averaged over the spike growth period (as defined above). Also:

\[
\text{GN} = \text{SDW}_a \times \text{Grains/SDW}_a
\]

where the ratio of grains : SDW_a, initially proposed as a cultivar-specific trait (Fischer 1984), is now termed the spike fertility index (SFI). It can be usefully disaggregated as well:

\[
\text{SFI} = \frac{\text{Competent florets} \times \text{SDW}_a \times \text{grain set} \times 100}{100}
\]

in which competent florets have plump anthers just before AN, and grain set, refers to those competent florets which progress through pollination, fertilisation and early grain survival to bear grains at maturity. Grain set is important, and can fall significantly below 100% under stress, and even sometimes under apparently favourable conditions, especially in older cultivars (e.g. Evans et al. 1972), but will not be discussed further in the context of PY. Figure 1a illustrates the partitioning of dry matter to the growing spike, the associated water-soluble carbohydrate (WSC) changes, and the formation of competent florets in the simple situation of a single main stem, while Fig. 1b shows partitioning in wheat crops, and Fig. 1c the relationship of competent florets to SDW_a across spikes taken from crops of a given variety.

From the above model, traits D_s and CGR capture the important environmental determinants of GN. Thus, major climatic influences are seen in the simple PTQ ratio during spike growth mentioned earlier, with D_s inversely proportional to T_mean, and CGR proportional to solar radiation and relatively-stable radiation-use efficiency (RUE, crops under PY conditions usually intercept all the incident solar radiation before the onset of the spike growth stage). However, this simplification ignores several generally weaker influences of climate on RUE, such as low vapour pressure deficit (vpd) and a high ratio of diffuse to total solar radiation improving RUE and thus CGR (see review by Stockle and Kermanian 2009), as well as possible independent effects of minimum temperature (T_min). In addition, the influence of photoperiod on D_s should be included, as seen in Serrago et al. (2008) and illustrated experimentally in Fig. 1d. The positive effect of lower T_min (but not approaching freezing levels) has received attention lately in rice, but may also operate in wheat (Lobell et al. 2005), possibly because of greater freezing losses on warmer nights, but data are lacking.

Despite the strong association between yield progress through breeding and GN, genetic effects on the above determinants of GN are less widely reported. Following Eqn 1, D_s did not vary in a tall versus short isogenic comparison (see references in Fischer 2007) nor in the comparison of modern Argentine wheats (Abbate et al. 1998), so apart from Serrago et al. (2008) above, cultivar effects on D_s have yet to be described. However, large Argentine cultivar differences in the duration of the phase (TS/SE to AN) in °C (at least 2-fold for a given photoperiod) were reported by Whitechurch et al. (2007), and these may reflect differences in D_s, which falls largely within TS/SE to AN. Also, Gonzalez et al. (2005a) showed a highly significant relationship between SDW at flowering and solar radiation intercepted over the TS to AN phase, when its duration was varied by photoperiod extension across photoperiod-sensitive alleles in the Mercia background.

For CGR during spike growth, most studies find no genetic differences (e.g. Sayre et al. 1997; Abbate et al. 1998). However, a positive effect of genetic progress (year of release) on RUE
between start of SE and AN, and on SDW, was seen in UK winter wheats released between 1972 and 1995 (Shearman et al. 2005). Indirect evidence for a similar relationship underlying spring wheat GN and yield comes from positive correlations of pre-anthesis stomatal conductance (g,) and light-saturated photosynthetic rate (Pmax) with GN progress in north-west Mexico (Fischer et al. 1998), and from similar pre-anthesis conductance/Pmax correlations with yield in a warmer Mexican environment (Reynolds et al. 2000). Short erect leaves tending to have a higher specific leaf area and specific leaf N, common in the latest winter and spring cultivars (Fischer et al. 1998; Shearman et al. 2005), could also be contributing to the CGR increase through higher RUE. These observations hinting at increased GN associated with photosynthesis and CGR immediately before flowering have support from similar results with modern versus older rice cultivars in Japan (see Fischer and Edmeades 2010).

Dwarfing genes clearly enhanced F, the partitioning of dry matter to growing spikes (e.g. Fischer 1984, 2007; Abbate et al. 1998; Sláfer et al. 1999). The explanation is that shorter stems, growing at the same time as spikes, compete less for limited assimilate, permitting spikes to acquire more, but the real control mechanisms are likely to be much more complex (Fischer and Stockman 1986; Bancal 2008). On the other hand, for a given genotype, Fischer (2007) demonstrated under controlled conditions that F, was quite stable across different total assimilation amounts, and even different potential spike sizes, as caused by early photoperiod effects on spikelet number. Abbate et al. (1998) found only small differences in F, (range 0.29–0.34) among modern semi-dwarf Argentine cultivars. Reynolds et al. (2001) reported that the GN advantage associated with LR19 from Agropyron was associated with a proportional increase in F,.

Significant genetic variation in SFI was first noted in modern Argentine cultivars (Abbate et al. 1998); values ranged from 61 to 106 grains/g, entirely explaining GN variation among five cultivars. Shearman et al. (2005) also reported genetic variation in SFI (range 73–129 grains/g) but no significant increase with year of release, nor association with GN. It is also evident that there can be some environmental effects on SFI. In particular, in controlled environments, heavy shading in the critical stage just before AN reduced the number of competent florets per unit spike weight at AN (Fischer and Stockman 1980). This probably also happens in the field, especially in lower order tillers, which are already disadvantaged in the canopy, as was clearly shown by Wall (1979). Several other issues can further complicate the study of SFI: in the field crop AN takes place over several days across the main culms and tillers, blurring precision with respect to stage of development. Second, a spike does not finish growing until several days after first anthesis (see Fig. 1a, b), by which time grains are beginning to grow; such grains need to be removed if spike weight is to be correctly determined4. Finally, it is tempting to use chaff weight at maturity to calculate SFI (e.g. Stapper and Fischer 1990a, who found fairly consistent cultivar differences on this basis), but chaff weight can be 20–50% greater than spike weight at AN, both in controlled environments and in the field (Wall 1979; Fischer and Stockman 1980; Stockman et al. 1983), for reasons that need to be better understood.

