Chapter 17

Breeding Evolution for Conservation Agriculture

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Introduction

It is now over 30 years since Peter Cornish first published his considered thoughts on delivering improved crop and pasture varietal performance for changing farming systems, including then new conservation agriculture (CA) regimes (Cornish 1987). Since this time breeding programs have changed markedly to accommodate the many genetic, phenotypic and statistical tools that enable increased rates of genetic gain and/or reduced cost in varietal development. Most crop and pasture breeding programs have since become privatised, increasing competition to facilitate the uptake and efficient use of new technologies. Returns to breeding companies are captured through seed sales and for some crops through End Point Royalties (EPR) where a levy is returned on seed or hay delivered for sale. Breeding has become less of an ‘art’ and more of a science with an explosion in genome-based understanding and how genes and their expression can be exploited to deliver improvements in selection. Notwithstanding, elements of traditional breeding have been maintained owing to the need for breeders to understand better and exploit those traits contributing to improved disease resistance, quality and adaptation in their gene pools.

The adoption of CA was targeted to improve the environmental and economic sustainability of farming systems. Farming systems evolved as factors limiting performance and profitability became better understood; in particular, how increased water productivity could be achieved by changing sowing date, improved crop sequences and addressing increases in on-farm input costs. The breeding evolution was globally-led and independent of the evolution in farming systems. Yet while genetic gain in wheat prior to 1987 was stable at 0.6% per year (Fischer *et al.* 2014), it has remained so since, even with the improved understanding of the genome and factors affecting adaptation with CA.

The opportunities to improve water use efficiency in rain-fed systems have been highlighted previously (*e.g.* Kirkegaard and Hunt 2010, Flohr *et al.* 2018, see also Chapter 13). Yet the literature does not acknowledge a strong capacity for exploiting genotype × management interaction in elite breeding lines (*e.g.* Cooper *et al.* 2001) presumably because the breeders’ gene pools are genetically narrow or environmental factors such as rainfall, temperature and soil type dominate genotype ranking in multi-environment studies. That aside, CA-adapted germplasm has been identified when genotype × tillage studies are broadened to include very diverse overseas germplasm (Trethowan *et al.* 2012). Further, assessment of mapping populations has identified genomic regions with potential to improve adaptation with CA (Trethowan *et al.* 2012).

This chapter focuses on breeding activities targeting genetic improvement in high yield systems and does not address low-input or organic agriculture (see Wolfe *et al.* 2008). We report on recent advances in breeding and on future opportunities to incorporate new genetics to improve performance in CA systems. We also report on how a physiological framework has allowed for an improved understanding of factors limiting the performance of crops, especially wheat under CA, and the targeting of novel genes not present in commercial breeding programs. Finally, we discuss how better understanding of the genetic architecture of key traits has permitted more rapid breeding and delivery of germplasm to commercial breeding programs. Our focus here is on wheat, as it is the dominant crop in rain-fed farming systems in Australia and receives the most breeding investment. However, the principles are also applicable to other major crops.

The evolution in breeding methods

The breeding of crops can be summarised as a continuum of activities commencing with parent identification and crossing, population development and early-generation screening, and extensive testing in multi-environment trials culminating in cultivar release (Robertson *et al.* 2015). The significant effort in managing this complex and integrated series of processes reflects many years of sustained effort and both considerable financial cost and risk to the breeder. The skill of the breeder commences and is limited by the identification of the optimal parents and their crossing as these set the population mean and genetic variance from which genetic gain will be subsequently made. The breeder must then identify and target which tools to employ, and when, to reduce the time and cost between cross and release, and increase the likelihood of delivering a highly competitive variety into the marketplace. Many of the tools developed for improved breeding over the past 30 years are discussed briefly.

Biotechnology

Perhaps the greatest evolutionary change in breeding over the past 30 years has been in the capacity to move beyond selection of a phenotype to selecting directly for a targeted gene. Advances in biotechnology have provided plant breeders with the opportunity to increase the rate of genetic gain when breeding new varieties. Molecular markers have been the main biotechnological tool used in this respect and, through their application, increased understanding of the genetics underlying both simple and complex traits has been attained. The usefulness of molecular markers arises from the ability to detect DNA sequence variation between individuals and through the association of this genotypic variation with phenotypic variation (Langridge *et al.* 2001).

Numerous types of molecular markers have been developed over the past 30 years, including:

- random amplified polymorphic DNAs (RAPDs);
- restriction fragment length polymorphism (RFLP);
- amplified fragment length polymorphisms (AFLPs);
- simple sequence repeats (SSRs, commonly referred to as microsatellites); and
- single nucleotide polymorphisms (SNPs).

In recent years SNPs have become the dominant molecular marker platform, due to their abundance within genomes and the availability of low cost, high-throughput systems for their detection. The most beneficial application for markers in breeding is to select for desirable alleles of a phenotype of interest, in a process termed marker-assisted selection (MAS). In plant breeding, MAS has been used to increase the efficiency of back-crossing, combine (pyramid) genes for traits of interest, and reduce linkage drag (Collard *et al.* 2005, Francia *et al.* 2005). The advantages of MAS, when compared with traditional phenotypic selection, are greatest for traits that show low heritability, are difficult to phenotype, or are not expressed in single plants (Dreisigacker *et al.* 2016). In these instances, increases in genetic gain in breeding programs is achieved by increased selection accuracy and reduced generation time.

