Chapter 2
History of Wheat Breeding: A Personal View

R. A. (Tony) Fischer

Abstract For more than a century, breeding has delivered huge benefits as a major driver of increased wheat productivity and of stability in the face of inevitable disease threats. Thus, the real cost of this staple grain has been reduced for billions of consumers. Steady breeding progress has been seen across many important traits of wheat, currently for potential yield averaging about 0.6% p.a. This yield progress continues to rely of extensive multilocational yield testing but has, however, become more difficult, even as new breeding techniques have improved efficiency. Breeding will continue to evolve as new approaches, being proposed with increasing frequency, are tested and found useful or not. High throughput phenotyping (HTPP), applying modern crop physiology, and molecular markers and genomic selection (GS) are in this phase right now. Such new techniques, along with pre-breeding for new traits, will likely play a larger role in this future improvement of wheat. New tools will also include genetic engineering (GE), as society's need for its benefits become more urgent. The steady privatization of breeding seems unlikely to cease in the developed world but will continue to struggle elsewhere. It would seem wise, however, that a significant portion of the world's pre-breeding research remains in the public sector, while maintaining close and equitable contact with those delivering new varieties.

Keywords Yield progress · Plant pathology · Grain quality · Biometrics · Pre-breeding · Privatization

2.1 Learning Objectives

- To know about and be proud of the past achievements of wheat breeders
- To understand the successful techniques making for this progress and the importance of breeding × agronomy interactions
- To be aware of the new breeding technologies but mindful of the need for validation in the real world

R. A. (Tony) Fischer (✉)
Agriculture & Food, CSIRO, Canberra, Australia
e-mail: tony.fischer@csiro.au

M. P. Reynolds, H.-J. Braun (eds.), *Wheat Improvement*,
https://doi.org/10.1007/978-3-030-90673-3_2

- To appreciate the evolution towards larger multidisciplinary breeding teams and the continuing key role of teamwork and strong leadership.
- To recognize the ongoing place for public research in wheat breeding which is steadily privatizing.

2.2 Introduction

I am not a wheat breeder, rather I have been a crop physiologist/agronomist specializing in wheat for most of my long career in Australia and in Mexico at CIMMYT. Therefore, it is both an honour and a special challenge to contribute to this book targeting young scientists, many early in wheat-breeding careers. The challenge is to tell you something of past and present wheat breeding that is of value for your future career in agriculture. I say agriculture because many of us finish in other often-related fields than where we start. This is not bad, for I am firmly believe in scientific breadth, as well as depth in some speciality, likely to be breeding in your cases. What I have in mind is commonly described as the T-trained person, the “jack-of-all trades and master of one”.

The inspiration that one derives from being amongst leading wheat breeders is important. In my case, in the early 1960s it was Albert Pugsley and Jim Syme at Wagga Wagga (where William Farrer Australia’s famous first wheat breeder had worked), then from 1970 to 1975 at CIMMYT, Norman Borlaug, Frank Zillinsky, Glenn Anderson and Sanjaya Rajaram, and all the US and Canadian breeders who were regularly in NW Mexico to attend to their winter nurseries of spring cereals. My second period at CIMMYT (1988–1995) as Wheat Program Director again put me in touch with wheat breeding around the world. For you, there will be others, your contemporaries, but I recommend that you read about your predecessors, especially Borlaug (e.g., Vietmeyer’s 2011 book [1], see also the vintage Borlaug 1968 IWGS presentation below). Successful wheat breeders of my vintage were very dedicated to breeding, hardworking, spending long hours in the nurseries and field plots, very focussed on their breeding goals and prepared to persist decades to achieve them. They led small teams of scientists and technicians with a firm hand and changed successful breeding strategies reluctantly. As a young scientist at the International Wheat Genetics Symposium in 1968 in Canberra, I witnessed crop physiologist Professor Colin Donald deliver for the first time his radical concept of a wheat ideotype [2]; it did not go down very well with the assembled breeders from around the world. Borlaug’s description of his already remarkably successful breeding program in Mexico, with its unique emphasis on efficiency and broad adaptation, along with his fiery ridicule of bureaucrats and “band wagons” for hampering scientific progress in agriculture, was much more popular [3]!

Since that congress when my wheat career was just beginning, many things in wheat breeding around the world have gradually changed, while breeding progress in key traits has been maintained almost uninterrupted. Lessons have been learnt, supporting technologies have advanced in almost unimaginable ways, and the organization of breeding has altered notably. Some things have however not changed., nor should they as we look to the near future. The rest of this Chapter will deal with these issues, briefly given the space available and since many will reappear in detail in later Chapters.