The close link between dry matter accumulation in the growing spike, floret survival (for many more florets are initiated than ever survive to competency, see Fig. 1a), and competent floret number, exists whether spike weight is varied by shading, dwarfing genes, photoperiod, and photoperiod x photoperiod-sensitive alleles (Fischer and Stockman 1980, 1986; González et al. 2003, 2005a, 2005b); even photoperiod shortening in the field is reported to increase duration and spike size (M. Vasquez, unpubl. data). Subsequently there has been a detailed exploration of this relationship by González et al. (2005c), Bancal (2008, 2009) and Ghiglione et al. (2008). There seems little doubt that distal florets, especially in basal and distal spikelets, are the most vulnerable, and that florets begin visibly to ‘die’ early in the spike growth period; death begins at ~10% final spike weight when SDW accumulation is approaching the maximum rate. It is around the time that WSC concentration in the spike normally peaks (Fischer and Stockman 1980; Bancal 2008; Ghiglione et al. 2008; also Fig. 1a). This appears to confirm the link between floret survival and carbohydrate supply. Subsequently, florets continue to ‘die’ up until close to AN, at differing rates and durations of floret failure which are poorly understood. Ghiglione et al. (2008) found large differences in the expression of many genes associated with the greater levels of floret death under long compared to short photoperiods, but was unable to conclude much about the causality of death. In a departure from shading and photoperiod treatments, Ugarte et al. (2010) applied differing red:far red light ratios to spaced wheat plants over the whole period from SE to AN; there were interesting but difficult-to-interpret effects on rate of floret development and spike growth.

In conclusion, much research recently has focused for obvious reasons on GN determination: exploring the relationship to SDW, seems to remain a sound approach. It agrees with the observation that the final GN always equates to only a small percentage of the initiated florets, and with the notion that a floret competent to bear a grain represents a significant relatively fixed dry matter investment in spike structure, something which can, however, vary between cultivars. Searching for underlying mechanisms and even molecular controls of floret survival (e.g. Ghiglione et al. 2008) has been unsuccessful and indeed seems futile if the dry matter cost at anthesis of competent florets remains fixed. It may be more rewarding to note that the spike growth period is only the latter part of the TS/SE to AN phase, and to manipulate assimilate supply, and other aspects of the environment (e.g. temperature, red/far red radiation, ethylene), over sub-periods within the period, as in Fischer and Stockman (1980) and Stockman et al. (1983). Examining the nature of spike sink strength (essentially ratio F, above) and the basis of genetic differences in this ratio, may

4The study of Abbate et al. (1998) sampled crops at 7–9 days after 50% anthesis (GS65), and removed developing grains. Spearman et al. (2005) sampled at GS61, which may be too soon for SDW in a crop. For individual culms at 16.4°C, grain weight as a % of non-grain spike weight increases 3.6% per day from the 2nd to 9th day after first anthesis (R. A. Fischer, unpubl. data).
also be more fruitful for achieving SDWₜ increase. On the other hand, any changes which increase GN via increased SFI should note the tendency for a trade-off between SFI and potential grain size (e.g. Fischer and HilleRisLambers 1978; Dreccer et al. 2009).

**Grain weight**

Final GW in wheat is traditionally considered as the product of the duration of linear grain growth and the rate of this growth. Following Bingham (1969), Fischer (1984) proposed it to be the result of an interplay between the potential GW (the sink), being the GW reached when the assimilate supply is not limiting grain growth, and the actual supply of assimilates per grain during grain filling (the source). For wheat crops under PY conditions, it is often reported that grain-filling source exceeds the sink capacity of grains; this was clearly the case with older cultivars, but still seems to be so with the most modern cultivars (see below). At the same time GW is under the strong influence of grain-filling Tₑ (a negative relationship with slope of 2–7°C for Tₑ between 15 and 28°C (Wardlaw and Wrugley 1994)), and of cultivar, although genetic yield progress has generally not raised GW. There is also a weak positive GW response to grain-filling solar radiation independent of temperature (Fischer 1984). The negative effect of temperature is related to a shortening of grain filling (in days, not in degree-days), which is not fully compensated for by an increase in grain growth rate. Cultivar differences in GW tend, however, to be largely related to differences in filling rate.

The above simple notions, including that of a cultivar-specific potential GW, have proved useful, but now need to accommodate the fact that recent research has shown GW to be affected by conditions before anthesis, in particular spike temperature in the period between booting to AN, and especially heading to AN: even though the duration of leaf area during grain filling was unaffected, higher temperature just before AN reduced carpellate size at AN, and then GW (Calderini et al. 1999, 2001; Ugarte et al. 2007). There was a positive relationship between GW and carpellate size, which seems to apply not only as a result of temperature variation immediately pre-anthesis (Calderini et al. 1999), but also with cultivar differences (Calderini and Reynolds 2000; Calderini et al. 2001), with variation in floret position along the spikelet rachilla, and with variation in their apparent assimilate supply in the period (e.g. pre-anthesis floret removal treatments in Calderini and Reynolds 2000). The GW versus carpellate weight relationships tended to be curvilinear downwards; temperature and floret thinning treatments a week after AN had no effect on GW in this work (Calderini and Reynolds 2000). Potential GW therefore appears to be determined by carpellate size and not solely by endosperm cell division occurring in the week or so after AN as was believed earlier. Work has continued, seeking to relate GW to early grain expansion and hence to the size of the pericarp, already present in the carpellate, and following the expression of expansin-coding genes in elongating pericarp cells, expression which correlated well with early grain expansion (Lizana et al. 2010).