MAS had been touted as having the potential to revolutionise plant breeding and lead to the occurrence of another 'Green Revolution' (Naylor and Manning 2005). Presently however, MAS is routinely used in plant breeding programs only for selecting alleles with large effects on traits with simple inheritance, such as flowering time, height, and qualitative disease resistance (Zou *et al.* 2017). While these activities provide evidence of the value of MAS, many traits of agricultural importance (such as yield, quality, abiotic stress tolerance, and resistance to certain diseases) are under polygenic control, and successful application of MAS for such polygenic traits is highly desirable. Indeed, Mohler and Singrun (2005) suggest that the incorporation of loci that contribute to variation in quantitative traits (quantitative trait loci, QTL) into breeding programs is the principal task of MAS. MAS for QTL can theoretically be achieved simply by selecting for the presence of specific marker alleles that are tightly linked to, or flank, favourable QTL alleles. However, despite an explosion of reports on the identification of molecular markers linked to QTL for many traits, MAS for quantitative traits is mostly unsuccessful (Bernardo 2008).

Francia *et al.* (2005) have described several reasons why MAS for QTL tracking can fail. These include:

- uncertainty of the QTL position;
- deficiencies in QTL analysis leading to under-estimation or over-estimation of the number and magnitude of effects of QTL;
- an inability to detect a QTL-marker association in divergent backgrounds;
- the possibility of losing target QTL due to recombination between marker and QTL;
- difficulty in evaluating epistatic effects; and
- difficulty in evaluating QTL × environment interactions.

Marker-assisted recurrent selection (MARS) is extension of MAS for genetically complex, polygenic traits. MARS uses recurrent selection to accumulate multiple markers through selection, crossing and reselection within the same cross before incorporating new alleles in crossing with other parents (Bernardo 2008). It has proven to be an effective low-cost breeding system targeting genetically-complex traits in some crops (*e.g.* improving maize under drought, Bankole *et al.* 2017).

Genomic selection (GS) was devised to overcome the restriction of tracking only a limited set of markers linked to QTL with large effects on traits of interest. By using all molecular markers to predict the performance of an individual, GS seeks to capture the additive genetic effects of all QTL affecting the trait of interest (Meuwissen *et al.* 2001). The implementation of GS requires a training population that has been phenotyped in the target population of environments and densely genotyped (Voss-Fels *et al.* 2019). The genotypic and phenotypic information from the training population is then used to develop models that predict the genetic value of unobserved individuals using their genotypic data alone. The GS models allow plant breeders to select individuals with the highest genomic estimated breeding values (GEBVs) for further evaluation, and to design crossing strategies to accelerate the rates of genetic gain for traits of interest. Simulation and empirical studies have shown that GS outperforms traditional MAS, leading to accelerated genetic grain both by improving selection accuracy and by shortening breeding cycles (Heffner *et al.* 2010, Arruda *et al.* 2015).

Genomics

Genomics linked to improved field and controlled environment phenotyping has been useful in identifying genes associated with improved performance. Transcriptomics enables high-throughput investigation of changes in mRNA expression levels while proteomic and metabolomic profiling has enabled investigation of the effects of post-transcriptional and post-translational gene regulation. Genetic engineering permits the identification and transfer of foreign DNA to a new recipient genome. Resulting 'Genetically Modified Organisms' (aka GMOs) provide novel genetic diversity not present within the broader crop gene pool and include varietal resistance to glyphosate herbicide. Genome editing relies on targeting of specific nucleotides monitored and selected following mutagenesis. The generation of mutants is rapid and relatively inexpensive although less precise than for genetic engineering. However, unlike GM, Australian government approval is not required if the DNA-cutting proteins allow the host cell to repair the break naturally and do not use a template containing genetic material to direct the repair process.

Quality phenotyping

Accurate prediction for complex traits is dependent upon high-quality phenotypic data. Emerging reports are supporting additional gains in prediction accuracy for complex traits such as yield, when GS is combined with high-throughput phenotyping (HTPP). Technologies such as LiDAR, thermal imaging, and spectral reflectance are being deployed using manned and un-manned vehicles, generating a wealth of field phenotypic data that was not previously available to breeders (Deery *et al.* 2016, Jimenez-Berni *et al.* 2018, Rodrigues *et al.* 2018). Although several studies have demonstrated that prediction accuracy for grain yield improves when secondary traits captured by HTPP (*e.g.* canopy temperature and normalised difference vegetative index [NDVI]) are used for GS model training (Rutkoski *et al.* 2016, Crain *et al.* 2018), incorporation of HTPP in GS approaches is still in its infancy, requiring further research.

‘Managed Environment Facilities’ (MEFs) have been constructed across Australia to provide a set of nationally coordinated research sites where traits and other pre-breeding outputs can be assessed side-by-side and under the same controlled, managed conditions (Rebetzke *et al.* 2013). Such facilities provide the understanding from which a clear value proposition can be delivered for new traits, methods or technologies relevant to breeding. While originally developed for assessment of putative drought tolerance traits, the careful control within the MEFs can be readily extended to include other constraints (*e.g.* subsoil and nutrient limitations) and capacity to assess different farming systems toward better understanding of genotype × management interaction (*e.g.* time of sowing).

Considered here as a component of phenotyping, the Australian National Variety Trialling (NVT) program is globally unique in the distribution and testing of advanced commercial breeding lines independent of the breeding companies themselves. The program is funded and coordinated through grower levies by the Grains Research Development Corporation, and aims to provide growers and agronomists with grain yield, quality and agronomic information to aid in the selection of varieties for on-farm use.