2.3 Past Wheat Improvement at the Farm Level and in the Breeders' Plots

World *wheat yield* has increased remarkably linearly at about 40 kg/ha/y over the last 60 years (Fig. 2.1); for projection to meet future demand, the key number is this slope relative to today's yield of 3.5 t/ha, namely 1.16%. Fischer and Connor [4] argue that while this rate of increase is probably adequate to balance world wheat demand growth, a greater rate would help poor consumers by reducing pressure on prices, would protect against negative contingencies, and would reduce the pressure for greater wheat area (including clearing new land to achieve this). Yields in most wheat-growing countries and regions reveal similar close-to-linear increases at various rates clustered around the world figure [5] (also see Chap. 4). For example the irrigated Yaqui Valley of NW Mexico, where CIMMYT's major yield testing and selection is undertaken, shows one of the higher rates of absolute increase (Fig. 2.1,

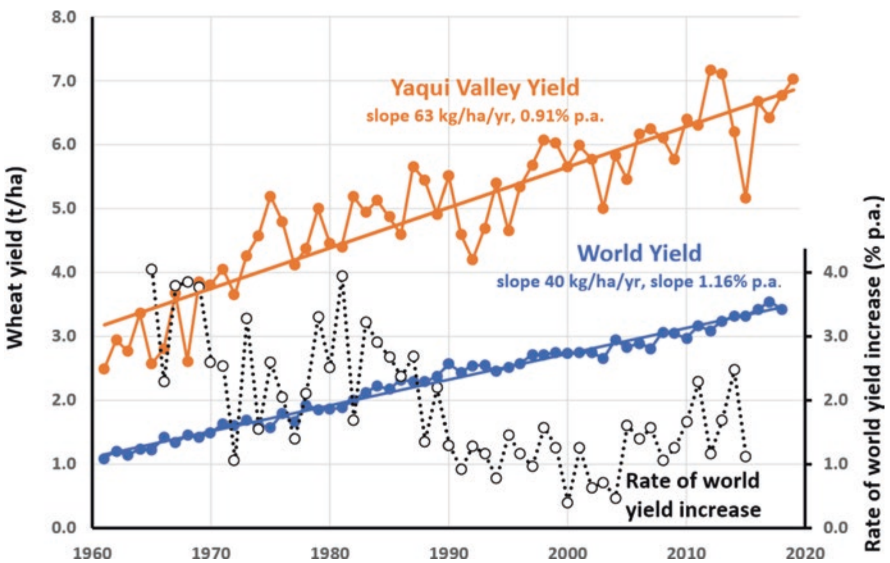

Fig. 2.1 Annual wheat yields from 1961 to 2019 for the world and the Yaqui Valley of northwest Mexico, also, relative rate of increase of world wheat yield with time based on 7 year moving average and plotted against the middle year. Note % p.a. slopes are expressed relative to the yield at the end of any period. (Sources: World yields (fao.org/faostat/en/#data/QC, accessed 17 September 2020); Yaqui Valley yields (various official sources in the State of Sonora, Mexico))

63 kg/ha/year, but currently only 0.91% p.a.), reflecting this breeding effort and the concurrent modernization of crop management by the Mexican farmers.

The percentage rate of increase in yield is a reasonable measure of productivity progress. Although it has fallen steadily with time – in % not in kg/ha – as shown for the world in Fig. 2.1, it is still strongly positive. I say wheat improvement because the yield progress has involved new varieties, new agronomy (or crop management), and the positive interaction between the two (G × M). The key agronomic changes include mechanized planting giving better plant populations and more timely sowing, increased fertilizer use, more irrigation, and improved weed and disease control. There has been endless discussion as to whether breeding or agronomy has played the greater role, but neither discipline alone could have achieved even half this progress; they have been complementary throughout, with agronomy continuing to create new challenges and opportunities for breeding.

The primary target of modern wheat breeding has been increased yield, through eliminating yield-related deficiencies such as lodging and shattering, fixing optimum height and flowering date, and seeking to raise inherent yield. *Breeding progress for yield* is commonly measured in vintage trials [6]. If management is excellent, water adequate, and diseases are absent or controlled, this measures potential yield (PY) under the best agronomy and weather of the time, thus including progress due to G × M. If water supply is inadequate as in many rainfed regions, we have water-limited potential yield (PYw). There are now new ways to measure such progress for multilocational multiyear national trials [6]. Throughout it is argued that progress is most usefully expressed, as above, relative to yield of the most recent cultivars in any series. Recent reports of breeding yield progress in wheat from around the world have been complied [7]: from 34 case studies the average rate of progress was 0.58 ± 0.034 % p.a., ranging from 0.2% to 1.1% p.a. There was no significant difference in rates of progress between spring and winter wheats, nor between PY and PYw. Recent rates of breeding yield progress with rice, maize and soybean averaged also around 0.6% to 0.7% p.a. [7].

Wheat breeders made yield progress under a *variety of breeding schemes* suitable for self-pollinated crops (see Chaps. 5 and 7). What is common to all systems is massive investment in yield measurement in field plots, beginning as early as F5 in home fields, then in steadily reduced numbers of advanced lines at increasing numbers of locations representing the target population of environments (TPEs). Since the middle of last century there has been no big change in this general scheme; new developments have continually been proposed, and if worthwhile, incorporated into the scheme to improve breeding efficiency.

