

Wheat physiology: a review of recent developments

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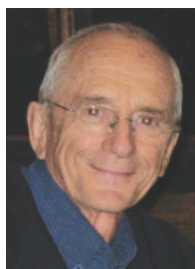
Abstract. This review focuses on recent advances in some key areas of wheat physiology, namely phasic development, determination of potential yield and water-limited potential yield, tolerance to some other abiotic stresses (aluminium, salt, heat shock), and simulation modelling. Applications of the 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 $G \times E$ 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



Tony Fischer was born in January 1940 and grew up on a wheat–sheep farm in the Riverina of NSW, where he has still maintained a close links until recently. He completed his secondary education in Melbourne, with B. Agric. Sci., (University of Melbourne), graduating in 1961. He then obtained a Master's of Agricultural Science degree (also from University of Melbourne) in 1964, and a PhD in Plant Physiology from the University of California (Davis) in 1967. Tony has worked for NSW Department of Agriculture at Wagga Wagga, CSIRO in Canberra, CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo) in Mexico (1970–95, 1988–95), and finally for ACIAR (The Australian Centre for International Agricultural Research) from 1995 to 2005. He is currently an Honorary Research Fellow at CSIRO Plant Industry. Whilst at CIMMYT, Tony was the Director of the Wheat Program from 1988 to 1995 and later has been a member of the Board of Trustees of GRDC, ICARDA and IRRI. His research interests have always been the physiology, agronomy and genetic improvement of wheat, which has been gradually expanded to include the role of crop science in international agricultural development. Tony has published over 100 peer-reviewed papers. Tony was awarded the CM Donald Medal in 2004, the William Farrer Memorial Medal in 2007 and Member of the Order of Australia (AM) in 2007 for services to agricultural research.

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 phenology or phasic development which describes the occurrence of key growth and development events. Date of anthesis (AN) is the first appearance of dehiscent 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*)¹. 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-B1* 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-A^m1*), 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.

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-1*) and the vernalisation genes (*Vrn-1*, *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)

Cultivars		Genes and alleles			Classification	Sowing date
	<i>Ppd-D1</i> ^A	<i>Vrn-A1</i> ^B	<i>Vrn-B1</i> ^B	<i>Vrn-D1</i> ^B		
<i>Australia (Farrer's and CIMMYT's legacy)</i>						
Purple Straw (19th C)	<i>b</i>	<i>v</i>	<i>v</i>	<i>v</i>	Typical winter cultivar	
Federation (1901)	<i>b</i>	<i>b</i>	<i>a</i>	<i>v</i>	First early spring cultivar	
WW15 (1969)	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>	First CIMMYT parent in Australia	
<i>Western Australia 1990s</i>						
Osprey	<i>a</i>	<i>v</i>	<i>v</i>	<i>v</i>	Very long season	April
Halberd, Spear	<i>b</i>	<i>a</i>	<i>a</i>	<i>v</i>	Long season	Late April–early May
Eradu, Aroona	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>	Mid season	May
Kulin, Gutha	<i>a</i>	<i>a</i>	<i>a</i>	<i>v</i>	Short season	Late May onward
<i>Pugsley's isolines</i>						
Triple Dirk	<i>b</i>	<i>a</i>	<i>a</i>	<i>v</i>	Unresponsive to vernalisation	
Triple Dirk D	<i>b</i>	<i>a</i>	<i>v</i>	<i>v</i>	Unresponsive to vernalisation	
Triple Dirk B	<i>b</i>	<i>v</i>	<i>a</i>	<i>v</i>	Small response to vernalisation	
Triple Dirk E	<i>b</i>	<i>v</i>	<i>v</i>	<i>a</i>	Small response to vernalisation	
Triple Dirk C	<i>b</i>	<i>v</i>	<i>v</i>	<i>v</i>	Typical winter type	

^A*a* is dominant-insensitive allele, *b* recessive sensitive; Triple Dirk data from H. Eagles (pers. comm.).

