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Wheat Improvement

Food Security in a Changing Climate

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Chapter 1
Wheat Improvement

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Almost certainly the first essential component of social justice is adequate food for all

Norman Ernest Borlaug

Abstract Wheat is a staple for rich and poor alike. Its improvement as a discipline was boosted when statisticians first distinguished heritable variation from environment effects. Many twentieth century crop scientists contributed to the Green Revolution that tripled yield potential of staple crops but yield stagnation is now a concern, especially considering the multiple challenges facing food security. Investments in modern technologies – phenomics, genomics etc. – provide tools to take both translational research and crop breeding to the next level. Herein wheat experts address three main themes: "Delivering Improved Germplasm" outlining theory and practice of wheat breeding and the attendant disciplines; 'Translational Research to Incorporate Novel Traits' covers biotic and abiotic challenges and outlines links between more fundamental research and crop breeding. However, effective translational research takes time and can be off-putting to funders and scientists who feel pressure to deliver near-term impacts. The final section 'Rapidly Evolving Technologies & Likely Potential' outlines methods that can boost translational research and breeding. The volume by being open access aims to disseminate a comprehensive textbook on wheat improvement to public and private wheat breeders globally, while serving as a benchmark of the current status as we address the formidable challenges that agriculture faces for the foreseeable future.

Keywords Breeding precedents · New-technologies · Interdisciplinary research · Proof of concept · Food security · Wheat breeding benchmark

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1.1 Learning Objectives

- Provide background to the rest of the textbook and crop breeding generally.
- Highlight the need for integration among disciplines.
- Outline factors involved to achieve proofs of concept and impacts.

1.2 Background on Crop Breeding

Wheat is one of approximately 300,000 potentially edible plant species, of which just over 100 are commonly cultivated (Fig. 1.1). Of these just three – maize, rice, and wheat – provide nearly 60% of all human calories [2] and wheat alone provides approximately 20% of all calories and protein [3]. Plant breeding has been evolving since humans first selected among plants and their seed, for whatever purpose. Wallace et al. [4] and Fernie and Yan [5] divided the evolution of breeding into four stages. Stage 1 was phenotypic selection by farmers, stage 2 the era of hybridization. Most current breeding programs are in stage 3, characterized by use of biotechnologies like marker-assisted breeding, genomic selection, transgenics and use of bioinformatics. We are now entering stage 4, breeding by design, i.e. genome editing and precision breeding supported by big data analysis targeted to develop crops

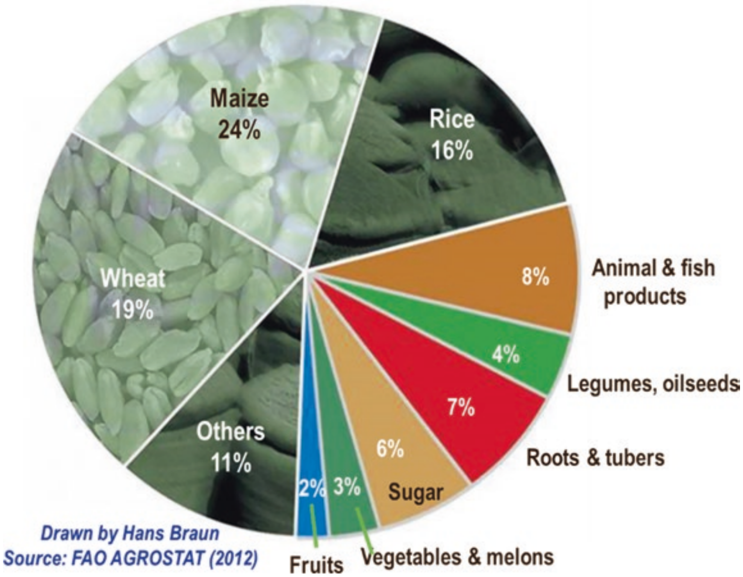

Fig. 1.1 The proportions of crops produced globally as a % of their total dry matter (approximately 3 billion tons annually). (Figure drawn by Hans-Joachim Braun with data from Ref. [1])

that meet farmer and consumer expectations in terms of yield and yield stability, biotic and abiotic stress tolerance, and nutrition and quality.

Interestingly, no new plant domestication has occurred in modern history, clear evidence of the formidable challenges associated with crop 'domestication'. There is one partial exception, namely triticale a relative of wheat [6], but even that was a hybridization of two domesticated species, wheat and rye, and has been quite difficult to commercialize despite its robustness to stress and multiple potential uses.