Borlaug's unique strategy of shuttle breeding was controversial: it delivered greater efficiency through two generations a year but was novel in that selection alternated between two distinct environments in Mexico, preceding widespread testing in collaborating programs around the world. This testing was adopted by CIMMYT when it began in 1966 which, along with ICARDA starting in the 1970s, and building on early efforts by USDA and FAO, gave rise to the extensive and unique international network for testing and germplasm distribution [8], which continues to this day. The strategy of selecting and testing in many environments has been vindicated with the production of a number of superior cultivars having *broad adaptation,* meaning good performance across locations and years (e.g., Siete Cerros 66, Pavon 76, Anza (via California), Seri 82, Attila or PBW343 (via India), Borlaug100). Other breeding efforts have also delivered a small number of varieties which have dominated over large and seemingly diverse regions (e.g., Florence Aurore from Tunisia, Gabo from Australia, Bezostaya from Krasnodar in Russia, Capelle Deprez from France). As mentioned, the relative yield progress seen in PYw, or at lower soil fertility levels, is unabated compared to that under PY conditions and what's more, the cultivar ranking generally changes little across a large range of such resource inputs (e.g., recent references [9, 10]). In fact, after allowing for differences in flowering date, which can be important in particular years, amongst low latitude spring wheats there are few significant crossover interactions in the absence of disease; the characteristic fan pattern of variety yield response to site mean yield, popularized long ago by Finlay and Wilkinson [11] in barley, remains valid even today. Finally, some advocate intrinsic yield stability, which is of limited value since it tends to mean low average yield; yield responsiveness (to good years and management) is what modern farmers need!

In the case of wheat, the second target for breeding, taking up to one half of the breeding effort, is aimed at *biotic stress resistances*, strengthening, and then maintaining genetic resistance to diseases (see Chaps. 8, 9, 19 and 20). This is adding a useful type of stability but is rarely related to PY. Also included is a smaller investment directed against insect pests and nematodes (see Chap. 20) for which biocides are less effective and more dangerous. Plant pathology has been the discipline most closely linked with wheat breeding since its outset, indeed many pathologists have become successful breeders. The first single genes identified were major rust resistance genes, and many years later, in 2003, the first wheat rust gene was sequenced. Being a serious disease that knows no borders, rust was the reason for the first international screening nurseries, as already mentioned. Since then, this collaboration has grown and a host of major and minor rust resistance genes have been identified, catalogued, sometimes sequenced, and freely shared and utilized by breeders around the world. Early warning systems and ongoing deployment of new major genes and more durable minor ones have meant that wheat yield losses due to rust are lower now than ever, notwithstanding the apparent uniformity of modern wheats. This is a powerful tribute to unfettered international collaboration amongst wheat breeders and rust pathologists; the current Borlaug Global Rust Initiative (BGRI) is the latest iteration in this process.

Since there are so few yield losses due to rust these days, rust breeding is now directed more at maintaining resistance with the deployment of more durable resistance genes including GE solutions. Attention has also passed to the multitude of other diseases of wheat, for many of which host plant resistance can be effective. There is, however, never any room for complacency, with new diseases and new virulences likely to threaten wheat at any time and readily spread in our interconnected world. The latest wheat example is the occurrence of a wheat blast (*Magnaporte oryzae* pathotype *Triticum*), first seen in Brazil in 1985, and now in Asia (Bangladesh in 2016) and Africa (Zambia in 2018). Genetic biotic stress resistance, including GE solutions, will probably become even more important if societies only partly justifiable fear of biocides continues to grow.

The *industrial quality of wheat* (its suitability for products for human consumption, in particular the many forms of bread and noodles) has been the third major target for breeders (see Chap. 11) and an important element of productivity gain not captured in yield statistics. Rapid low-cost tests for various quality traits were widely used for screening early generations from the 1960s onwards, and overall industrial quality has generally been improved even in the face of the inevitable decline in grain protein concentration with yield improvement. (e.g., [12, 13]). Market price premiums for desirable quality are essential, so farmers as well as consumers see the benefit.

In the last 30 years, concern has grown for the *nutritional and health qualities* of wheat, especially its inherently low concentrations of iron and zinc, values which had tended to fall as wheat PY had been lifted by breeding. A variety have recently been released in India with improved grain zinc levels, and there are genotypes in the pipeline with other health-giving properties (e.g., high iron, soluble fibre, fructans). These issues are likely to receive more attention in the future (see Chap. 12).