^B*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-1* (insensitive allele *a*, or sensitive allele *b*), and the vernalisation genes *Vrn-1*, *Vrn-B1* and *Vrn-D1* (all having dominant-insensitive allele *a*, or sensitive allele *v*; *Vrn-1* 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-1* and *Vrn-1*, *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-1 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*, *vav*, *vva*). This explained the greater delay in flowering with winter wheats (*vvv*) the warmer the site. Finally the photoperiod-sensitive allele (*Ppd-1 b*) was estimated to delay heading on average 7 days compared to the insensitive one (*Ppd-1 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 alleles³, 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-1*,

³There 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 (PID) and vernalisation sensitivity (PIV) were fitted across 105 site-years, following which PID parameter values were fitted to the known photoperiod alleles, and PIV 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 of varieties of different maturity classes as shown in Table 1. A degree of vernalisation responsiveness is obviously needed with early sowings when photoperiods are longer, and in general gives the least delay in flowering per day delay in sowing [typically around 0.3 day, Syme (1968)], but this is not enough.

A second and greater novel challenge with the new knowledge is to ask whether it matters which combination of major gene alleles produces a given date of AN (see also below). For the wheat physiologist, phasic development not only includes AN, but also the timing of key events within this period such as floral initiation, terminal spikelet (TS), end of tillering/start of stem elongation (SE), flag leaf emergence, and meiosis, and that of events during grain filling (Slafer *et al.* 2009). Vernalisation of sensitive cultivars accelerates events to floral initiation and sometimes TS, while longer photoperiods appear to accelerate development right up to flowering, and increased temperature accelerates all development (Slafer and Rawson 1994; Slafer *et al.* 2009), although the base temperature for a constant degree-day response appears to increase, and clearly exceeds 0°C for the later stages of development (e.g. Fischer 1985). The relationship between the duration of the various phases and the production and survival of numerical components of grains m⁻² (tillers, spikes, spikelets, florets, grains) has been soundly established (e.g. Slafer and Whitechurch 2001; González *et al.* 2005a). Lately most interest has focused on the period in the crop most critical for the determination of grains (per m²), namely that of spike growth (dry matter accumulation in spike structure), with the view to manipulating development genetically so as to lengthen the period around spike growth, preferably at the expense of earlier periods, thus not changing time to AN.

Fischer (1984) defined the spike growth period as that when the spikes in a crop accumulate the last 95% of final dry weight

excluding grains (for a single culm, approximately the interval from penultimate leaf emergence, well after TS/SE, to AN (see Fig. 1)). Only photoperiod and temperature appear to directly control the duration of spike growth as defined, since they appear to also control the duration of the subtending longer period, TS/SE to AN (Fischer 1985; Slafer and Rawson 1994), and even the last part of this period, namely flag leaf emergence to AN (e.g. Whitechurch and Slafer 2002). Reduced duration with artificially extended photoperiod in this period (and before the period, via a memorised effect) had been shown in the field in Mexico (Wall 1979; Fischer 1985), and later confirmed in the Canberra Phytotron (Miralles *et al.* 2000) and in the field in Argentina (Whitechurch and Slafer 2002; González *et al.* 2003, 2005a). With Chinese Spring chromosome substitution lines, the TS–AN period appeared to be sensitive to photoperiod in the presence of the *Ppd-B1b*-sensitive allele, but not the *Ppd-A1b* or *Ppd-D1b* ones; in shorter photoperiods the period was notably longer only with *Ppd-B1b* (Whitechurch and Slafer 2002). However, the same Argentine laboratory found a longer duration (and sensitivity to photoperiod) with the *Ppd-D1b*-sensitive allele and little response to the *Ppd-B1* one in Mercia vernalised isolines (González *et al.* 2005a). These latter authors admit to many remaining uncertainties in understanding the genetic control of duration of this critical phase.

