

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Achieving sustainable cultivation of wheat

Volume 1: Breeding, quality traits, pests and diseases

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Introduction

A strong case can be made for wheat as the most important plant for humans. Wheat, along with barley, was the first plant to be domesticated. This happened around 10,000 years ago in the Middle East and formed the base for the development of agriculture, which, in turn, laid the foundations for the development of Western civilisation (Tanno and Willcox, 2006; Bilgic et al, 2016). Today wheat is grown in over 120 countries across the temperate world (Figure 1) and covers an area of over 220 million hectares with a total production of over 725 million tonnes (FAOSTAT, 2017). It accounts for 11% of total crop production and is our most widely cultivated plant, occupying 16% of cropped land (Figure 2). Wheat's adaptation to cool, temperate climates allows it to grow at quite low temperatures, and this has placed it in a unique position in cropping rotations with rice, maize, soya bean and cotton.

In addition, wheat is the most traded agricultural commodity, making it of critical importance in global food security. In 2013, 23% of the world's wheat production (162 million tonnes) was traded compared to 12% of maize and only 5% of rice produced (FAOSTAT, 2017). The amount of wheat traded globally has increased steadily from 40 million tonnes in 1961 to over 160 million tonnes in 2013 (Figure 4). Consequently, fluctuations in wheat price and availability have a large impact on food security.

The importance of wheat for food security lies not only in its role as a stable, easily transportable foodstuff but also in its nutritional value and multiple end uses. Wheat is a major source of carbohydrates for much of the world's population and accounts for around 20% of our protein and provides dietary fibre and minerals. The FAO estimates that wheat provides almost 16 g protein per day per person, compared to less than 4 g for maize and 10g for rice (FAOSTAT, 2017). Wheat's many uses depend largely on the grain hardness, protein content and gluten or dough strength. For leavened breads, hard wheat is usually preferred with pan breads made from strong dough while medium or

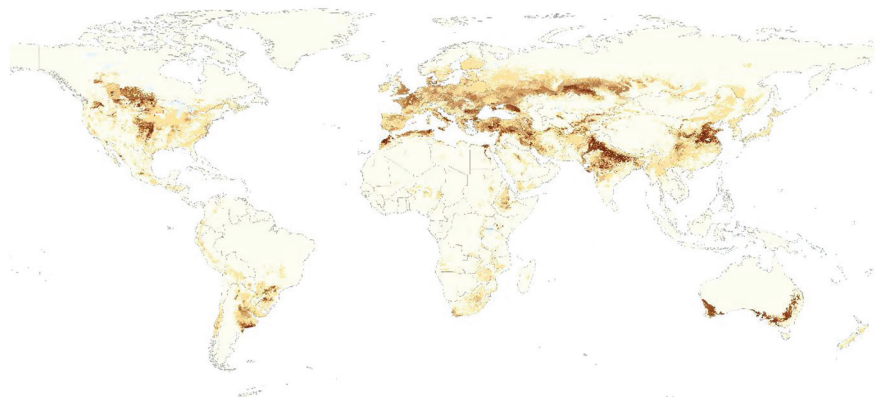


Figure 1 Global wheat production (You et al, 2014 MapSpam). Colour intensity relates to the proportion of land devoted to wheat production.

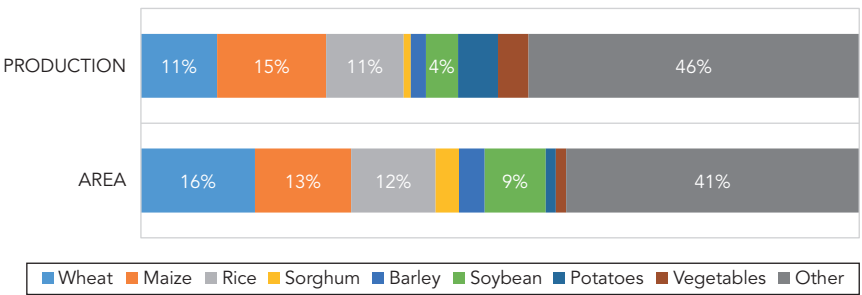


Figure 2 Comparison of wheat production and area with other major crops. The percentages of total global crop production and area are shown for the most widely grown and produced crops with all remaining crops grouped under ‘Other’. Data from FAOSTAT, 2017.