The principles of breeding are similar across most crops since they are cultivated in similar ways, and new cultivars face similar types of challenges in their respective growing environment. These include resisting or tolerating diseases and pests, and since most crops are field-grown, they must also adapt to variable temperatures, water supply, light and soil conditions, while flowering and maturing within defined time windows. Crop management can optimize the plant's environment to some degree, including for nutrients, control of biotic threats, as well as through choice of sowing dates, crop rotations, and irrigation where feasible. However, significant yield gaps in most annual cropping systems [7, 8], attest to the importance of selecting for heritable traits through plant breeding. Once obtained, a new cultivar can normally be relied on to express desirable traits, including yield and other agronomic and commercial expectations, as well as robustness to seasonal variation that may include a range of abiotic stresses, within a given target population of environments. In other words, guided hybridization and heritable-trait selection is a highly effective way to boost and/or protect crop productivity, since changing cultivars is one of the easiest interventions to achieve at the farm level [9].

1.3 Crop Improvement in Pre-history

Domestication of wild plants to fit agriculture is believed to have started in the Neolithic age at least 12,000 years ago in the fertile crescent, that finally led to the around 100 species that we cultivate today; though in fact a much larger number of plant species (7000) are considered semi-cultivated [10] if we include herbs, spices, medicinal plants etc. Considering the characteristics that have been passed down through history, and in comparison to wild ancestors, it is clear that early plant breeder/farmers selected for three main trait classes: (1) Preferential growth of edible organs to maximize yield; (2) Palatability and nutritional value; (3) Adaptation to a range of biotic and abiotic stresses, a problem challenging breeders to the present day [11, 12]. In short, modern day breeding is qualitatively the same discipline as our ancestors practiced; the principal selection objectives remain much the same though the breeding tools have changed.

1.4 Breeding in the Industrial Age

Mendel's work led to the first scientific proof of hereditary principles and the new discipline of genetics catalyzed crop research with the objective of boosting productivity through breeding. Gartons Agricultural Plant Breeders in the UK was one of the first companies to commercialize higher yielding cultivars. William Farrer in Australia bred the first rust resistant wheat strain. Meanwhile Nazareno Strampelli in Italy bred several high yielding, early maturing, rust resistant and short strawed wheat lines using the *Rht 8* dwarfing gene. Some of his lines made global impact and were exported to the Americas and China [13], and also used decades later as parents by Norman Borlaug. The new discipline of statistics enabled traits to be dissected genetically allowing a quantitative distinction between heritable variation and environment effects on trait [14].

These efforts and the work of Gonjiro Inazuka in Japan created the foundation of the Green Revolution leading to a paradigm shift in plant breeding and crop management. This was kick started by the dissemination of semi-dwarf genes in wheat and other cereals in the 1960s. Before the adoption of shorter lines, cereal yields were limited by lodging if plants became too tall as a result of yield-boosting inputs like N and irrigation water. It took over 10 years to achieve effective introgression of Rht1 from Norin-10, but its pleiotropic effects improved harvest index (HI) and nitrogen use efficiency (NUE), as well as lodging resistance, spearheading the Green Revolution [15]. The new generation of semi-dwarf spring wheat lines were also photoperiodic insensitive which was of paramount importance for their wide adoption; Borlaug himself admitted that this was a case of serendipity – 'an unplanned collateral effect of shuttle breeding'.

The Green Revolution in the 1960s, based in wheat on *Rht1* and *Rht 2* dwarfing genes and breeding genetic backgrounds to suit them, and the biotechnology revolution from the 1980s onwards, have delivered increasingly sophisticated methodologies for crop improvement. In the meantime, breeding programs have been efficiently meeting the demands of a fast-growing global population through steady genetic gains and broad-spectrum resistance to pests and diseases in wheat and other staple crops, with exceptionally high returns on investment documented [16]. Some suggest that this success has led to complacency, and both public and private sectors struggle to achieve the investments needed to match predicted human food demand by mid-century. The situation is especially ironic, given that many breeding programs now struggling for operational funds – have already made initial investments in modern technologies such as phenomics, genomics and informatics that are crucial to further increase genetic gains. In addition to helping increase the efficiency of selection for mainstream traits – yield, and yield stability, abiotic and biotic stress tolerance, phenology, quality and nutrition – these technologies can be powerful tools in translational research aimed at achieving step changes in yield and adaptation to emerging stresses.