One weakness in the above studies is that actual spike growth duration is not a development phase, and was not measured, although it is clearly only the later portion of the TS/SE to AN phase. Indeed it has been too loosely defined since its beginnings in Fischer (1984). In reality spike growth is sigmoidal and continues for a few days after AN (see Fig. 1). The author (unpubl. data) has shown that in a single culm the growth duration, defined now as the interval between 5 and 95% final dry weight, as suggested in Abbate *et al.* (1997), for the main shoot of the cultivar Yecora 70, is 300 degree-days (above 4.5°C) at 11-h photoperiod and only 200 degree-days at 17-h; commencement was well after SE, at 22 and 17 days before AN, respectively, and termination 3 days after AN (mean temperature (T_{mean}) was 16.4°C). Abbate *et al.* (1997) reported a similar duration in field crops, and suggested the duration to be 4.5 phyllochrons. Serrago *et al.* (2008) also measured growth duration directly, albeit somewhat differently, and showed it to be reduced by longer photoperiod in two cultivars, but not in another (but see below). In summary we remain far from the goal of Fischer (1985) and Slafer and Rawson (1994) of boosting yield through lengthening the duration of spike growth at the expense of earlier periods. Whether via exploiting natural genetic variation in the independent photoperiod sensitivities of different periods, as the early work of Wall (1979) and others (see Slafer and Rawson 1994) suggest may exist, or such variation in *Eps*, or via exploiting the burgeoning functional genomic knowledge pertaining to photoperiod sensitivity (e.g. Dwivedi *et al.* 2008), it remains a very worthwhile challenge.