Statistical methodology

The large datasets encompassing genetic, pedigree, phenotypic and environmental information are becoming fully integrated as ‘big data’ available for genetic and environmental prediction of breeding line performance. Statistical modelling has moved from least squares based analyses to likelihood based modelling permitting delivery of unbiased estimates of genotype prediction where data are incomplete. Complementing the statistical analysis of data has been an evolution in crop modelling relevant to uptake for use in commercial plant breeding. Improved models have provided understanding of the potential for different traits to contribute to improved adaptation, and trait value toward a value proposition important in prioritising breeding objectives (Robertson *et al.* 2015). The greatest value in crop modelling for breeders has most likely been through the interpretation of large genotype × environment interaction in breeders’ own and national variety trials. From those trials sampled environments are characterised and the performance of genotypes interpreted relative to performance of known genotypes for an historic set of environments (Chenu *et al.* 2011). The environmental characterisation has largely been defined around timing and amount of soil water but could be extended to other factors including soil constraints and non-optimal temperature regimes (*e.g.* frost and heat, Watson *et al.* 2017).

Other tools

A range of other technologies have been developed to reduce the cost or increase the confidence in commercial breeding. For example, speed-breeding methods aimed at reducing the time from cross to line testing (*e.g.* doubled-haploids and environmental manipulation to hasten the interval between successive generations) and use of off-season nurseries for testing and seed-increase have potential to reduce the time to commercial release of cereal varieties by 3 to 5 years.

An evolution in output trait understanding and delivery

The revolution with CA has relied on the appropriate genetics to complement dramatic changes in the farming system while maintaining the same or improved genetic gains. Coinciding with this revolution has been a gradual change in the climate and its effect on drought and air temperatures to affect productivity (Lobell *et al.* 2015, Hochman *et al.* 2017). The genetic diversity in Australian wheat breeding programs is relatively small following a gradual reduction in genetic variability particularly following the widespread use of CIMMYT germplasm in the 1970s following the Green Revolution (Joukhadar *et al.* 2017).

New genetics and breeding strategies are required to maintain genetic gain given the reduction in effective population size and development of large linkage blocks throughout the genome. Given the emphasis on maintaining high milling quality, disease-resistant gene complexes, targeting new genetics from overseas breeding programs, is key (Joukhadar *et al.* 2017) yet must be relevant to our climate and specifically to our farming systems. One strategy is to source genetics targeting traits aimed at overcoming current and future agronomic and climate constraints. In some cases the genetics does not reside in Australia and must be sourced elsewhere (*e.g.* increased crop competitiveness for suppressing herbicide-resistant weeds) while in others much of the genetics is already contained in older Australian wheat varieties (*e.g.* awnless wheats for frost risk mitigation and greater coleoptile length for improved establishment).

Table 1. Current and future agronomic challenges confronting growers, and those traits and their capacity for selection and delivery in commercial wheat breeding programs

Breeding target	Trait	Genetic variation?	Genetic complexity	Screening method(s)
Challenges with early growth				
Establishment with deep sowing/stubble retention	Greater coleoptile length	Yes[B]	Complex	Molecular markers/phenotypic screening
Early sowing in warm soils	Greater coleoptile length	Yes[B]	Complex	Molecular markers/phenotypic screening
Dry sowing and false breaks	Reduced seed dormancy	Yes[B]	Unknown	Phenotypic screening
Late-sowing cereals	Rapid early leaf area/biomass	Yes[B]	Complex	Phenotypic screening
Overcoming hard soil constraints	Greater early vigour/thick coleoptile	Yes[B]	Complex	Molecular markers/ phenotypic screening
Challenges with reproductive growth				
Optimising flowering date	Development	Yes[A]	Simple	Molecular markers
Frost mitigation	Awnless milling and hay wheats	Yes[A]	Simple	Molecular marker
Challenges with managing stubble				
Reducing stubble loads	Reduced height	Yes[B]	Simple	Molecular markers
Challenges with disease and insect pests				
Stubble-hosted diseases (*e.g.* yellow leaf spot)	Disease resistance	Yes[A]	Complex	Molecular markers/ phenotypic screening
Soil-borne diseases (*e.g.* crown rot, Rhizoctonia)	Disease resistance	Yes[A]	Complex	Molecular markers/ phenotypic screening
Invertebrate pests (*e.g.* snails, slugs, nematodes)	Pest resistance	For some[A]	Simple/ complex	Molecular markers/ phenotypic screening
Challenges with weeds				
Herbicide-resistant weeds (*e.g.* annual ryegrass)	Crop weed competitiveness	Yes[B]	Complex	Phenotypic screening

[A] Variation present in commercial breeding programs; [B] Variation not present in breeding programs

The value in using a physiological approach to understanding limits to adaptation with CA was highlighted in Rebetzke *et al.* (2014b). A surprising phenomenon, given the many improvements in the structural and biological properties of soils in CA systems, is the observed reduced early seedling vigour and poor establishment with commercial wheat varieties. Wheat germplasm containing novel high early vigour genes developed leaf area and biomass more rapidly than commercial wheat varieties in hard, undisturbed soils. In modelling the benefits of greater early vigour in wheat, Zhao *et al.* (2019) demonstrated a benefit with greater establishment and seedling vigour throughout the Australian wheat-belt. Table 1 describes those traits aimed at genetically addressing constraints to productivity in Australian cereal-based farming systems. A discussion of some output traits is provided elsewhere (*e.g.* see Chapter 18) while brief descriptions of some selected key traits is provided below.