1.5 Technologies That Have Impacted Crop Breeding in Recent Decades

This volume attempts to present the most relevant disciplines and research approaches that are likely to impact wheat breeding for the foreseeable future, building on tried and test approaches as well as new and emerging technologies.

Among these the most important effort, at least from the point of view of sustainable crop production and in addition to selecting for incremental yield gains, is breeding for resistance to pathogens and pests (i.e. maintenance breeding), this being a task that only becomes harder as agriculture intensifies. Maintenance breeding is reminiscent of the legend of Sisyphus, whose task started over and over again just as he had nearly finished, and so it is with the constant evolution of new pest and disease races, as well as the periodic emergence of new threats that jump host-species barriers, such as wheat blast [12]. For many diseases the challenge is made even harder since new sources of resistance are mainly found in relatively exotic materials such as landraces and wild relatives. This continuous challenge to find resistance genes against new disease pathotypes follows the same principals as the need to develop new vaccines effective against new CoVID-19 variants [17]. Molecular technologies can now be applied in breeding for resistance to many diseases where the genes are of relatively large effect. With recent advances in gene-cloning and gene-stacking, it is now technically possible for example, to combine stem rust resistance genes so that they do not recombine and are inherited like a single trait [18] and thereby underpin durable resistance. All rust resistance genes used in the stack originate from wheat and closely related genomes (i.e. cisgenics). However, since genetic modification (GM) technology can be used to stack the wheat resistance genes, policy makers and consumers must first accept such products. Then gene stacking technology could be expanded to other diseases, having fundamental impacts in terms of durable and sustainable crop protection and reducing agro-chemical footprints globally.

The approaches and technologies used to deliver new, higher yielding, broadly adapted, disease resistant wheat lines, many with specific quality and nutritional characteristics, are described in Part II of this volume entitled “Delivering Improved Germplasm”. This section outlines the theory and practice of wheat breeding and the disciplines it routinely integrates to deliver on farmer and consumer needs. These methods underpin food security, especially in countries where many external inputs such as fungicide or insecticide are out-of-reach for resource poor farmers. Resistance to biotic stresses also helps safeguard farmers, agricultural communities and ultimately consumers from the potential hazards of widescale application of such chemical protectants.

On the other hand, for any complex genetic trait – such as many associated with yield potential and climate resilience – the chances of cloning a causative gene or identifying reliable molecular markers decreases with the numbers of genes involved in its expression. Hence genomic selection for yield involves modelling of largely random markers in order to train QTL-based models of yield prediction; exercises which have underscored the importance of genetic background and environment in determining which alleles impact crop performance. Nonetheless, the process remains largely stochastic and is challenging to apply on all of the complex traits that have been shown – and will be shown – to be involved in yield determination and adaptation to biotic and abiotic stresses. In order for breeding to reach the final 'deterministic' stage and catch up with the technological revolutions that are happening in phenomics, genomics, in silico breeding, etc. an even larger integration of disciplines is required.

1.6 Integration of Disciplines

Crop improvement relies on integration and application of many disciplines and has been exemplary in achieving this, having underpinned global food security since the Green Revolution, during which time human population has more than doubled. During this time frame, namely the last half century, the area sown to cereals globally – has not changed significantly while yields have tripled. It is clear that crop research has achieved outstanding impacts on breeding and crop management, while policy and the adaptability of farmers to embrace new technologies have had life-saving outcomes [19]. Nonetheless, the challenges that agriculture faces now are not just to feed nearly 10 billion people within the next 3 decades, but to achieve it sustainably under a warmer and more unpredictable climate, and often with less water, less N and declining soil quality [20]. Clearly research, breeding and agronomy must become even more effective and responsive to a range of stakeholders.