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

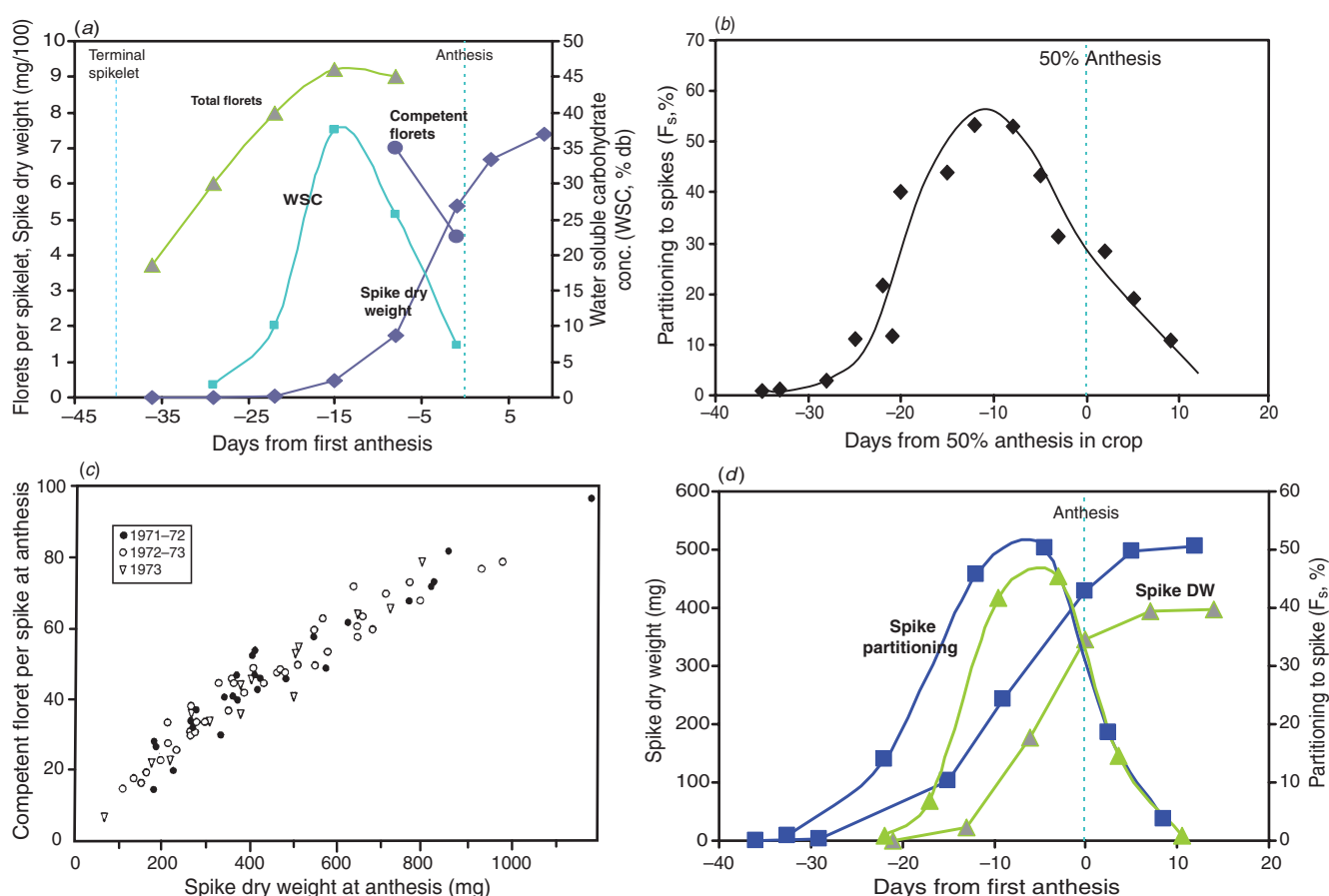


Fig. 1. (a) Spike growth (d.w., mg), water-soluble carbohydrate concentration (WSC, % d.b.), and total and competent floret number in central spikelet; cultivar WW15, main stem only, controlled environment. (b) Partitioning of dry matter to spikes (F_s , %) in short cultivar crops; irrigated, Griffith, New South Wales, 1987. (c) Relationship of competent floret number per spike to spike dry weight; individual spikes sampled at first anthesis in irrigated crops of cultivar Yecora 70 in Mexico. (d) Spike growth (d.w., mg) and dry matter partitioning to spike (F_s , %) under 11-h (triangles) and 17-h (squares) photoperiods; cultivar Yecora 70, main stem only, controlled environment. Data sources: (a) Fischer and Stockman (1980), (b) and (d) R. A. Fischer, unpubl. data; (c) Fischer (1984).

world, PY progress drives farm yield growth hence its importance (Fischer and Edmeades 2010). Solar radiation, temperature and photoperiod, interacting with genotype, in turn determine PY.

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_{mean} and solar radiation seem to underpin the flowering date for maximum yield in wheat. At low latitudes ($\sim 30^\circ$), optimum flowering date is a compromise, following closely upon the early spring maximum in photothermal quotient [$\text{PTQ} = \text{solar radiation} / (T_{\text{mean}} - 4.5^\circ)$] 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_{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/m² (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/m²) 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 Slafer 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:

$$\text{SDW}_a = D_s \times \text{CGR} \times F_s \quad (1)$$

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:

$$\text{GN} = \text{SDW}_a \times \text{Grains}/\text{SDW}_a \quad (2)$$

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:

$$\text{SFI} = \text{Competent florets}/\text{SDW}_a \times \text{grain set} (\%/100) \quad (3)$$

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 respiratory 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, González *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_a, 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_s) and light-saturated photosynthetic rate (P_{max}) with GN progress in north-west Mexico (Fischer *et al.* 1998), and from similar pre-anthesis conductance/ P_{max} 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_s , the partitioning of dry matter to growing spikes (e.g. Fischer 1984, 2007; Abbate *et al.* 1998; Slafer *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_s 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_s (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_s .

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 $\times$ 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 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 $\sim 10\%$ 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_a 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_s 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_a 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 SDW_a 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 T_{mean} (a negative relationship with slope of $2\text{--}7\%/^{\circ}\text{C}$ for T_{mean} between 15 and 28°C (Wardlaw and Wrigley 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 carpel size at AN, and then GW (Calderini *et al.* 1999, 2001; Ugarte *et al.* 2007). There was a positive relationship between GW and carpel 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 carpel 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 carpel 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 carpel, 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 sheaves. 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 tipping 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 P_{max} 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 WCS 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: WCS 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 WCS at around anthesis (Shearman *et al.* 2005). Considerable research is now underway on WCS reserves, which tend to peak at the onset of grain filling, when most measurements are focused. Spring wheat populations revealed a large range in WCS 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 Borrás *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 (Rathey *et al.* 2009).