While potential GW may be determined by events up to about a week either side of AN, realisation of this potential across all grains in the crop (the grain-filling sink) depends on an adequate supply of assimilates during the grain-filling period (the source), both from current assimilate and WCS stored at AN in the crop, principally in stems and sheathes. Arguments about the importance of source versus sink during grain filling in wheat are legion (Evans 1993; Sinclair and Jamieson 2006; Fischer 2008) and the outcome will obviously depend at least to some extent on the weather before relative to that after AN. While low radiation (as simulated by post-anthesis shading) and high temperature can reduce GW by tippering the source-sink balance towards source limitation, in most wheat studies GW is quite insensitive to artificial manipulation of source/sink, such that in the control crop, sink limitation appears to dominate during grain filling (Borras et al. 2004; Miralles and Slafer 2007). A component of this apparent insensitivity is seen in the increased Pₘₐₓ during grain filling when GN was artificially increased in four modern varieties (Reynolds et al. 2005).

The apparently low level of source limitation during grain filling in commercial cultivars under potential conditions is probably ultimately related to the market penalty for grains which are not plump, but the physiological mechanisms could be multiple. Thus, as breeders have lifted GN and PY, they may have (unwittingly) increased WSC levels at anthesis; these reserves can be translocated relatively efficiently to the grain and buffer GW against reduced current assimilate as argued by Borras et al. (2004). This appears to have happened in UK winter wheats lately: WSC content rose significantly with genetic yield progress, at a rate of ~20 mg for each extra grain, and the most modern varieties have ~4 t/ha WSC at around anthesis (Shearman et al. 2005). Considerable research is now underway on WSC reserves, which tend to peak at the onset of grain filling, when most measurements are focused. Spring wheat populations revealed a large range in WSC concentration at the onset of grain growth, a moderate to high narrow-sense heritability, complex genetic control across up to 10 QTL, and an association with larger GW, less grain shrivelling, but in some backgrounds, also earliness (Rebetzke et al. 2008; Dreccer et al. 2009). Borras et al. (2004) also suggest that the insensitivity of GW to source variation could be due to the early establishment in wheat of the potential or maximum GW, at a time when GN is also being determined, thereby facilitating adjustment of the grain-filling sink to the potential source. Another likely factor is that green area and photosynthetic activity are maintained longer into the grain-filling period in modern varieties [as is widely recognised in modern maize hybrids, Fischer and Edmeades (2010)]. Certainly RUE levels during grain filling have improved (e.g. Miralles and Slafer 1997), and some modern varieties appear to show better 'stay green' (Christopher et al. 2008). Finally it appears that grain-filling photosynthetic activity can actually be increased by a larger GN sink (see above). It would also seem very likely that any gain in post-anthesis assimilate production has required greater levels of leaf N late in the life of the canopy, something which might constrain the N harvest index (HI) (N in grain as a % of total N uptake by the crop).

Homeostasis of propagule size (e.g. GW in wheat) is a strong force in nature (Sadras and Denison 2009). This appears to have persisted through yield improvement by breeding: genetic variation in GW is common and an easy selection target, but it has not generally contributed to higher PY. In reviewing this
general phenomenon Egli (2006) points out, as did Borras et al. (2004) above, that temporal overlap in the determination of GN and potential GW aids compensation or trade-off between these components. The indication of a strong negative genotypic relationship between potential GW and SFI in Fischer and HilleRisLambers (1978), suggests one such compensatory mechanism. Another could arise when GN increase is associated with more grains per spikelet [i.e. more grains in rachilla positions 3 and 4 with lower potential GW (Miralles and Slafer 1995)]. But such relationships do not explain why there seems to be overcompensation, such that in most comparisons across wheat genotypes, as GW increases, GN falls faster, so that PY also falls. However, before concluding that future breeding progress will be a question of continuing to maintain GW rather than increase it, it is worth noting that recent PY progress in spring wheat at CIMMYT appears also to be associated with GW increase (Aisawi et al. 2010). Whether their large-grained parent Baviacora or Babax (Sayre et al. 1997) is an exception to the rule, or the beginning of a new rule, is unknown, but the GN-GW nexus appears also to have been weakened in the CIMMYT-derived Seri-Babax mapping population studied intensively in Queensland (Rattey et al. 2009).

**Harvest index and lodging resistance**

Following Donald and Hamblin (1976), crop physicists tended to relate wheat grain yield to total biomass and HI. This model suffers physiologically because many processes are integrated into these two components; nevertheless its simplicity and the moderate heritability of HI are advantages. Fischer (2007) recently pointed out that the highest values of HI in winter wheats (~0.50), and especially spring wheat (0.45), leave scope for some improvement, if an upper limit of 0.62 (Austin 1980) is accepted, and if we note that modern varieties of rice and maize are approaching an HI of 0.55 (Fischer and Edmeades 2010). But as the height of modern wheat varieties settles at an apparent optimum of ~70–100 cm (Flintham et al. 1997), there is already a tendency for recent PY progress in spring wheat at CIMMYT appears also to have been weakened in the CIMMYT-derived Seri-Babax mapping population studied intensively in Queensland (Rattey et al. 2009).