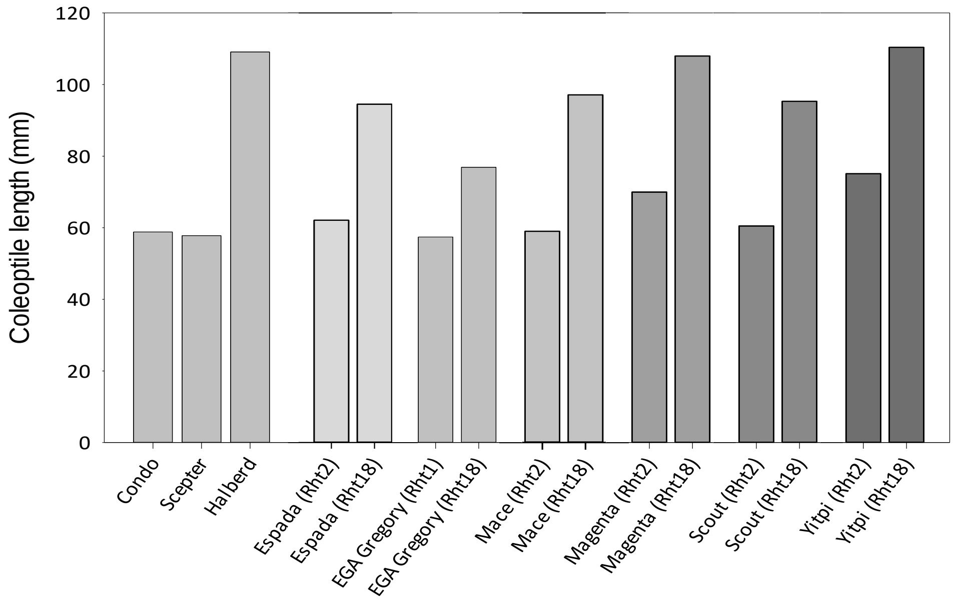

Figure 1. Average coleoptile length for backcross three-derived *Rht2* and *Rht18* dwarf near-isogenic lines in six wheat genetic backgrounds assessed at soil temperatures of 23°C. Semi-dwarf varieties Condo and Scepter, and tall variety Halberd are included for comparison (average LSD for all mean comparisons was 9 mm)

Improving crop establishment

Development of wheat varieties with the capacity to emerge from deep sowing would benefit growers in arid regions (Kirkegaard and Hunt 2010). Often sufficient moisture for germination is available deeper in the soil profile but the shorter coleoptiles of current semi-dwarf wheats prevent successful establishment if sown deep into this moisture (Schillinger *et al.* 1998, Flohr *et al.* 2018). Deeper sowing into stored soil moisture will also allow sowing programs to commence earlier. This will have the impact of increasing yield at both the farm and field scales (see Chapter 18). Deep sowing commonly results in few typically later-emerging seedlings producing small relative growth rates and slower leaf area to reduce seedling biomass (Hadjichristodoulou *et al.* 1977, Rebetzke *et al.* 2007a). In turn, later emerging plants have smaller biomass at anthesis, fewer spikes and lower final biomass and yield (Rebetzke *et al.* 2007a). Other factors contributing to poor establishment include stubble residue on the soil surface (Rebetzke *et al.* 2005, Soane *et al.* 2012), diseases such as crown rot and increasing soil temperatures associated with earlier sowing and/or climate changes. Modern semi-dwarf wheats containing the *Rht1* (syn. *Rht-B1b*) and *Rht2* (syn. *Rht-D1b*) dwarfing genes produce c. 45% shorter coleoptiles at 27 *vs* 15°C soil temperatures (Rebetzke *et al.* 2016a).

Genetic increases in coleoptile length will improve crop establishment with deep sowing, stubble retention and warmer soil temperatures. Shorter coleoptiles and poor emergence have commonly been associated with presence of the *Rht1* and *Rht2* dwarfing genes (Schillinger *et al.* 1998, Rebetzke *et al.* 2007a, b). Many of the alternative, gibberellin-sensitive dwarfing genes (*e.g. Rht4, 8, 12, 13 and 18*) reduce plant height with little or no effect on coleoptile length (Rebetzke *et al.* 2012a) or coleoptile diameter (Rebetzke *et al.* 2004). The increase in coleoptile length in replacing *Rht2* with *Rht18* is shown in Figure 1 where *Rht18* near-isogenic lines (NILs) produced an average 50% longer coleoptile when grown at 23°C soil temperature. The increase in coleoptile length was consistent across six genetic backgrounds with coleoptile length equivalent to that of the long coleoptile tall check variety, Halberd. Three *Rht2* and *Rht18* NIL pairs were separately assessed with deep-sowing at 120 mm at Merredin in 2018.

Figure 2 summarises a 50-90% increase in numbers of emerged seedlings in lines containing the GA-sensitive *Rht18* dwarfing gene. There was no statistical difference in establishment at the shallow (*i.e.* 40 mm) sowing depth (data not shown). Other studies have also demonstrated the potential of the *Rht8* dwarfing gene in the development of semi-dwarf, long coleoptile wheat targeted at sowing depths exceeding 110 mm (Schillinger *et al.* 1998, Rebetzke *et al.* 2007a) and where stubble loads are high (Rebetzke *et al.* 2005). Together with genomic regions linked to increased coleoptile length (Rebetzke *et al.* 2007b, 2014a), new gibberellin-sensitive dwarfing genes have been delivered in elite genetic backgrounds to Australian wheat breeders for population development.