The explosion in fundamental plant science of recent decades has uncovered the physiological and genetic basis of many traits as well as genetic markers in model species. Nonetheless, many of these outputs have yet to be tested and translated into applied breeding. Clearly, the need for investment in translational research is more critical than ever. Sequencing of the wheat genome, in conjunction with thorough phenotypic characterization of elite material in appropriate field environments, will lead to a comprehensive physiological and biochemical basis of crop yield and adaptation. Such information will enable modelling the effects of and interactions among candidate traits and genes in different target locations, and help inform and refine breeding strategies. Meanwhile, advances in phenomics and genomics have the potential to be mainstreamed in three main areas of crop improvement: (1) Characterizing candidate parents to help design more strategic crosses; (2) Screening progeny at breeding scale to identify genotypes that express the targeted traits; (3) Facilitating the exploration of vast collections of relatively underutilized crop genetic resources. Advanced phenomics approaches – such as use of hand-held androids, drones and plane/satellite mounted sensors – make screening of such collections much more feasible at scale [21]. At the same time, genomics is also mobilizing to the field, with portable genotyping kits that have the potential to revolutionize global disease surveillance, potentially averting pandemics [22]. Such technologies scale readily to mainstream breeding and are equally valid for biotic and abiotic factors.

For these reasons, the volume includes a dedicated section entitled ‘Part III Translational Research to Incorporate Novel Traits’, covering biotic and abiotic challenges. Translational research in this context, is defined as the application of any scientific knowledge to crop improvement. Translational research of this kind provides an essential link between more fundamental research and crop breeding, adding value to both. The challenge however, is to demonstrate genetic gains using up to date and representative germplasm, in relevant environments. Therefore, translation often takes time and can be off-putting to funders and scientists who feel pressure to deliver near-term impacts. As a result, relatively few scientists occupy the applied research space where proofs of concept for crop improvement hypotheses are rigorously tested in a breeding context. Nonetheless, it can be accelerated with newer tools and technologies and these are discussed in the final part of this volume ‘Part IV Rapidly Evolving Technologies & Likely Potential’.

1.7 Networking and Sharing

No matter how advanced the understanding of a component of a problem, holistic understanding is required to solve many cropping-system level challenges. New tools and approaches can help fill knowledge gaps and potentially accelerate genetic gains directly. A recent review involving industry and academia set out to define major knowledge gaps with potential to improve crop productivity across a broad

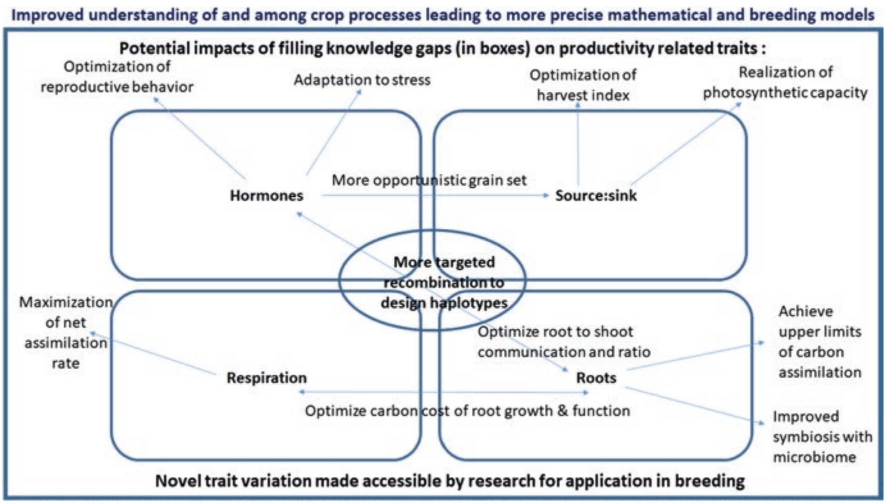

Fig. 1.2 Current trait-knowledge bottlenecks and potential research outcomes on crop productivity. (Reprinted with permission from Ref. [23])