2.4 Past Activities Associated with Greater Breeding Success and Efficiency

Genetic variation is essential to breeding success: especially since the middle of the twentieth century there has been a big increase in collection and conservation of *wheat genetic resources*, ranging from wild wheat ancestors through land races to named varieties and genetic stocks (see Chaps. 16, 17 and 18). Fortunately, genetic resource scientists moved quickly to collect such materials as modern varieties began to replace land races in farmers' fields. However, because of linkage drag, the utilization of these materials by breeders has been slow. Disease resistance and some quality genes are the best examples of useful introgression into modern cultivars. Also, some accessions have now been identified as sources for increase in yield, this includes 1B/1R, 1A/1R, 2NS, and the LR19 translocation from *Agropyron*. This process has been helped partly through the large effort that CIMMYT has put into creating synthetic wheats with new accessions of *Triticum tauschii*, and incorporating them into its breeding program where they have demonstrated both increased PY and PYw; success with such material in Sichuan, China, is a recent example [14]. Wheat genetic resources are safely conserved but their exploitation in breeding, which is a form of pre-breeding, remains too slow due to underfunding.

Breeding efficiency over the last 50 years has been greatly facilitated by *allied fields of technology and science* combining with breeder ingenuity. This includes the mechanization of seeding and harvesting (see Chap. 15), the acceleration of generation advance (see Chap. 30), and automation of all repetitive tasks, including NIR-based measurement of quality traits and molecular markers for difficult to measure qualitative traits (see Chap. 28). Biometrics has brought large *advances in trial design and computing* for processing of data and applying complex algorithms to field measurements correcting for spatial variation in ever more efficient plot designs (see Chap. 13). This progress is probably now reaching the limits imposed by measurement error and soil spatial variation. This is a special problem as the relative yield gains being sought become smaller (note 0.6% p.a. is only a 3% jump every 5 years). Finally, the ever-present G × E (genotype × environment) driven by both locational and annual variation in E remains a special challenge. Many statistical models have been applied over the years, with factor analytics the most recent (see Chap. 3). Also, crop simulation modelling is valuable for characterizing environments, especially rainfed ones (e.g., [15]. Such modelling is now based on sufficiently-sound physiological knowledge to also allow the exploration *in silico* across TPEs of the effect of changes in some key traits (e.g., phenological ones), but such modelling is very unlikely to be a substitute for accurate multilocational yield testing (see Chap. 31). The past failure of many breeders to adequately measure their environments (soil, weather), and thus facilitate a better understanding of the basis of G × E, has always been a weakness, but national and global weather services are now filling this gap.

In the late 1960s it was expected that *physiology* would help breeders accelerate yield progress, explaining why CIMMYT first hired me, a disciple of the physiological thinking of Lloyd Evans and UK physiologists, especially Roger Austin, and breeder John Bingham. Much is now known about the crop physiological changes behind the yield progress since 1960: generally flowering date is unchanged or slightly earlier, height is substantially reduced (from >120 cm to <90 cm), harvest index has increased as has grain number (/m^2), but not necessarily spike number (/m^2). Stomatal conductance and leaf photosynthetic rate have increased along with leaf erectness, and lately biomass is also increasing, as is grain weight in some places. Apart from earliness and height reduction, and with a few exceptions such as erect leaves, almost nowhere in the world were the other changes either pre-emptively identified by crop physiologists, and/or deliberately selected by wheat breeders. There are lessons in this observation: maybe physiology should not have been so focussed on retrospective studies, missing opportunities for testing traits in breeders' populations and in early generation indirect yield selection, some of which such as harvest index, fruiting efficiency and stomatal conductance/canopy temperature are discussed in depth recently in Fischer and Rebetzke [16]. One constraint was that physiological studies often paid little attention to the crowded crop situation in which yield is to be delivered. Donald [2] in 1968 pointed out how much smaller than the isolated wheat plant was the plant under heavy competition in the crop and argued that for higher yield the crop plant needed traits that made it less competitive and more "communal"; lately this neglected notion has received solid support in retrospective studies of yield progress. Another constraint with early physiology was that trait measurement was too slow/expensive for use in selection by breeders, and a final constraint, physiology often did not work sufficiently closely to and cooperatively with real breeding programs. HTPP has been proposed lately as one way of dealing with the trait measurement constraint (see Chap. 27), but there still needs to be an intimate link with open-minded and well-resourced breeders.

These days widespread *pre-breeding* aims to transfer to elite materials (and validate) potentially useful physiological (and morphological) traits, for their subsequent easier incorporation into better varieties by other breeders who generally don't have the resources for risky pre-breeding (see Chap. 25). Dwarfing genes, alternatives to those which catalysed the Green Revolution, are a potentially useful target for such exploitation. Another current use of physiological knowledge, undertaken in CIMMYT Wheat Fisiologia, is in the selection of parents with measured physiological traits which are likely to be complementary for yield [17].

Over the last century, other new techniques to aid crop genetic improvement have, like physiology, been highlighted but have often failed to realize their early claims of success. Simmonds [18] disparagingly called them "***band wagons***" and his list includes induced polyploidy, mutation breeding, physiology (again), and somaclonal variation; F1 hybrids for wheat could also be added, but that effort continues in several breeding programs, encouraged by successes with hybrid rice since the 1980s. The lesson for the breeder regarding band wagons, and they appear with regularity, seems to be to hasten slowly, change currently successful programs gradually and only after solid evidence of efficiency gains has been gathered. We shall return to this, for Simmonds also included biotechnology in his bandwagon list!