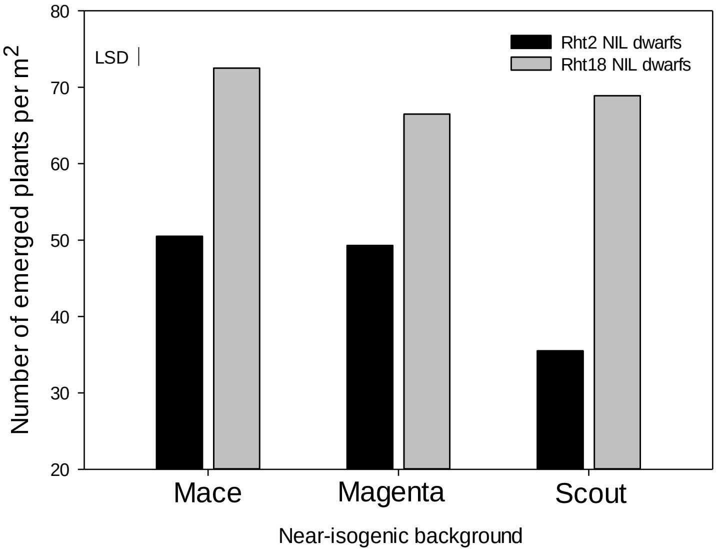

Figure 2. Average numbers of emerged seedlings (per m²) for backcross three-derived *Rht2* and *Rht18* near-isogenic lines in Mace, Magenta and Scout genetic backgrounds when sown at 12 cm sowing depth at Merredin in 2018

Crop weed competitiveness

The uptake of CA systems has prompted greater use of herbicides to place significant pressure on current herbicide modes of action (MOA). In turn, greater reliance on herbicides has increased selection pressure on weeds to evolve widespread herbicide resistance (D'Emden and Llewellyn 2006, Broster *et al*. 2019). In Australia, more than 500 unique cases of herbicide-resistant weeds have been identified showing resistance to 23 of the 26 known MOA (Heap 2019). The ongoing identification of new herbicide resistance emphasises the need to develop and implement alternative, non-herbicide protection strategies. Implementing 'Integrated Weed Management' (IWM) tools is a targeted strategy which aims to maintain the longevity of new and existing chemistries (see Chapter 10). Crop competition is one non-herbicide IWM control tool complementing agronomic methods, including changes in sowing density and sowing orientation as competition strategies. There is also evidence that early growth is impeded in no-till systems (Verhulst *et al.* 2011, Rebetzke *et al.* 2014b). Although compensated by more rapid later development, this provides an environment for greater weed growth early in the season. A greater sowing density increases competition by the crop for resources, mirroring the mass-competitor strategy of weeds to the advantage of the crop (Weiner *et al*. 2010). Similarly, optimally orientating the sowing of rows can limit the light available for weeds growing between rows. For example, changing the row orientation to an east-west sowing in wheat and barley in Western Australia decreased weed biomass by 37-51% (Borger *et al*. 2010). A third less-used competition strategy is to modify the crop variety itself to have a competitive advantage. This strategy is easily implemented with other IWM tools and moreover has low cost and low risk, assuming such varieties are commercially available.

Early vigour, defined as more rapid leaf area development through wide leaves and greater biomass at stem elongation, is a common mechanism for plant-to-plant competition in natural plant communities (Aerts 1999). Greater leaf area should shade and thereby suppress the competing weeds early before canopy closure. Wheat varieties with greater early vigour should provide an effective ideotype for crop-competition in managed farming systems as they do in natural plant-plant competition. The challenge globally is that very few competitive crop varieties have been released commercially and very few are wheats with greater early vigour. A reason for the lack of released vigorous competitive varieties might be the lack of early vigour in wheat germplasm arising from the over reliance of *Rht1* and *Rht2* dwarfing genes following the green revolution (Rebetzke and Richards 1999). To address this, a global survey of over 2000 overseas and Australian wheat genotypes were screened under controlled environment conditions for width of leaves 1 and 2, and early leaf area. The 28 most vigorous genotypes were then selected for intermating in the development of a structured high vigour, recurrent selection population. The resulting 38 F1 progeny were self-pollinated to produce S0 progeny and then 40-50 S0:1 progeny. Seed were sized to a common weight and screened under controlled conditions for leaf 1 and 2 widths. Lines containing the largest mean leaf widths were transplanted and used for subsequent crossing and generation of a new cycle. Several new crosses were performed resulting in 80 new cycle 1 populations. The process was then repeated over multiple cycles (Zhang *et al.* 2015).

Weed competitive genotypes were developed from crosses between vigorous cycle 3 selections and widely adapted Australian cultivars Wyalkatchem and Yitpi (Zerner *et al.* 2016). High vigour-selected lines were assessed for competitiveness under field conditions using cultivated oat, barley, winter ryegrass and/or canola as weed surrogates. In particular, two of the cycle 3-derivatives (W470201 and W640704 – both top-crosses from Australian wheat varieties) stood-out in early leaf area development and biomass while maintaining spring habit and semi-dwarf stature. Both lines suppressed the competitor by up to 97%. Figure 3 shows the difference in suppression of weed-mimic canola between Scout, a commercialised adapted Australian cultivar, and the developed line W470201.