**Water-limited potential yield**

**A simple model**

The prevailing paradigm for understanding water-limited potential yield ($\text{PY}_w$) starts with the quantity of water available for the crop, namely the available water in the root zone at sowing plus rainfall on the crop. Assuming there is no incrop run-off or deep drainage, nor any available water in the soil at maturity, this quantity equals crop evapotranspiration (ET). By definition, water limitation implies that ET is no more than say two-thirds of potential ET for the crop. $\text{PY}_w$ is then usefully described by three components:

$$\text{PY}_w = (\text{ET} - E_s) \times \text{TE} \times \text{HI}$$

where $E_s$ is soil evaporation in the crop, so that $\text{ET} - E_s$ is transpiration (T), TE the transpiration efficiency, and HI. These relatively independent components are reasonably well understood (see review of Passioura and Angus 2010). The original proponents of Eqn 4 had shown that in southern Australia, $E_s$ was typically ~100 mm, with $\text{PY}_w$ rising in linear proportion to additional ET at a rate of 20 kg/ha.mm (French and Schultz 1984). Sadras and Angus (2006) suggest that the slope for modern varieties could now be approaching 22 kg/ha.mm.

The distribution of rainfall during the crop cycle can be more important than Eqn 4 suggests, especially in low water-holding capacity soils, such that if water stress is evident at AN, and there is no further rain, post-anthesis stress will be severe and HI very low. Approximately 30% of ET must occur after AN for the maximum HI, as determined by cultivar and other aspects of climate, can be reached. Use of the wheat simulation model APSIM (see later) has further improved consideration of the effect of rainfall distribution, and simulations with historical weather suggests that $\text{PY}_w$ is best represented by a boundary function of about the same slope as determined by French and Schultz (1984), but which cannot be reached in all years because of poor rainfall distribution or water losses through deep drainage, run-off, or very late rain events (Hochman et al. 2009b).

**Traits for improved $\text{PY}_w$**

The phasic development framework for dry conditions have been broadly determined empirically, initially for Australia by William Farrer himself, but there is need for greater flexibility than for PY because sowing date is governed more by rainfall occurrence, and nowadays, seasonal climate forecasts (see later) can drive tactical adjustments by the farmer. $\text{PY}_w$ is usually very sensitive to sowing date delays: improved pre-sowing agronomy and better seeding machinery have helped guarantee early seeding and germination. Physiology has also contributed with a natural herbicide-resistance trait permitting dry seeding, and hopefully will further assist with the search for long coleoptile wheats which can emerge from deep moisture-seeking seed placement (Richards 2006). An unstressed plant height of 70–100 cm is optimum for $\text{PY}_w$, and most wheat cultivars achieve this with one of the Norin-10 dwarfing genes (Rht-B1b, Rht-D1b), but these GA-insensitive semi-dwarf wheats have short coleoptiles and do not emerge well from deep seeding especially in warm soils. Alternative GA-sensitive dwarfing genes with longer coleoptiles are being sought and tested with success (Rebetzke et al. 2007). Finally, optimum flowering date for $\text{PY}_w$ may be earlier than that for PY because of climate considerations, even though it brings an increased risk of spike frost in mid-latitude spring wheat environments like Australia or Argentina. Researchers are
again targeting resistance to spike frosting, but progress has been very slow in wheat although somewhat promising in barley (ACPFG 2010a); quantification of the likely benefit through simulation modelling would be helpful.

Significant soil evaporation ($E_s$) occurs whenever solar radiation reaches wet soil (once the soil surface dries $E_s$ drops markedly and is less radiation-dependent); $E_s$ is thus an important wasteful component in rain-fed cropping systems (ranging from 30 to 70% of ET), obviously being smaller where cover, whether by the crop or by surface residue, is less. For a given cover, the $E_s$ saving relative to no cover is greater when rains are frequent, potential evaporation is low and soil texture is heavy (Gregory et al. 2000). A rapid approach to substantial cover by the crop itself can therefore reduce $E_s$ losses in winter-rainfall environments. As well it needs to be noted that partial cover and a dry soil surface can cause significant energy transfer from the soil to the canopy and its atmosphere (e.g. Gregory et al. 2000), further favouring higher green cover and pointing to the importance of micrometeorology to our full understanding.

Equation 4 assumes the crop uses all available soil water. Sometimes, however, available water is found at maturity deep in the root zone, even when the crop has been severely stressed. Such water could have been used during grain filling very efficiently since it is not subject to evaporative losses and all assimilation then goes to the grain: thus Kirkegaard et al. (2007) measured grain efficiencies of up to 60 kg/ha.mm when crops were subirrigated at depth during grain filling. Unused deep water points to insufficient deep roots arising from physical or chemical restrictions in the subsoil. To the extent that the water is replenished between crops or in wet years, [which is not always the case (Lilley and Kirkegaard 2007)], it is a wasted resource. Genetic tolerance of roots to high boron is believed to benefit subsoil water extraction where subsoil boron is high (Millar et al. 2007); molecular characterisation is being pursued (ACPFG 2010b). Variation in root depth and water extraction between genotypes has been shown by Manschadi et al. (2006) and Lopes and Reynolds (2010); it is also evident that longer cycle wheat tend to have deeper roots (Fig. 2a). Interest in this previously neglected area of wheat physiology is now high (e.g. Pahta and Watt 2009).