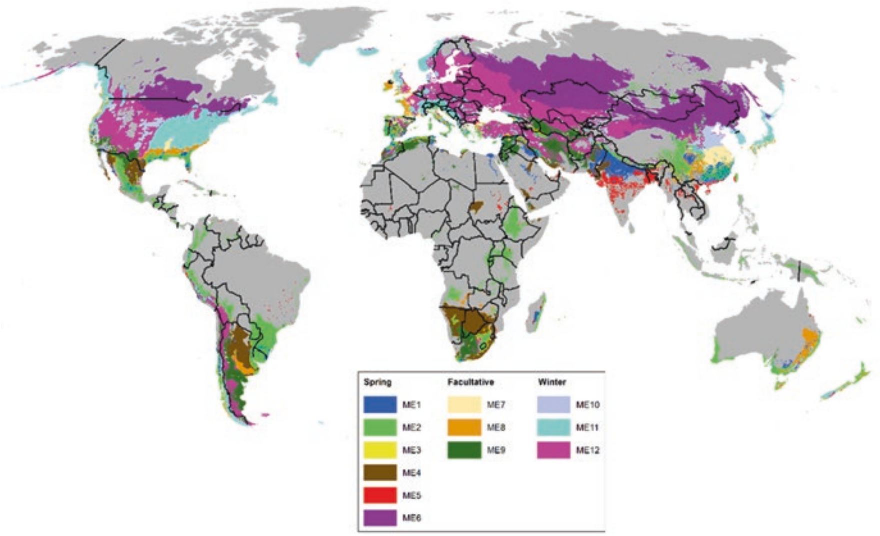

Fig. 1.3 The International Wheat Improvement Network (IWIN) embraces a global collaboration of wheat scientists testing approximately 1,000 new high yielding, stress adapted, disease resistant wheat lines each year. Breeding is directed towards 12 different ME, representing a range of temperature, moisture, and disease profiles. Spring wheat: *ME1* irrigated, high yield, *ME2* high rainfall disease prone environments, *ME3* acid soils, *ME4* water limitation, *ME5* heat stress, *ME6* temperate, high latitude.; Facultative wheat: *ME7* irrigated, moderate cold, *ME8* high rainfall, moderate cold, *ME9* low rainfall, moderate cold.; Winter wheat: *ME10* irrigated severe cold, *ME11* high rainfall/irrigated, severe cold, *ME12* low rainfall, severe cold. (Figure drawn by Kai Sonder and adapted from Ref. [3])

range of crops and environments. These research bottlenecks if addressed can also be expected to complement existing knowledge (Fig. 1.2), thereby also capitalizing on previous investment. However, other gaps exist in our understanding of how to maximize the output and stability of cropping systems. Since many challenges to wheat production are experienced across continents (Fig. 1.3), global collaboration offers many advantages, in terms of efficiency of scale, encompassing representative sites within and among target environments, and by coordinating efforts across a range of stakeholders thereby avoiding costly duplication of effort [24]. In summary, maximizing the impacts from crop research requires cross-stakeholder interaction to share know-how tailored to stakeholder requirements [25].

1.8 Choosing Crop Improvement Approaches

A young crop scientist may be overwhelmed by the volume of scientific literature available, and the many different theories about how crop productivity can or should be boosted. In addition, there are bandwagons in crop science [26] that both funding bodies as well as peer-pressure ‘encourage’ the science community to board. Joining can be a useful learning experience, positive for the career and possibly lead to impacts. However, the true scientific mind goes where the evidence takes it. Luckily science still upholds its internal standards through the institution of voluntary, anonymous peer-review, helping to maintain the scientific bar high in terms of objectivity and rigor. However, no one is without bias and keeping an open mind is always a worthy challenge. As an example, a recent study challenged a growing movement that believe – with some justification – that an industrial model of agriculture with its intensive farming practices, make society more vulnerable to unpredictable climate and other environmental impacts. The study looked specifically at the impact of winter wheat selection in North Europe under intensive inputs, with respect to its genetic gains across a range of high and low input systems. The results showed that the genetic gains achieved at high input stood up when tested across all levels of input [27], mirroring similar findings in Spring wheat breeding [28]. However, such results, valuable and practical as they are, should be taken at face-value and not be used to make sweeping generalizations about one cropping system over another. For example, while crop yields tripled over the last 60 years, Nitrogen (N) application increased tenfold [29]. Only research conducted objectively can provide the answers we need as contributors to food security; and proofs of concept can only come from outputs of research that are tested directly in the appropriate plant breeding and crop management contexts, before they can be scaled to meet the challenges that agriculture must face in the future.

The future of food security will depend on a combination of the ecological prudence of the past and the technological advances of today (M.S. Swaminathan)

1.9 Main Objectives of the Textbook ‘Wheat Improvement – Food Security in a Changing Climate’

While the scientific context for each main section of this volume has been presented already, outlines of individual chapters are not listed here, as the information is readily accessible in the Table of Contents and in the Abstracts of each chapter. However, it is worth mentioning the why. The textbook was developed with three main objectives. One was to put together in a single volume, a compendium of knowledge about the theory and practice of wheat improvement to serve as a guide to full-time students of the field as well as scientists from a given discipline wishing to brief themselves on areas outside of their own expertise. Among the authorship are world authorities in their respective fields which certainly lends weight to the content. There is a CIMMYT bias in authorship, partly a tactic to ensure timely delivery of the book as a whole, but also reflecting the paramount role that CIMMYT has played on wheat breeding globally for more than half a century, currently impacting around 70% of all wheat grown globally and generating an estimated extra revenue of $2–3 billion dollars annually for farmers in the Global South alone [16].