2.5 Some Future Considerations for Breeding

History is of little use if it doesn't guide the future. Field grown wheat will be around for your lifetime and field testing of yield in crop-like plots will remain paramount. But what may change are the breeding tools, the natural environment, and the agronomy. Indeed. innovation never ceases and wheat breeding is now engaging with a suite of new tools (band wagons if you like) proposed to improve the efficiency and effectiveness of the breeding, as described in the Chaps. 16 to 32 on translational research. Unfortunately, space limits attention to these issues here.

The first consideration which must be emphasized, however, is an ongoing problem with field testing, namely *bias in plot trials*. In small plots (< say 3 m^2) which are harvested without trimming, yield can easily be biased by as much as the breeding progress expected to be achieved in 5 years (only 3% at best). There is little doubt that cultivars can perform differently in plot ends and edge rows than in inside bordered-rows, and that where paths are narrow (<50 cm) plants in edge rows can compete for light and nutrients (and moisture if rainfed) with adjoining plots; all this distorts or even negates their performance relative to inner rows [19]. Larger sown plots and/or edge trimming is essential, while certain simple measurements (e.g., path NDVI) can help detect and perhaps correct for such bias.

New tools offer help with the biggest specific challenge facing wheat breeding, the need *to continue to lift potential yield*. After 100 years of success in this area, relative rates of breeding progress for yield have, as we have seen, slowed to currently around 0.6% p.a., yet breeding investment in real terms has probably increased. Does this herald an approach to the biological limit for yield? Probably it does. But can new tools and pre-breeding lift rate of progress and/or ultimately push back this limit? Is greater progress to be achieved by focussing now more on specific adaptation, better exploiting the locational component of G × E which is so often noted in multilocational trails (see Chap. 3)? Will seed production and heterosis be improved enough for F1 hybrid wheat to become a reality? These are exciting questions which will be resolved one way or another in the next 20 years of your breeding careers.

HTPP and *GS* have already been mentioned for predicting yield advance; together they could be even better (e.g., [20]). GS allows the shortening of the generation cycle: while HTPP must be applied to segregating populations if it is to be truly useful (e.g., [16]). The new environments predicted by climate change modellers could be another target, but this needs to proceed cautiously because of the uncertainties. Besides the best way to adapt to climate change is to be field testing widely, due to the simple fact that a significant proportion of years across locations in any decade predict better than any model those of the next decade!

GE (often less usefully abbreviated to GM) and gene editing must be part of the near future for wheat breeding, but they will have great difficulty raising potential yield simply because of the genetic complexity of this quantitative trait, the product of millennia of evolution and over a century of breeding. The numerous promising reports on GE crop plants in controlled environments, where mainly photosynthetic, partitioning and drought resistance traits were targeted, have so far failed to deliver extra grain yield in the field [21, 22]. However the first GE event to enhance wheat yield (HB4, see [23] has now been approved in Argentina: substantial yield increases (>20%) have been measured in multi-year large plots and fields when dryness has restricted yields to less than 2 t/ha, while there are no yield penalties at higher levels. Another promising wheat GE event has been the modification of pericarp expansins to give larger grains apparently without the compensatory negative genetic trade-off commonly seen in crops between grain weight and grain number ($/m^2$) [24]. In the meantime, we desperately need *GE to enhance other traits* besides potential yield: the scientific prospects are much better because many such traits are less complex than yield, and there is now often precedent from other crops. Such traits in wheat could include improved nutritional value, such as high iron wheat [25], better resistance to rust (see Chap. 19), or environmentally desirable traits like biological nitrification inhibition. Regulatory barriers to GE traits will fade as society accepts their proven safety and realizes it cannot do without their manifest benefits.

Passing to the *changing natural environment of cropping*: CO_2 is rising inexorably (currently about 2 ppm p.a.), related to this climate is changing (largely warming but maybe drying in middle latitudes, and greater frequency of extreme heat events). Atmospheric pollution (aerosols, ozone in particular) is rising (and declining in some regions where pollution controls are enforced). Finally, water scarcity in irrigated systems is increasing, especially in Asia, due to overextraction of aquifers. The optimal genetic makeup of cultivars will interact with all these changes.