Strictly speaking TE refers to the ratio of photosynthesis to transpiration, but in Eqn 4 it refers to net dry matter accumulation (above ground) relative to crop transpiration. It is strongly controlled by an inverse relationship to daytime vpd, and is notably greater for crops with the C4 photosynthetic pathway than C3 crops like wheat. Nevertheless, Farquhar and Richards (1984) found TE in wheat to show useful cultivar variation, which in accord with theory, was related inversely to $^{13}$C isotope discrimination ($\Delta$). This knowledge fired research in the area, and some 20 years later cultivars began to be released with the high TE trait (Richards 2006). It was learnt that in wheat, high TE is mostly associated with lower $g_s$ and $P_{\text{max}}$. This trade-off meant high TE was only superior in environments where growth tended to rely more on soil stored moisture and $E_s$ was low [conversely $\Delta$ is positively related to PY (e.g. Fischer et al. 1998)]. Several issues remain: little research has compared high TE/low $g_s$ genotypes with low TE/high $g_s$ cultivars on a scale sufficiently large to be fully relevant to farmer fields. One such attempt (Condon et al. 2002), based on 10-ha fields of each type, was frustrated by the poorer growth of the former, but did suggest that $T$ (and hence TE) differences driven by $g_s$ differences, were relatively less than seen in leaf gas exchange studies because...
of the uncoupling of the crops from the atmosphere (i.e. the presence of a significant atmospheric resistance to energy and gas interchange within and immediately above the crop canopy), again pointing to the importance of micrometeorology. Another issue is suggested here: in most latitudes crop growth before flowering is often occurring at suboptimal temperatures for leaf expansion, if not for photosynthesis [although frost can have lasting effects on the latter (Koh et al. 1978)]; there must be implications for TE but little research now focuses on this, or on the underlying genetic variability.

The final component in Eqn 4, HI, is especially sensitive to water stress just before flowering and again during grain filling. The former is related to the sensitivity of pollen viability at the young microspore stage, which actually occurs at around flag leaf emergence in any culm, ~10 days before AN. Some of the effect of this stress may operate via reduced photosynthesis, as sheflects in reduced final SDW, but there is little doubt that many cultivars show an additional depression in GN per spike due to male sterility (Fischer 1973), effectively reducing SFI; Fig. 2b illustrates this for a drought-affected wheat crop. The physiology of the sterility has been related to changes in histology, hormones, and gene expression (Koonjul et al. 2005; Ji et al. 2010). Importantly the latter paper found repeatable genotypic differences (as did Fischer (1980)), and related susceptibility to an inability to maintain carbohydrate supply to the anthers, as reflected inter alia in changes in their fructan-transferase gene expression.

The second aspect of HI currently under intense scrutiny is the role of WSC storage at AN as a useful trait in grain-filling terminal drought. As already mentioned under PY, the WSC content shows genetic variation, and van Herwaarden and Richards (2002) were able to relate the grain yield of cultivars under dry conditions to the WSC levels at AN. However, definitive confirmation of the benefit of this trait under terminal drought from the recombinant inbred populations (RIL) of Rebetzke et al. (2008) and Dreccer et al. (2009) has yet to surface. Lopes and Reynolds (2010) recently suggested that WSC at AN might be competitive with deep roots (it must also be competitive with spike growth); also it is apparent that the amounts of WSC may be quite small if there is water shortage before flowering (Dreccer et al. 2009).

Interestingly, van Herwaarden et al. (1998a) were able to advance understanding of the grain shrivelling or ‘haying-off’ phenomenon in high N crops under terminal drought, by showing that WSC reserves were actually reduced in such crops.

Many other traits have been proposed as important for understanding and advancing PYw in wheat (e.g. Tambussi et al. 2007; Reynolds and Tuberosa 2008). Many of these and the above-mentioned traits are also discussed in detail in Richards et al. (2010), who go on to consider the vital issue of proper strategies for their validation and subsequent utilisation in breeding, an issue often neglected in the past.

What does PYw variation in the real world tell us?

Many years ago, physiologists started looking at grain yield variation and trait associations among cultivars, then there were comparisons of isolines with and without given traits, and lately RIL and bulk segregant analyses have come to dominate. With each step the linking of yield variation, through traits to genes, has been advanced, but at the same time, greater complexity has been revealed. Recent studies with an elite × elite CIMMYT population (Seri-Babax) of more than 160 RILs are illustrative (Olivares-Villegas et al. 2007; Rattey et al. 2009). Averaged over 3 years at a single location in north-west Mexico under controlled terminal drought (RIL mean yield range 100–450 g/m²), the former reference showed yield to be weakly correlated with days to AN (phenotypic r = −0.26), strongly with height (r = 0.67) and canopy temperature (r = −0.72 to −0.78 for the average of measurements on 5–7 days), and very strongly with GN (r = 0.97); it was postulated that differences in soil water extraction explained these associations, and later work with extremes from the population confirmed this (Lopes and Reynolds 2010). This could be considered a reasonably satisfactory result. When Rattey et al. (2009) tested the material in south-east Queensland over three locations and 5 years (only six environments, with yield range 202–660 g/m²), the mean yield of the RILs ranged from ~350 to 500 g/m², and were correlated with days to AN (genotypic r = −0.50), GN (0.52), HI (0.47), and biomass (0.36) and weakly with GW (0.22) and WSC at anthesis (0.25). Canopy temperature relationships with yield were weaker than those in Mexico (A. Rattey, pers. comm.). McIntyre et al. (2010) went on to map yield and traits in the Queensland study, identifying many significant QTL, but none of better than weak explanatory value. The weaker relationships seen in Queensland are likely to be more realistic of a breeding program target, reflecting natural drought and soil variation, and suggest no simple path to improved PYw. On the positive side, it does seem the population produced some RILs combining high GN and GW, and yielding significantly more than the parents and the best local checks.

Other abiotic stresses

Wheat is subject to many other abiotic stresses (salinity, aluminium and boron toxicity, water logging, high temperature, low temperature and frost, ozone, pre-harvest rain, etc.), all of which reduce yield (and/or quality) to a significant extent in different parts of the world. The physiology of response to and tolerance of most of these appears to be simpler than that for water stress, even if some may be linked to water stress (e.g. salinity), and genetic differences are easier to demonstrate. It is therefore to be expected that physiology has progressed further in understanding and exploiting these differences, especially as agronomic solutions tend to be unavailable, or expensive (e.g. drainage, liming). Space permits brief attention to only three examples, the first two of which reveal excellent progress and good chances of impact, a welcome contrast with the frustrations of advancing PYw.