Nonetheless, readers should not assume this volume to be a definitive, last word on wheat improvement. Authors of all chapters were asked to cite the literature in a selective way, so as to give readers access to other sources that complement understanding and in many cases provide alternative perspectives. Furthermore, while the attempt was made to cover key disciplines, it is recognized that what may be priorities from a global perspective (reflecting the professional background and bias of the editors), can allow important challenges and disciplines to be overlooked. For example, there is no chapter in this volume on chilling and freezing stress tolerance which are especially important for winter wheat. The fall sown winter wheat crop must survive harsh frosts and snow cover without incurring irreversible tissue damage caused by internal ice crystals. They must also be able to fix carbon on cold but sunny winter mornings when chilling can be an important factor that causes photo-oxidative damage; readers are referred to Muhammad et al. [30] for an up to date review on cold stress acclimation in wheat. While micronutrients are addressed in the chapter covering microelement deficiency and toxicity, macronutrients are not covered in this volume. Despite wheat being a good nitrogen scavenger, there is much interest in breeding for nitrogen and other macronutrient use efficiency, for example [31], while a body of literature on the impact of the microbiome on crop nutrition is starting to accumulate, including possible genotype effects [32]. Neither was a chapter on roots commissioned but readers are referred to "Wheat root systems as a breeding target for climate resilience" just published [33]. Lodging resistance is missing despite its persistent negative impact on wheat (and other crops), but readers are referred to a comprehensive review on the subject for cereals [34] and more recent efforts to identify genetic bases in wheat [35].

A second objective is to disseminate the information in this book as much as it can be useful since (i) wheat is the most widely grown crop globally, (ii) many wheat colleagues – particularly in the Global South – work with very restricted budgets, so access to costly literature is therefore limited, and (iii) potentially to serve as a technical reference point for the many stakeholders involved in wheat improvement. Through a grant from the Bill and Melinda Gate's Foundation, the cost for publishing this volume as open access is covered, so the whole volume can be shared electronically, printed locally, and even translated to other languages if desired without restrictions.

Finally, as with any textbook, this volume benchmarks the state-of-the-art in wheat breeding, but at a key moment in the history of agriculture. Decisions and actions that are taken now will be pivotal to future food security for a number of reasons, for which crop breeding – if adequately resourced – can provide at least partial solutions. The factors are well known and have already shown global impacts: a less predictable and generally harsher climate; declining water resources; widescale attrition and disappearance of arable soils; a burgeoning population with increased demands for wheat products; grave concerns about the evolution of new pests and disease races and the threat of crop pandemics looming closer as some diseases are already jumping species barriers; an imperative to reduce the environmental footprint of agriculture to help avert devastating sea level rises for example, associated with global warming; a need to produce more on the same land to decelerate encroachment of agriculture into precious natural ecosystems, and the list goes on. These are significant challenges not only for breeding per se, but also to the way agriculture – the widely recognized cornerstone of civilization – will be conducted in the future. However, if you are reading this you have already embraced the challenge.

1.10 Key Concepts

Wheat breeding has a long history and excellent precedents Many new technologies can be applied to emerging problems; interdisciplinary approaches applied through collaborative research are likely to be more efficient than working in silos, assuming objectivity; proof of concept need to be achieved in the appropriate context before breeding pipelines are changed.

1.11 Conclusions

Wheat breeding has been extremely successful especially since the Green Revolution and much of the progress made was due to the open sharing of germplasm and knowledge among wheat scientists, which holds up until today. As long as hybrid wheat does not become a widely accepted reality, wheat research is likely to remain a critical activity in the public domain, in particular in the Global South where most wheat is produced. In order to match predicted demand and adapt the crop to a more challenging environment, crop scientists must demonstrate objectivity and rigor, in order to combine technologies – both old and new – that will deliver reliable productivity gains. We trust, this book will help to generate interest among young scientists to enter the exciting field of crop and in particular wheat improvement.

> *Nobody is qualified to become a statesman who is entirely ignorant of the problems of wheat (Socrates/Plato)*

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