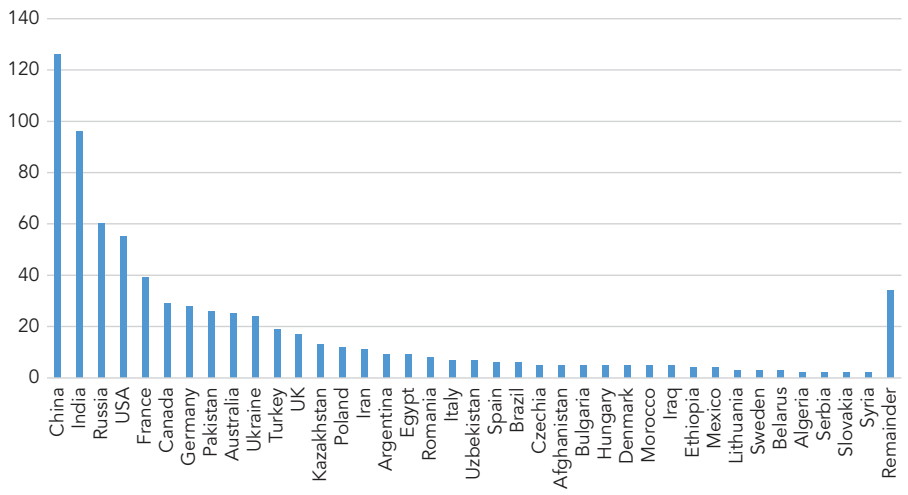


Figure 3 Wheat production by country in million tonnes. Countries that produced over 2 million tonnes in 2014 are presented with all remaining production under ‘Remainder’. Data from FAOSTAT, 2017.

weak dough strength is preferred for steamed breads. Medium hardness is preferred for unleavened breads such as Arabic flat breads, chapatti, tortillas and crackers. The many different types of noodles make use of both hexaploid bread and tetraploid durum wheat, while cookies, cakes and pastries use soft wheat. Durum wheat is also used for couscous in North Africa.

The world’s two biggest wheat producers (China and India, Figure 3) consume around 190 million tonnes annually and these two countries also account for one half of the world’s poor (FAOSTAT, 2017). Wheat is not only a major food source for the world’s poor; it is also of great importance as both a food and commercial commodity in the developed world with Russia, USA, France, Canada, Germany and Australia, all ranking amongst the world’s top ten producers (Figure 3).

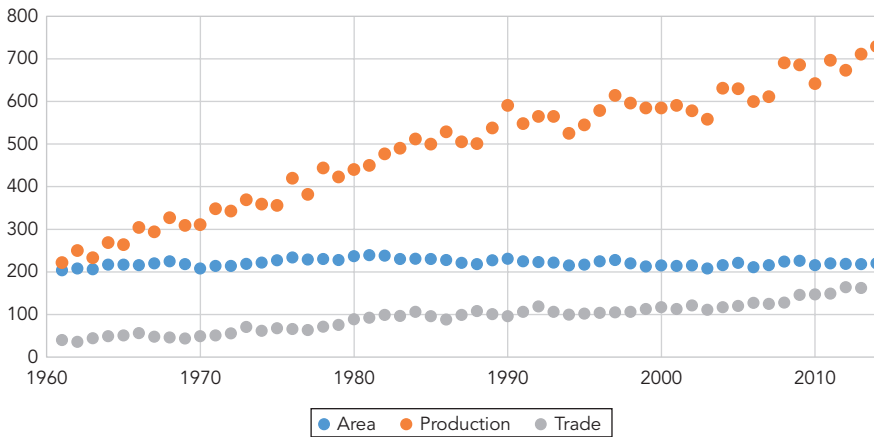


Figure 4 Global area sown to wheat, total production and trade since 1960. Scale is million tonnes for production and trade, and million hectares for area (data from FAOSTAT, 2017)