Related to natural environments changes are those in *wheat agronomy, and the cropping, farming and social systems* within which the wheat crop is grown, the input and product prices, and, ultimately, our social licence to farm, which relates to the increasing regulation of cropping practices. Breeders need always to be alert to these developments and hence remain in contact with agronomists and farmers, policy makers and ultimately the public. One example suffices: in southern Australia, Flohr and colleagues [26] recently describe a striking G × M change. Conservation agriculture had improved fallow storage of moisture; along with a gradual shift in rainfall patterns (probably linked to climate change), this opened opportunities for earlier than normal planting of wheat (April instead of May-June). Planting date could be advanced 4–8 weeks, but the optimum flowering date in the spring remained unchanged. Only new combinations of the wheat phenology alleles could deliver cultivars giving optimal flowering dates when being planted much earlier; essentially this meant a switch from spring wheats to fast winter types. The longer crop cycle (sowing to anthesis) had the bonus of bringing deeper roots; in many situations yield improved notably. This new system often requires deeper seeding hence it needed wheats with longer coleoptiles (= alternative dwarfing genes to the Norin10 ones) which was enabled by pre-breeding. Since the early planted winter wheat can deliver substantial winter forage to grazing sheep or cattle without grain yield loss, the whole transformation is aided by the notable rise in the ratio of meat/wheat prices on world markets. Of course, the wheat farming system must have access to grazing animals, which is the case in Australia (and West Asia-North Africa). This serves to remind us that wheat is part, not only of a cropping, but also a farming system.

2.6 Organization and Funding of Wheat Breeding

Ultimately the success of plant breeding (and your jobs as breeders) depends on how this complex task is organized and financed. The roots of modern breeding lie in the late nineteenth century, just before the rediscovery of Mendel's notions of genes and inheritance in 1900. Even then there were *private and public breeding organizations,* although *w*heat breeding has rarely had the protection of secrecy provided by commercial F1 hybrids (as with maize for example). Notwithstanding this, as time passed, the private wheat breeders became gradually stronger, especially in Europe. Plant variety protection under UPOV rules and seed sale royalties gave greater income security to the private sector, which had become formalized into farmer-owned cooperatives and companies. Following the 1964 Plant Variety and Seeds Act in 1964, a milestone was the full privatization of wheat breeding in the UK in 1987, in accord with the free market concepts of the time; there are valuable lessons in this disruptive experience [27]. Outside of Europe, apart from Argentina, the privatization of breeding was slower. However, this has now accelerated in the New World, especially USA and Australia but less so in Canada, and lastly has begun in Asia. Uniquely, in USA wheat breeding is supported by utility patents and licensing, accompanying check-off fees and royalties on seed sales, and in Australia support is entirely from end-point royalties on grain sales [28]. Payment for private varieties has always been a challenge with wheat since seed can and commonly is saved on-farm without fear of genetic change. Provided there is reasonable adherence to the relevant laws and regulations, the various schemes mentioned here have generally been successful in returning just rewards to the breeder and better varieties for growers.

Around 2020, the biggest multinational wheat breeding efforts are found in traditional breeding companies like Limagrain (French) and KWS (German) in Europe, where also there are several smaller ones such as RAGT Semances (France) and Staaten-Union, the latter uniquely strong in F1 hybrid wheat. Multinational life companies have, through mergers and takeovers in the last 25 years or so, also become significant players in wheat breeding: firstly Syngenta, then relative newcomers Bayer, BASF, and Corteva Agriscience: combining breeding and agricultural chemicals has both synergistic and, unfortunately, perverse elements. All these companies are moving cautiously into the developing world and the ex-Soviet Union, where there were only a few smaller home-grown private breeding companies (e.g., Mahyco (India), SeedCo (East Africa), Buck and Klein (both on Argentina)). Here the public system continues to take major breeding responsibility in the form of state and national wheat breeding institutions and some Universities; this will probably remain the case until and if F1 hybrid wheat becomes feasible. CIMMYT and ICARDA's wheat breeding which targets the developing world has, of course, remained public since its inception around half a century ago, with support from many governments, non-profit organizations and institutions. These two centers continue to play a vital role in supplying international trials of advanced breeding lines and facilitating collaboration amongst all of the worlds' wheat breeders, with germplasm and performance results distributed free of change to all *bona fide* breeders, whether public or private. Their impact has been huge [29]. With competing breeding entities in most countries, another very desirable component is publicly controlled independent testing of candidate varieties for yield and other important attributes, and the associated registration of new varieties. The final critical step in the breeding process is the national seed systems for getting new varieties to farmers (see Chap. 14).

Along with greater privatization and consolidation, wheat breeding has become obviously a big team effort, with the inevitable involvement of associated disciplines such as pathology, cereal quality and biometrics, aided often these days by service providers for routine trials and testing work. *Pre-breeding research* has emerged as a vital supporting activity, but generally is separated from breeding and still publicly funded, essentially because it is a long-term high-risk activity with potential benefits for society which are maximized if its fruits are widely shared. As mentioned, these activities range from genetic resource conservation, the discovery of novel useful genes (traits) in this material (or creation through GE or gene editing), and the incorporation of new traits into lines and populations having relevant modern genetic backgrounds for utilization by all breeders, commercial and public. Also included is strategic plant science aimed at understanding the physiological and functional molecular basis of important wheat traits, with a view to more efficient manipulation of the traits in breeding and selection strategies (see Chap. 28). It suffices here to emphasize that because of “market failure” pre-breeding research merits public investment, and this includes funding from major non-profit organizations as we have seen lately with the International Wheat Yield Partnership (IWYP) and the Heat and Drought Wheat Improvement Consortium (HeDWIC). In the future, more traits may be protected as intellectual property, as is usually the case with GE ones, but meeting equity goals will remain important to maximize benefit and societal acceptance.