Aluminium tolerance

Selection of wheat progeny tolerant of high levels of the soluble trivalent aluminium cation in the rhizosphere, a common problem of acid soils, has been practised for many years, often via solution culture screening. The role of malate secretion by root tips in this tolerance was recognised by Delhaize et al. (1993), malate precipitating the aluminium cation. Molecular markers for a major resistance gene were located (Riede and Anderson
and the gene itself was identified (TaALMT1) in tolerant wheat and sequenced by Sasaki et al. (2004), the first ever such plant gene. In an unusual reversal of the chronological order of things, the gene has been transformed into Arabidopsis where it is effective, and into barley, while its overexpression in a susceptible wheat cultivar leads to improved tolerance in an acid soil with a high % of exchangeable aluminium (Pereira et al. 2010). The effective allele appears to have a stronger promoter region leading to greater efflux of malate when activated by aluminium (Raman et al. 2008). A second gene, from the MATE family, has recently been found and sequenced in wheat: it is also aluminium activated but leads to citrate excretion (Ryan et al. 2009). Tolerance has been exploited in conventional breeding, while the transgenic approach offers further options.

Salinity

Salinity refers to high sodium chloride in the root zone and it imposes both an instant osmotic stress similar to water stress which reduces leaf growth, as well as a slowly developing stress due to toxic levels of Na⁺ in key leaf tissues which reduce photosynthesis and hastens senescence (Munns and Tester 2008). Bread wheat is moderately tolerant of salinity as a species, durum wheat less so, barley more so. Physiological studies of genotypic differences in tolerance in wheat point to the importance of differences in Na⁺ exclusion from leaves. Initially a single gene (Kna1) from bread wheat and known to exclude Na⁺ was located on 4DL (Dubcovsky et al. 1996). Lately extensive screening and QTL analysis of appropriate populations (tolerant × susceptible) have revealed two genes which exclude Na⁺ in durum wheat leaves, Nax1 and Nax2. Both genes derive from a wheat ancestor T. monococcum, but apparently an accession not involved in modern durum varieties. Nax1 is found on chromosome 2AL, removes Na⁺ from the root and leaf sheath xylem, and appears to be a member of the HKT (high affinity K⁺ transporter) family (Huang et al. 2006). Nax2 is found on 5AL and removes Na⁺ from the xylem in the roots; it appears to be homeologous to Kna1 of bread wheat (ancient chromosome translocations account for the different chromosome groups today) and is also a member of the HKT family (Byrt et al. 2007).

In accord with the above work on wheat, the amphiploid between the barley wild relative, highly salt-tolerant Hordeum marinum, and bread wheat, has intermediate salt tolerance, associated with leaf intersection of Na⁺ and intermediate leaf concentrations of glycinebetain and proline protectants (Islam et al. 2007). In another wheat-wide cross, some fertile wheat-like progeny from the somatic hybridisation with the salt-tolerant wheat wild relative Thinopyron ponticum Podp., appear to have salt tolerance when compared to the winter wheat parent, both in the laboratory and field, but the mechanism of tolerance may not be Na⁺ exclusion from the leaves (Chen et al. 2004).

The second major mechanism by which crops withstand salinity is tolerance to high leaf Na⁺, the apparent basis of cultivated barley’s tolerance. There is some evidence for genotypic variation in this trait in durum wheat but its importance is yet to be fully understood (Munns et al. 2006).

The development of transgenic salt-tolerant wheats, expressing a vacuolar Na⁺/H⁺ antiporter gene from Arabidopsis (AtNHX1), is noteworthy because it was taken through to successful field testing: the best lines appear to carry no yield penalty in the absence of salinity, yet outperform the original parent notably in its presence (Xue et al. 2004); both leaves and roots accumulate less Na⁺ and more K⁺ than the check in the presence of salinity.

In contrast to wheat performance with water limitation, the simpler trait, performance under salinity, has thus yielded somewhat to a combination of physiology and functional genomics. Much, however, remains to be done: Nax1 and Nax2 are currently being validated in modern durum cultivar backgrounds in saline fields (R. Munns, pers. comm.), while the wide cross and GM tolerances from China seem not to have had the apparent early progress confirmed. It is also ironic that salinity-tolerant bread wheat cultivars performing well in saline farmers’ fields in the north-west IndoGangetic Plains and in Egypt were developed empirically some time ago, but little is known of the underlying mechanisms of tolerance (Munns et al. 2006).

Heat shock tolerance

The negative effect of raised Tmean (chronic heat) on yield and yield components has already been mentioned. Here reference is made to the negative effect of shorter periods (1–4 consecutive days) of maximum temperature (Tmax>around 32°C) during the grain-filling period, noting that such heat shocks can be common at middle and low latitudes, and are expected to become more common. Heat shock can reduce GW, and also sometimes GN if it is soon after AN, and can cause serious damage to wheat quality. Asseng et al. (2011) showed that there are already on average 1–5 days with Tmax>34°C during grain filling at locations across the Australian wheat belt. Their modelling suggested a yield reduction of ~0.2 t/ha for each such day, because of an assumed dramatic acceleration of leaf senescence in proportion to the number of such shocks, something probably influenced by the level of soil water and warranting further experimental validation because, in contrast to this mechanism, it has earlier been proposed that heat shock specifically inhibited soluble starch synthase in the grain, and not assimilate supply (Jenner 1994).