Harvest index and lodging resistance

Following Donald and Hamblin (1976), crop physiologists 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 breeding progress to be less linked solely to HI, and more to both HI and biomass, or even biomass alone (e.g. Shearman *et al.* 2005; Aisawi *et al.* 2010). In addition a recent thorough physical analysis of dry matter costs of reducing stem lodging in heavy wheat crops to a tolerable risk, limits HI to closer to 0.50, and involves extra dry matter investment in surface roots for reduced root lodging risk (Berry *et al.* 2007); in addition, for a given yield level and HI, a larger spike size and corresponding culm diameter, via reducing culm number, is more efficient for reducing lodging than more smaller spikes borne by narrower culms. There seems little doubt that further PY increase in wheat will depend more on increased biomass, necessarily accompanied by a HI, which is as high as possible: culling progeny with HI below 0.40 or 0.45 would seem a sensible breeding strategy, and rapid determination of HI thus a worthwhile goal.

Water-limited potential yield

A simple model

The prevailing paradigm for understanding water-limited potential yield (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 in-crop 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. PY_w is then usefully described by three components:

$$PY_w = (ET - E_s) \times TE \times HI \quad (4)$$

where E_s is soil evaporation in the crop, so that $ET - E_s$ 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 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 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 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. 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 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 PY_w may be earlier than that for PY because of climate considerations, even though it brings an increased risk of spike frosting 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 (ACPGF 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. Fischer (1979) was surprised by marginal water-use efficiencies for dry matter as high as 150 kg/ha.mm with growth (cover) enhancing treatments (earlier sowing, higher fertiliser and greater seed density) at Wagga Wagga and Tamworth. In heavy-textured infertile soils in the dry winter-rainfall environment of Syria (<300 mm annual rainfall), N and P fertiliser so boosted crop cover that the replacing of E_s by T alone explained much of the substantial yield increase (Cooper *et al.* 1987). Similarly it is postulated that selection for greater early vigour in wheat, for which there is substantial genetic variation, can significantly boost growth at little overall cost in ET (Richards and Lukacs 2002).

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 (salinity, acidity, high boron) 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 (ACPGF 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. Palta 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 C_4 photosynthetic pathway than C_3 crops like wheat. Nevertheless, Farquhar and Richards (1984) found TE in wheat to show useful cultivar variation, which