The smooth transfer of products of pre-breeding in an equitable way so that all commercial breeders benefit is a challenge yet to be solved. Europe seems to have made most progress in imbedding independently funded pre-breeding research into the private breeding process in a mutually beneficial manner. CIMMYT and ICARDA’s wheat improvement teams are rare in that they have had for many years carried out pre-breeding alongside their breeding of advanced lines for variety release by NARS, but efficient in-house collaboration can still be challenging. How much further along would CIMMYT be if the early promise for yield advance seen with cumbersome stomatal conductance measurements on F2 plants [30] had been pursued a little longer, thereby encountering the huge efficiency gains in conductance measurement coming from infrared thermometry. This demands open and enlightened leadership, multidisciplinary teamwork, and adequate long-term stable financial support. Balancing this with the need to consider the endless stream of breeding innovations being proposed is a critical challenge: effective breeding programs should only be adopting new technologies when these have been tested in pilot mode and found to deliver!

2.7 Key Concepts

- The goals of wheat breeding have changed little, increased potential yield and host plant resistance remain paramount
- The technology and science of breeding has changed gradually but reliance on multilocational yield testing remains essential
- Genetic engineering and gene editing are starting to deliver valuable trait opportunities for breeding, as is innovative agronomy (examples in Sect. 2.4)
- Multidisciplinary breeding teams have become more important and their effective leadership remains a challenge
- Privatization of wheat breeding grows steadily, but there remains an essential role for the public sector breeding research and pre-breeding and a challenge linking it closely to variety production.

Acknowledgements The author thanks the Editors, and John Passioura and Richard Richards for their input, and especially Stephen Baenziger and William Angus for detailed comments on the manuscript.

References

1. Vietmeyer N (2011) Our daily bread; the essential Norman Borlaug. Bracing Books, Lorton
2. Donald CM (1968) The breeding of crop ideotypes. Euphytica 17:385–403. https://doi.org/10.1007/BF00056241
3. Borlaug NE (1968) Wheat breeding and its impact on world food supply. In: Proceeding of the 3rd international wheat genetics symposium Canberra 1968. Canberra, Australia, pp 1–36
4. Fischer RA, Connor DJ (2008) Issues for cropping and agricultural science in the next 20 years. Field Crop Res 222:121–142. https://doi.org/10.1016/j.fcr.2018.03.008
5. Fischer RA, Byerlee D, Edmeades GO (2014) Crop yield and global food security: will yield increase continue to feed the world, Monograph 158. Australian Centre for International Agricultural Research, Canberra. https://aciar.gov.au/publication/mn158
6. Fischer RA (2015) Definition and determination of crop yield, yield gaps, and the rates of change. Field Crop Res 182:9–18. https://doi.org/10.1016/j.fcr.2014.12.006
7. Fischer RA (2020) Advances in the potential yield of grain crops. In: Gustafson JP, Raven PH, Ehrlich PR (eds) Population, agriculture and biodiversity: problems and prospects. University of Missouri Press, Columbia, pp 150–180
8. Byerlee D, Lynam JK (2020) The development of the international center model for agricultural research: a prehistory of the CGIAR. World Dev 135:105080. https://doi.org/10.1016/j.worlddev.2020.105080
9. Voss-Fels KP, Stahl A, Wittkop B, Lichthardt C, Nagler S, Rose T, Chen T-W, Zetzsche H, Seddig S, Baig MM, Ballvora A, Frisch M, Ross E, Hayes BJ, Hayden MJ, Ordon F, Leon J, Kage H, Friedt W, Stützel H, Snowdon RJ (2019) Breeding improves wheat productivity under contrasting agrochemical input levels. Nat Plants 5:706–714. https://doi.org/10.1038/s41477-019-0445-5
10. Mondal S, Dutta S, Crespo-Herrera L, Huerta-Espino J, Braun HJ, Singh RP (2020) Fifty years of semi-dwarf spring wheat breeding at CIMMYT: grain yield progress in optimum, drought and heat stress environments. Field Crop Res 250:107757. https://doi.org/10.1016/j.fcr.2020.107757
11. Finlay KW, Wilkinson GN (1963) The analysis of adaptation in a plant breeding programme. Aust J Agric Res 14:742–754. https://doi.org/10.1071/AR9630742
12. Laidig F, Piepho H-P, Rentel D, Drobek T, Meyer U, Huesken A (2017) Breeding progress, environmental variation and correlation of winter wheat yield and quality traits in German official variety trials and on-farm during 1983–2014. Theor Appl Genet 130:223–245. https://doi.org/10.1007/s00122-016-2810-3
13. Guzmán C, Autrique E, Mondal S, Huerta-Espino J, Singh RP, Vargas M, Crossa J, Amaya A, Peña RJ (2017) Genetic improvement of grain quality traits for CIMMYT semi-dwarf spring bread wheat varieties developed during 1965–2015: 50 years of breeding. Field Crop Res 210:192–196. https://doi.org/10.1016/j.fcr.2017.06.002
14. Tang Y, Wu X, Li C, Yang W, Huang M, Ma X, Li S (2017) Yield, growth, canopy traits and photosynthesis in high-yielding, synthetic hexaploid-derived wheats cultivars compared to non-synthetic wheats. Crop & Pasture Sci 68:115–125. https://doi.org/10.1071/CP16072
15. Chenu K, Porter J, Martre P, Basso B, Chapman S, Ewert F, Bindi M, Asseng S (2017) Contribution of crop models to adaptation in wheat. Trends Plant Sci 22:472–490. https://doi.org/10.1016/j.tplants.2017.02.003
16. Fischer RA, Rebetzke GJ (2018) Indirect selection for potential yield in early-generation, spaced plantings of wheat and other small-grain cereals: a review. Crop & Pasture Sci 69:439–459. https://doi.org/10.1071/CP17409
17. Reynolds M, Langridge P (2016) Physiological breeding. Curr Opin Plant Biol 31:162–171. https://doi.org/10.1016/j.pbi.2016.04.005
18. Simmonds NW (1991) Bandwagons I have known. Trop. Agric. Assocn. Newsl. 11:7–10