Interestingly, selection for wider leaves one and two has been shown to carry through to enlarged size and area for all leaves. Greater leaf area promotes a denser more shaded canopy that can readily suppress later germinating weeds. Greater early leaf area also reduces soil evaporation and means that a greater proportion of soil water is transpired through plant leaves with a resulting increase in water productivity.

The research and delivery work of developing competitive wheat lines is ongoing with aims to supply growers with another non-herbicide IWM tool for controlling weeds. Current weed-competitive donors include cycle 6 high vigour derivatives with populations derived from modern Australian varieties so as to maintain excellent milling quality and yield. To facilitate rapid delivery to growers, there is strong collaboration with wheat breeders with over 5000 back-cross and top-cross breeding lines now distributed.

Figure 3. Commercial Australian cultivar Scout and developed weed competitive breeding line W470201 sown with (+canola) and without (control) competition from weed-surrogate canola at Condobolin NSW Australia in 2017. Wheat was sown at 160 plants m^{-2} in all plots and canola sown at 60 plants/m^2 in +canola plots. The experiment was designed with three replicated paired plots with the same suppression identified

Soil-borne and leaf diseases

Tillage moves and disturbs the spores and mycelium that cohabit together in the zone of soil disturbance. Tillage also reduces soil water potential to slow the movement of water-mobile pests (*e.g. Pythium* spp.), incorporates disease-infected residues (*e.g.* yellow spot and Fusarium crown rot), and reduces bulk density to permit greater rates of root elongation away from soil borne pathogens such as *Rhizoctonia solani* and *Pseudomona*s spp. (Simpendorfer *et al.* 2002). Movement to RT or NT must factor these changes and the capacity for varieties to tolerate and preferably resist biotic constraints to growth (see Chapter 11).

Globally, RT and NT have been associated with increased incidence of both soil-borne diseases including take-all (*Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici* J. Walker), pythium seed and root rot (*Pythium* spp.), rhizoctonia root rot (*Rhizoctonia solani* Kuhn), common root rot (*Bipolaris sorokiniana*) and crown rot (*Fusarium pseudograminearum*) (Bockus and Shroyer 1998, Wildermuth *et al.* 1997), and leaf diseases including yellow spot (*Pyrenophora tritici-repentis* (Died.) Drechs), fusarium head blight (*Fusarium graminearum* Schwabe), septoria tritici blotch (*Mycosphaerella graminicola*.) and septoria glume blotch (*Stagonospora nodorum* (Berk.) Castellani & E. G. Germano) (Bockus and Shroyer 1998).

Crop rotation and fungicides are key to control many of these diseases as genetic resistance either does not exist, is partial in its control or is genetically complex. That said, significant breeding efforts for improved resistance to *Septoria tritici* and glume blotch, yellow spot, crown rot and *Pratylenchus thornei* for reduced-tillage systems are delivering wheat varieties with improved tolerance to these key diseases (McIntosh 1997, see Chapter 11).

Shorter stem lengths to reduce stubble loads

Significant amounts of stubble following harvest could previously be burned or grazed. With widespread adoption of CA, growers are less willing to use such techniques to deal with sometimes as much as 10 t/ha of residual leaf and straw. Further, efforts to speed harvest and thereby reduce the cost and duration of harvesting has prompted identification and adoption of innovative technologies such as use of stripper fronts borrowed from other crops. Furthermore, the retention of crop residues is widely regarded to reduce soil evaporation and enhance WUE. The move from tall to semi-dwarf cereals has changed the allocation of assimilates away from straw to grain to reduce crop lodging and increase crop yields. Total biomass has remained largely unchanged with increases in grain number reflecting increases in partitioning (or ‘harvest index’). As indicated, the green revolution GA-insensitive *Rht1* (syn. *Rht-B1b*) and *Rht2* (*Rht-D1b*) dwarfing genes are present in many of the world’s semi-dwarf wheats and so represent the most commonly adopted dwarfing genes in wheat breeding programs globally (Rebetzke *et al.* 2012a).

There is opportunity to reduce height further through the development of doubled- or sesqui-dwarfs: doubled-dwarfs containing combinations of GA-insensitive and -sensitive dwarfing genes (Rebetzke *et al.* 2012b). Figure 4 summarises changes in grain yield with reduction in plant height for a range of different dwarfing gene near-isolines (NILs) evaluated under irrigation at Yanco NSW in 2018. Reductions in plant height were associated with increasing grain yield up to a maximum of *c.* 65 cm height whereupon further reductions in height were linked to reductions in grain yield. Compared with the tall recurrent parent Halberd, almost all single-dwarf NILs were significantly greater in grain yield (except for the extreme height-reducing, GA-insensitive *Rht3* and *Rht10* NILs). Further reductions in plant height in the weaker sesqui-dwarfs were associated with additional increases in grain yield through greater harvest index (data not shown). By contrast, the extreme height and yield reduction with *Rht1+Rht2* doubled dwarfs reduces their potential. Extreme height reduction in cereals is problematic given their reduced capacity for mechanised harvest and reduced biomass and yield, especially in very dry seasons.