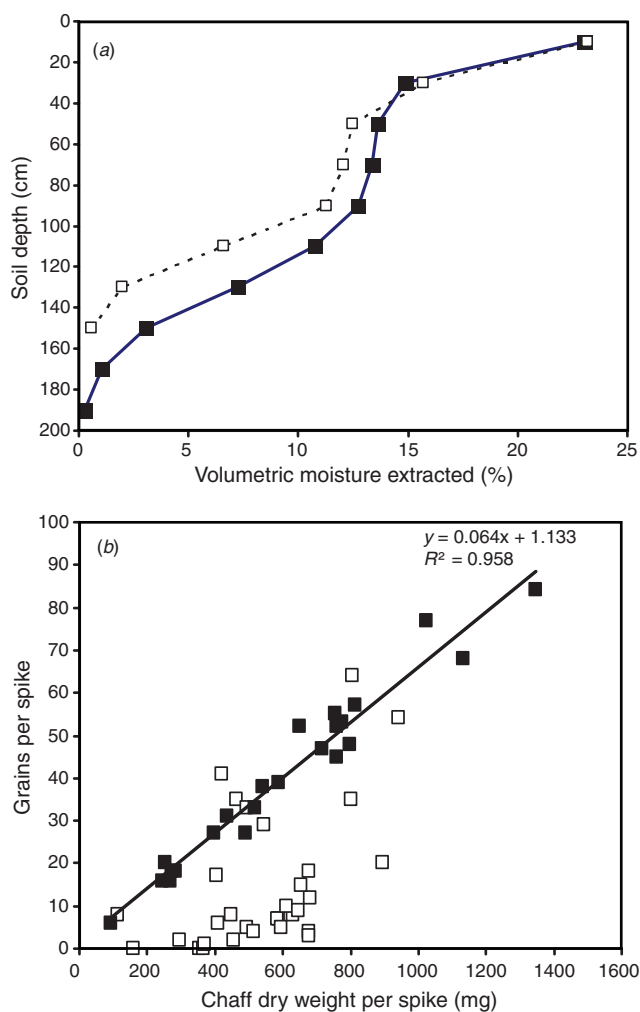


Fig. 2. (a) Pattern of soil water extracted at maturity following 12 weeks without rain under winter wheat cultivar S71 (closed symbols), sown 23 March, and spring wheat cultivar Egret (open symbols), sown 20 May; field, Gininderra Experiment Station 1987 (the late P. M. Bremner, unpubl. data). (b) Relationship of number of grains to spike weight at maturity (=chaff weight) for individual spikes of cultivar Ventura under drought (open symbols) and well watered conditions (closed symbols with regression); field, Boree Creek, 2007 (R. A. Fischer, unpubl. data).

in accord with theory, was related inversely to ^{13}C isotope discrimination (Δ). 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 $P_{\max}$. 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 Δ 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 reflected in reduced final SDW_a, 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 surely 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 PY_w 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 PY_w 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 PY_w. 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 PY_w.

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

1996), 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 $\times$ 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 intermediate leaf exclusion 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 T_{mean} (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 ($T_{\text{max}} > \text{around } 32^\circ\text{C}$) 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 $T_{\text{max}} > 34^\circ\text{C}$ during grain filling at locations across the Australian wheat belt. Their modelling suggested a yield reduction of $\sim 0.2\text{ t/ha}$ 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.* 1998b), 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 T_{max}) 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 g_s .

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)

	Control	Atmospheric stress			Atmospheric plus soil stress	
Air temp. (°C)	25	32	39	46	46	46
vpd (kPa)	Low	3.1	5.1	8.4	8.4	8.4
Ψ_{soil} (kPa)	>−0.1	>−0.1	>−0.1	>−0.1	>−0.2	>−0.3
<i>At the end of the 6-h heat shock period</i>						
Leaf RWC ^A (%)	96.0	91.5	92.4	81.4	67.0	<50
Grain RWC ^A (%)	94.6	93.0	91.2	89.5	87.4	84.8
Leaf temp. (°C)	–	30.0	32.2	39.0	43.2	46.2
Grain temp. (°C)	–	31.0	34.6	40.4	39.4	42.3
<i>24 h later</i>						
Leaf damage (%)	0	0	0	0	0	50–75
<i>At maturity</i>						
Grain weight (%)	100	97	95	87	83	72

^ARelative water content.

abiotic stress (Stone and Nicolas 1994; Wardlaw *et al.* 2002; Yang *et al.* 2002; Spiertz *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 $\times$ 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_w against which to benchmark the farmers’ yields; the latter averaged 77% of PY_w (Hochman *et al.* 2009b).

Yield Prophet simulated yield explains little more of the actual yield variation than did simulated ET alone (r^2 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 $G \times E$ (and $\times$ management (M)) and the prediction of trait change effects on yield. Because validation is