Not surprisingly, there is growing interest in genotypic differences in heat shock tolerance but problems arise with screening for such shock tolerance. These include the possible effects of preceding temperatures (hardening) as in Spiertz et al. (2006), exposure of roots to excessive heat when testing plants in pots (van Herwaarden et al. 1998), and the influence of soil water supply and vpd. Heat shocks are usually accompanied by dry winds and high vpd, and the escape effect provided by plant cooling relative to the air temperature can be substantial provided soil water is readily available as seen in Table 2 showing the influence of soil water (and of Tmax) with a single heat shock. Canopy and spike cooling by 5°C or more is not uncommon with irrigated wheat (Amani et al. 1996; Fischer et al. 1998): the effect is dependent on transpiration and is proportional to vpd and gs.

Notwithstanding the uncertainties of heat shock screening, wheat cultivars appear to differ in the sensitivity of GW to this
### Table 2. Effect of heat shock on physiological indicators and grain weight in wheat (cv. Gabo) grown in pots under moderate temperature and adequate water, then exposed to heat shock conditions for a single 6-h period at normal solar radiation level; average of single heat shocks at 10, 16, 24 and 31 days after anthesis (developed from Fischer 1980)

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<tr>
<td>Air temp. (°C)</td>
<td>25</td>
<td>32</td>
<td>39</td>
</tr>
<tr>
<td>vpd (kPa)</td>
<td>Low</td>
<td>3.1</td>
<td>5.1</td>
</tr>
<tr>
<td>Ψ&lt;sub&gt;soil&lt;/sub&gt; (kPa)</td>
<td>&gt;-0.1</td>
<td>&gt;-0.1</td>
<td>&gt;-0.1</td>
</tr>
</tbody>
</table>

**At the end of the 6-h heat shock period**

<table>
<thead>
<tr>
<th></th>
<th>Leaf RWC&lt;sup&gt;a&lt;/sup&gt; (%)</th>
<th>Grain RWC&lt;sup&gt;a&lt;/sup&gt; (%)</th>
<th>Leaf temp. (°C)</th>
<th>Grain temp. (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>96.0</td>
<td>94.6</td>
<td>30.0</td>
<td>31.0</td>
</tr>
<tr>
<td>24 h later</td>
<td>91.5</td>
<td>93.0</td>
<td>32.2</td>
<td>34.6</td>
</tr>
<tr>
<td>Leaf damage (%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Grain weight (%)</td>
<td>100</td>
<td>97</td>
<td>95</td>
<td>87</td>
</tr>
<tr>
<td>At maturity</td>
<td>72</td>
<td>83</td>
<td>83</td>
<td>72</td>
</tr>
</tbody>
</table>

<sup>a</sup>Relative water content.

...abiotic stress (Stone and Nicolas 1994; Wardlaw et al. 2002; Yang et al. 2002; Spriet et al. 2006). Looking specifically at a susceptible (Karl 92) and a tolerant cultivar (Halberd) grown at 20/18°C, exposed to 1–2 days of heat (38/25°C) at 10 days after pollination, Hays et al. (2007) found 25% grain abortion and 10% GW reduction in cultivar Karl, but no response whatsoever in Halberd, responses which were associated with a large increase in ethylene production in grains and leaves with heat in the susceptible cultivar. These researchers have gone on to identify, in a RIL population of Halberd × Susceptible, several QTLs significantly associated with heat tolerance (Mason et al. 2010), but they are still some way from gene identification.

**Simulation modelling**

Simulation modelling of the wheat crop has advanced greatly since the early efforts of Nix and Fitzpatrick (1969), in line with increased physiological understanding, more transparent model structures, and much more powerful computing capacity. A comparison by Jamieson et al. (1998) of five wheat models against carefully measured wheat crops under a wide range of water treatments in New Zealand (yields from 3.5 to 9.9 t/ha) showed that the AFRCWHEAT2 model from the UK to be best for yield prediction [root mean squared deviation (RMSD) = 0.64 t/ha, c.f. CERES 0.90 t/ha, and Sirius 0.90 t/ha]. In Australia, APSIM-Wheat was developed from CERES and now dominates (Asseng et al. 1998, 2011; Wang et al. 2003; Hochman et al. 2009a, 2009b; Ludwig and Asseng 2010). The model uses daily time steps and includes a phenological framework, leaf expansion, crop growth driven by either radiation interception and RUE or transpiration and TE (whichever is most limiting), root penetration and layered soil water and N uptake, water and N stress indices feeding back into leaf area and RUE, and finally estimates of GN and GW. Yield predictions are reasonable, e.g. RMSD of 0.40 t/ha for yield range of 1–4 t/ha in Western Australia (Asseng et al. 1998) and 0.74 t/ha for a range 1–7 t/ha in Queensland (Wang et al. 2003). The latest official version of APSIM-Wheat is to be found at: www.apsim.info/Wiki/Wheat ashx, accessed 21 January 2011. Good progress has also been made in modelling grain protein content of wheat (Martre et al. 2006; Jamieson et al. 2010). All the models referred to so far are one-dimensional, but Evers et al. (2010) have attempted to build a 3D-architectural model of the wheat crop, tracking individual leaves and tillers in space; however, success was limited and such complexity may not be necessary for most uses. Recently Jamieson et al. (2010) have again extensively reviewed the structure and performance of wheat modelling, pointing to many worthwhile applications while recognising scope for further improvement. Independently Hall and Sadras (2009) have pointed to three specific areas for model improvement, namely root morphology and function, biomass partitioning, and crop response to extreme temperatures.