The 10 to 15 cm reduction in stem length (Figure 4) and greater harvest index with sesqui-dwarfs highlights their potential to reduce crop residues. Given the now widespread development of markers linked to these dwarfing genes it should be straight-forward to select and enrich for combinations of key dwarfing genes early before the expensive process of yield and quality testing. Further, the physiology of the GA-sensitive dwarfing genes provides opportunity for use of plant growth regulators to manage crop architecture for different times of sowing and seasonal conditions.

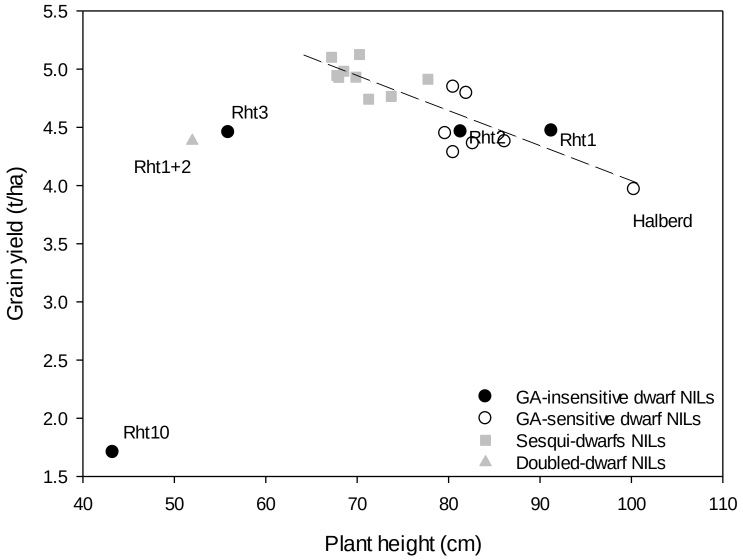

Figure 4. Relationship of plant height and grain yield for gibberellic acid (GA) -insensitive and -sensitive single and doubled dwarfing gene near-isolines (NILs), and original tall parent Halberd when grown with partial irrigation at Yanco Managed Environment Facility in 2018 (Line of best fit is Y = 7.061 - 0.031.X, $r^2 = 0.74$, $P<0.01$)

Awnless cereals for frost-prone regions

Drought- and frost-affected crops have reduced grain yields and quality and, owing to significant on-farm input costs, their incidence later in the season can result in a substantial loss of profitability to growers. Frost costs the Australian grains industry ~$700M AUD each year in direct costs (An-Vo *et al.* 2018). Affected crops may be fed to livestock but enterprises without animals have little option but to cut and bail for hay that has significantly reduced value. This reduced value reflects the presence of the awns – 'thread-like appendages extending from the tips of each spikelet'. All Australian wheat varieties lacked awns until delivery in the 1970s of *Rht1* and *Rht2* dwarfing gene wheats from CIMMYT containing awns. Dried awns are sharp and brittle, and can penetrate the gums and cheeks of animals when grazed. Awns have also been linked to increased pre-harvest sprouting and weather damage (King and Richards 1984), greater disease susceptibility in the ear and developing grain, and a predisposition to frosting of the ear itself (R.A. Richards pers. comm.). There is strong grower interest in a return to awnless cereals, and their potential for grazing and baling for hay in main-season sown crops. This interest is particularly strong in regions with a greater risk of frost damage at flowering.

Long awns are considered an important component trait of the high yielding wheat ideotype, particularly for wheat grown under water-limited conditions (Reynolds and Tuberosa 2008). Studies have demonstrated a grain yield advantage for awned wheats of up to 16% and particularly under drier conditions (*e.g*. Motza and Giunta 2002). Yet awns are often the first photosynthetic organ to desiccate under drought, and commonly senesce well before senescence of the upper canopy. In experiments conducted across 23 irrigated and rain-fed environments in Australia and Mexico, grain yields were the same for more than 40 BC_1F_6-derived awned and awnless NILs representing four genetic backgrounds (Rebetzke *et al.* 2016). Awnless wheats produced significantly greater numbers of grain per spike (+5%) reflecting more fertile spikelets and more grain in tertiary florets. The increased grain number was compensated by reductions in grain size (-5%) and an increased frequency of 'screenings' to reduce seed-lot quality of awnless NILs. It appears that allocation of assimilate to large and rapidly developing awns decreases spikelet number and floret fertility to reduce grain number particularly in distal florets. Kernel size is subsequently increased to reduce screenings and increase test weight particularly in droughted environments. Despite the average reduction in kernel size, awnless lines were identified in most backgrounds that combined higher grain yield with larger grain size, increased grain protein and reduced screenings.

Is there a place for late-sown cereal varieties?

Australian cereals are bred and managed for typically early-to-late May sowings. A return by breeding programs to the development of longer-season wheats for early sowing demonstrates the capacity to modify the timing of vegetative and reproductive growth to increase water use efficiency and provide valuable feed in mixed farming operations where the likelihood of early rainfall is high (Hunt *et al.* 2019, see also Chapter 18). New cereal varieties with appropriate vernalisation and photoperiod genes have been released with advanced breeding lines from across multiple breeding programs currently in the Australian NVT system (Flohr *et al.* 2018).