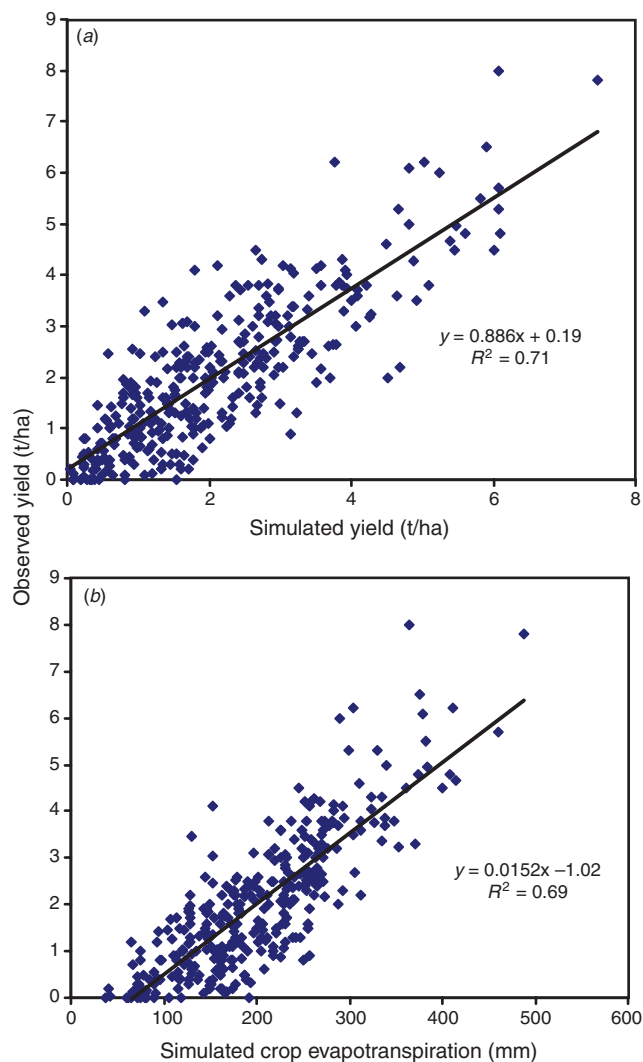


Fig. 3. Actual crop yields versus (a) Yield Prophet-simulated yield, and versus (b) Yield Prophet-simulated evapotranspiration; 334 crops across Australian wheat belt in 2004–07 seasons (Hochman *et al.* 2009a).

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.* 1998, 2010). With climate change-related applications of wheat modelling (e.g. Ludwig and Asseng 2010; Asseng *et al.* 2011), there are added uncertainties, about future climates themselves, especially rainfall, and about likely adaptation of agronomy and of cultivars to higher CO₂ levels and to the new climates, and more caution is urged.

Notwithstanding abundant physiological uncertainties, the newest application of modelling is the linking of genes (in fact alleles of genes) to phenotype (G-to-P) through incorporating trait physiology into models like APSIM. Indeed this is seen by

many as a key way forward for crop breeding, including the genetic engineering of yield. A courageous start has been made with genes in models of other crops like beans, soybeans, and barley, and with wheat phenology mentioned earlier (White *et al.* 2008), while APSIM is the vehicle by which the task is being approached in sorghum (Hammer *et al.* 2005), maize (Messina *et al.* 2009), and very recently, wheat (Chenu *et al.* 2010). But the initial efforts on traits and yield in wheat have been less ambitious. For example, Asseng and van Herwaarden (2003) have attempted to simulate the effect of a hypothetical increase in pre-grain-filling assimilates (a trait for which there is genetic variation) on wheat yield at a dry location in southern New South Wales: there was some validation against observations (but not of the genetic effect), and the positive simulated effects on yield at intermediate yield levels (1.5–4 t/ha) were plausible. Recent efforts on modelling traits to yield in wheat have been more ambitious. Thus, Ludwig and Asseng (2010) simulated five hypothetical trait combinations related to early vigour in wheat across three locations in Western Australia, two soil types, two N levels, and 50 years of historic weather, with and without many climate change scenarios. Even staying with historic climate and CO₂, interactions abound and it becomes daunting enough to describe the modelled effects on yield of trait changes, let alone explain them, although greater early vigour, as created in the model, seems to boost yield except at the wettest coolest site on heavy soil. However, the absence of any trait validation is a major blow to credibility. This wheat case, using modern computer power to tackle huge simulation tasks, does not differ from those of other crops above, illustrated by Messina *et al.* (2009) who modelled the effects of variation in five hypothetical traits (in all combinations) with APSIM-Maize. In all cases there is a serious lack of validation of the consequences for yield of hypothesised trait changes, and of the linking physiology; there is also daunting complexity. What is lacking is a simpler stepwise approach which could start with, for example, modelling the effect a single *Ppd* allele change, a change for which trait (flowering date) and phenotype (yield) data are already available from winter wheat *Ppd/ppd* isolines (e.g. Worland 1996; Foulkes *et al.* 2004; González *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_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 coleoptiles, where direct selection for the major new dwarfing alleles may be the most efficient way forward. But it goes without saying that the use of 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_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!

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