APSIM-Wheat is certainly sufficiently accurate and user friendly to inform farm management decisions, especially in dryland situations where rain is uncertain, and yield response risk needs to be quantified, and adjusted according to somewhat skilful seasonal forecasts and unfolding seasonal weather; in this role in Australia it has been renamed Yield Prophet (Hochman et al. 2009b). Model accuracy across a sample of 334 crops of ‘elite’ farmers over 2004–07, however, remains an issue; farmers want 0.5 t/ha accuracy while currently the RMSD of model versus observed is 0.8 t/ha, and there was a bias towards yield underestimate at high yield levels (Hochman et al. 2009a, Fig. 3a). Incorrect inputs (climate and especially key soil properties) and ignored biotic stresses (e.g. weeds, disease) could be part of the error; inadequate physiology is presumably the rest. Interestingly, the model, using ‘best bet’ values for plant density, N and time of sowing, gives an estimate of PY<sub>w</sub> against which to benchmark the farmers’ yields; the latter averaged 77% of PY<sub>w</sub> (Hochman et al. 2009b).

Yield Prophet simulated yield explains little more of the actual yield variation than did simulated ET alone (r² of 0.71 versus 0.69, Fig. 3b). Admittedly simulated ET values should take care of yield responses related to lost water through deep drainage or soil water left at maturity. Nonetheless it is a surprising result, for APSIM’s simulation of yield attempts to allow for the trading of soil evaporation for transpiration when, for example, higher soil N stimulated greater leaf area index (LAI), for the timing of rainfall via effects of plant water stress at critical stages, and for the influence of vpd on TE. The authors suggest that the substantial gap in both predictions may be partly due to ignoring the negative effects of extreme spring temperatures (frost and heat), in accord with Hall and Sadras (2009) above. Also the assumption of no biotic stresses is a weakness (although other evidence suggests these effects reduced yield no more than 5% for the crops sampled). There is little doubt, however, that simulation models which deal satisfactorily with biotic stress, in particular foliar disease are needed for better crop management.

There are several other common uses of wheat simulation models including the extrapolation in time and space of results from agronomic experiments, the exploration of likely effects on yield of past and future climate scenarios, and, in breeding, the understanding of G × E (and × management (M)) and the prediction of trait change effects on yield. Because validation is...
very difficult in these situations, model inaccuracies become more worrying. The reasonable yield predictions highlighted above often hide the fact that key internal physiological parameters like GN, GW and LAI are poorly modelled; compensating errors seem common because of the upper limits to growth and yield imposed by resource supply, and in fact one model does reasonably well ignoring GN and GW altogether (Jamieson et al. 2005a). In the meantime G-to-P simulation modelling will undoubtedly remain crop modellers’ greatest challenge. For readers who wish to see the latest courageous attempt to simulate the effect of real genetic variation in key traits (via QTL) on grain yield (in maize), Chenu et al. (2009) is recommended.

**Concluding remarks**

Today research on wheat physiology is undertaken usually with a stated view to impact, whether from improved crop agronomy or better cultivars: at the least, greater physiological understanding is invoked as showing the way forward. But resultant predictions are usually outputs not impacts, for while there has been steady progress in physiological understanding, impacts remain illusive. There may, however, be emerging greater confidence in physiological applications in agronomy than in breeding, although most scientists remain aware of the possibilities also of useful G × M interactions (Fischer 2009).

With agronomy, the questions relate to the strategic and tactical management of soil and soil water, the crop planting
date, its density, row spacing and fertilisation, and the management of biotic stresses, all done so as to maximise economic return at acceptable risk levels. Given the importance and uncertainty of weather in this endeavour, especially in rain-fed wheat cropping, capturing the physiological understanding through simulation modelling has become accepted as an essential tool, something strengthened by considering seasonal weather forecasts of improving skill (e.g. Moeller et al. 2008). Model calibration and validation against agronomic inputs is generally satisfactory, but should never be neglected and needs ongoing attention from physiologists, especially bearing in mind the new management opportunities that innovative agronomic technologies (e.g. precision seeding, nanotechnology) and new cultivars (e.g. herbicide resistance, adaptation to wide rows) can create. Better knowledge of root systems and rhizospheres may soon also need to be considered, and management models including biotic stresses are lacking.

It is with genetic improvement that the gap between physiological aspirations and impact is greatest, undoubtedly because the complexity of the path from gene through physiology to phenotype and yield, a route which far exceeds the complexities in going from agronomic management to yield. The examples given in wheat phenology and aluminium and salinity tolerance, where major genes and simple environmental cues, dominate, offer glimmers of hope for linking physiology to impact through manipulation of marked alleles for desirable and predictable effects in the field. This becomes much more difficult for quantitative traits, such that seeking understanding at deeper levels than that of trait physiology may be counterproductive, and selection based at the trait level, already fraught by unanticipated trade-offs, will remain a better option. This seems to be the current experience with breeding for PY and PY\textsubscript{w}: in the examples given, the genes and alleles involved may remain indecipherable, but this does not preclude progress through seeking and assembling apparently desirable traits, some of which may associate with robust low cost molecular markers; but others may be more readily assessable through low cost direct measurement (e.g. remote sensing). It should be remembered that the greatest threats to world food security will come soon, in the next 20 years, and seeking to explain at the molecular level all the trait phenomena may be a costly distraction from seeking to exploit the traits. There are of course exceptions to the frustrations of chasing alleles, like selection of short wheats with longer row spacing, capturing the physiological understanding through simulation modelling to predict from the gene level to the quantitative phenotype will remain extremely difficult for a long time to come, while modelling from trait change to yield will be difficult enough and needs to proceed in adequately validated successive steps of increasing complexity.

This review has not canvassed genetic engineering for PY or PY\textsubscript{w} gain because, to date and despite claims to the contrary, there are no well validated field successes, and because the approach reflects excessive naivety with respect to the complex physiology of yield determination. Success from genetic engineering for yield potential is most likely to arise largely by chance, just as it does in conventional breeding, both in Farrer’s time, and even today, with conventional breeding still managing to raise wheat yields 0.5–1% per annum!

References


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