In reality, the likelihood of later sowing opportunities is much greater than for early sowing throughout much of the Australian wheat-belt. Yet there are no varietal wheat options for late-sowing (*i.e*. mid-June to mid-July), and late sowing is commonly associated with large reductions in grain yield (Shackley and Anderson 1995). Late-sown cereals have significant potential in:

- maintaining grain yields in regions where rainfall necessary for germination and early growth is late;
- managing herbicide-resistant weeds through double-knock herbicide strategies (see Chapter 10);
- delaying flowering to avoid frost in frost-prone areas; and
- more cost-effective nutrient management to reduce the risk of over/under supply of nitrogen with shorter duration crops.

In a farming systems context, a competitive, high biomass, early flowering cultivar for late-sowing would give farmers additional flexibility to plan and adjust their sowing operations with greater precision. More crop could be sown with an ideal agronomic package, the implication being that farmers could achieve higher average yields across the farm, and make better use of machinery capital, where the effective sowing window for wheat is increased with changing climate. It would also give additional opportunities for the use of double knockdown herbicide strategies in seasons with a late break.

There is potential to further exploit genotype × management interaction in development of rapid growing wheat varieties with potential for very late sowing. Growers have expressed strong interest in access to higher biomass cereals for late-sowing with 78% of 200 growers surveyed on social media (Twitter®) in 2018 in support of such varieties (G.J. Rebetzke unpub. data). Previously, more vigorous barley and triticale varieties, and wheat varieties like ‘H45’, could be sown mid-to-late July to outcompete late-emerging weeds and produce high grain yields. Commercial breeding programs have released developmentally faster wheat varieties including ‘Zippy’ and ‘Axe’. However, uptake by growers has been poor as, unlike H45, these recent wheat varieties have slow leaf area development resulting in reduced biomass and lower grain yields. Australian wheats are very conservative in their early shoot and root growth (*e.g*. Figure 5). Genetic variation for rapid early growth is available globally, and the CSIRO has been using novel S1 recurrent selection to accumulate rapid growth genes from 28 overseas wheats to increase early leaf area and biomass, and early root growth (Figure 5).

Conclusions

Wheat breeders have been successful in maintaining genetic gains of near 0.6% per year despite the widespread adoption of CA and associated changes in wheat-based, farming systems and increasingly variable climate. This gain has been achieved without compromising grain quality and resistance to key diseases particularly the different rust pathogens. Breeders will continue to release varieties addressing a wide range of farming systems needs but there is the real likelihood of future reduced genetic gains owing to an increasingly narrowing genetic base together with the potential for rapid gene fixation with genomic selection. Further, climate variability will likely increase genotype × environment interaction in breeders’ nurseries and the National Variety Trials to reduce confidence in selection and the identification of higher-yielding, broadly-adapted genotypes.

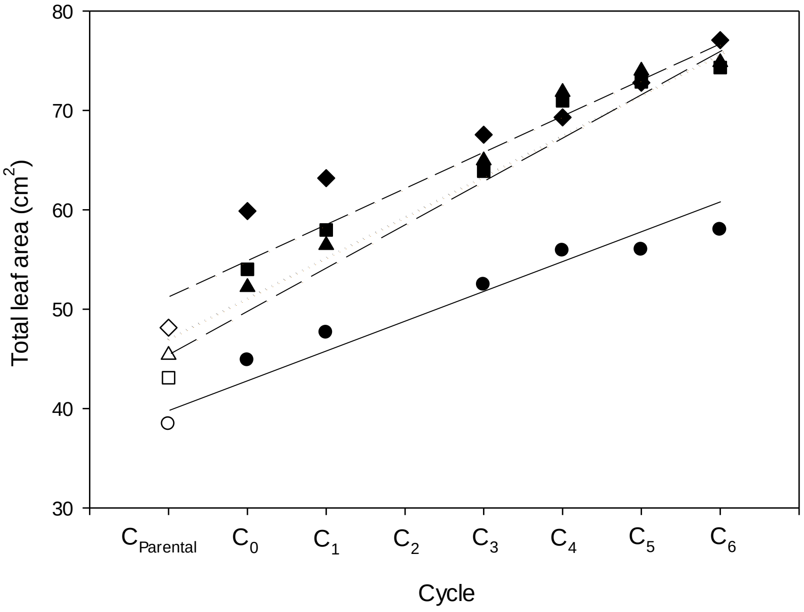

Figure 5. Relationship between cycle number and mean total seedling leaf area measured in four environments: Sow 1 (○; $r^2 = 0.93$**); Sow 2 (□; $r^2 = 0.94$**); Sow 3 (◊; $r^2 = 0.93$**); and Sow 4 (Δ; $r^2 = 0.95$**) (note that cycle 2 lines were accidently discarded during long-term seed storage) (Zhang *et al.* 2015)

Future crop varieties will require greater skill and attention in their selection around new disease and insect threats, greater weed competitiveness, tolerance of higher air and soil temperatures and drought through grain-filling, and with optimised flowering times to reduce the potential for damage from frost. There will also be changes to crop management that will require genotypes with new traits. Consideration towards a physiological framework in breeding is appealing as it allows for the creation of idealised genotypes targeting improved adaptation to those constraints limiting productivity. Further, such a framework permits the identification of new parental germplasm containing those genetics currently not present or at low frequency for implementation in breeding programs (*e.g.* weed competitiveness, high biomass for late-sowing and greater coleoptile length, modified root architecture). However, uptake of new output traits and genes will require clear and robust value propositions to effect changes in long-standing breeding objectives while their incorporation, selection and delivery in new varieties necessitates open and regular communication between the agronomists, physiologist, molecular biologist and the breeder.

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