19. Rebetzke G, Fischer RA, van Herwaarden AF, Bonnett DG, Chenu K, Rattey AR, Fettell NA (2014) Plot size matters: interference from intergenotypic competition in plant phenotyping studies. Funct Plant Biol 41:107–118. https://doi.org/10.1071/FP13177
20. Cooper M, Technow F, Messina C, Gho C, Totir LR (2016) Use of crop growth models with whole-genome prediction: application to a maize multienvironment trial. Crop Sci 56:2141–2156. https://doi.org/10.2135/cropsci2015.08.0512
21. Passioura JB (2020) Translational research in agriculture. Can we do it better? Crop & Pasture Sci 71:517–528. https://doi.org/10.1071/CP20066
22. Nuccio ML, Paul M, Bate NJ, Cohn J, Cutler SR (2018) Where are the drought tolerant crops? An assessment of more than two decades of plant biotechnology effort in crop improvement. Plant Sci 273:110–119. https://doi.org/10.1016/j.plantsci.2018.01.020
23. Gonzalez FG, Rigalli N, Miranda PV, Romagnoli M, Ribichich KF, Trucco F, Portapila M, Otegui E, Chan RL (2020) An interdisciplinary approach to study the performance of second-generation genetically modified crops in field trials: a case study with soybean and wheat carrying the sunflower HaHB4 transcription factor. Front Plant Sci 11:178. https://doi.org/10.3389/fpls.2020.00178
24. Calderini DF, Castillo FM, Arenas-M A, Molero G, Reynolds MP, Craze M, Bowden S, Milner MJ, Wallington EJ, Dowle A, Gomez LD, McQueen-Mason SJ (2020) Overcoming the trade-off between grain weight and number in wheat by the ectopic expression of expansin in developing seeds leads to increased yield potential. New Phytol. https://doi.org/10.1111/nph.17048
25. Beasley JT, Bonneau JP, Sánchez-Palacios JT, Moreno-Moyano LT, Callahan DL, Tako E, Glahn R, Lombi E, Johnson AAT (2019) Metabolic engineering of bread wheat improves grain iron concentration and bioavailability. Plant Biotechnol 17:1514–1526. https://doi.org/10.1111/pbi.13074
26. Flohr BM, Hunt JR, Kirkegaard JA, Evans JR, Trevaskis B, Zwart A, Swan A, Fletcher AL, Rheinheimer B (2018) Fast winter wheat phenology can stabilise flowering date and maximize grain yield in semi-arid Mediterranean environments. Field Crop Res 223:12–25. https://doi.org/10.1016/j.fcr.2018.03.021
27. Galushko V, Gray R (2018) Twenty five years of private wheat breeding in the UK: lessons for other countries. Field Crop Res 223:12–25
28. Alston JM, Gray RS (2013) Wheat research in Australia: the rise of public-private-producer partnerships. EuroChoices 12:30–35. https://doi.org/10.1111/1746-692X.12017
29. Alston JM, Pardey PG, Rao X (2020) The payoff to investing in CGIAR research. SoAR (Supporters of Agricultural Research). Virginia, pp. 156
30. CIMMYT (1978) CIMMYT report on wheat improvement 1978. 117–128. CIMMYT, Mexico, DF.