Wheat production has grown substantially from around 220 million tonnes in 1960 to over 700 million in 2014 with almost no change in the area sown to wheat (Figure 4). This rapid increase has come about through the Green Revolution, expansion in areas under irrigation and increased use of fertilisers, and has enabled producers to not only meet demand, but also to reduce real grain prices by about 40% (Everson and Gollin, 2003). However, studies indicate that the demand for wheat in the developing world will increase by 34 to 60% by 2050 and the current rates of gain are not adequate (Ray et al., 2013). There are several worrying trends. In North Africa and Western Asia, wheat imports have grown from around 4 million tonnes per year in the 1960s to over 40 million tonnes per year over the past decade (FAOSTAT, 2017). These are amongst the world's most unstable regions, and food security and import dependency are major issues.

The overall impact of increasing temperatures and climate variability are also expected to challenge wheat production in many regions (Vermeulen et al., 2014). For wheat, the advantages of increased photosynthetic rates due to elevated CO₂ levels are likely to be outweighed by elevated temperatures and reduced water availability for many major irrigation schemes (Lobell et al., 2011). A 1°C rise in global temperatures is predicted to lead to a decrease in wheat yields of between 4.1% and 6.4% (Liu et al, 2016).

Therefore, the target of lifting yields by 60% by 2050 to meet predicted rises in demand is challenging (OECD-FAO, 2015). The challenge is immediate since over the ten years wheat consumption is estimated to increase by over 60 million tonnes in the developing world (based on data from OECD-FAO, 2016).

The Wheat Initiative

The challenge of achieving a 60% increase in wheat production by 2050, is exacerbated by climate change, land degradation, reductions in water availability and pressure to reduce chemical inputs. International investment in wheat research will be critical since a close

linkage has been demonstrated between investment in research and growth in productivity (Alston et al 2010). In addition, there are significant changes in the nature of agricultural research and shifts in the role of public and private sector organisations. A recent analysis of global spending on agricultural R&D highlighted the growing role of the private sector and an increase in investment in middle-income countries such as China, India and Brazil (Pardey et al 2016). These trends are clearly visible in wheat research where there has been greater investment from the private sector, partially motivated by the potential and recent technological advances in hybrid wheat systems (Whitford et al, 2013).

The significance of the production challenge and the changes in the structure of research investment, coupled with the rapid technological advances, have provided an opportunity to re-visit the way in which wheat research priorities are established and coordinated at the international level. Many of the challenges are specific to particular countries or regions but all countries are facing problems in addressing adaptation to climate variability, reduction in inputs and the need to tackle pests and diseases.

This opportunity was recognised by the G20 Agriculture Ministries and led to the establishment the Wheat Initiative in 2011 as part of their action plan to contribute to global food security (G20 Agriculture Ministries, 2011). The vision and mission of the Wheat Initiative (Wheat Initiative, 2013) is as follows:

The Wheat Initiative aims to encourage and support the development of a vibrant global wheat public-private research community sharing resources, capabilities, data and ideas to improve wheat productivity, quality and sustainable production around the world.

This community comprises public and private researchers, educators and growers that, together, will have sufficient resources and capabilities to develop strong and dynamic national programmes on wheat in their country and, at the international level, through transnational collaborative programmes.

To answer the challenges of wheat research internationally, the Wheat Initiative will:

- 1 Develop a global strategic agenda for wheat research through the identification of research and outreach priorities and challenges beyond the capacity of single research groups/countries, and that can best be achieved by international coordination and collaboration between researchers, research institutions and funding organisations;
- 2 Encourage efficient investment in wheat research based on the capabilities of, and synergies among, national and international programmes;
- 3 Initiate the development of new collaborative programmes and coordinated actions across developing and developed countries;
- 4 Develop and coordinate knowledge sharing amongst the international wheat community;
- 5 Improve access of all to resources, services and facilities;
- 6 Support education of students and life-long learning of wheat researchers and farmers;and
- 7 Stimulate public/private collaborations.

In 2015, the Wheat Initiative developed a Strategic Research Agenda in collaboration with researchers from around the world. This Agenda set short, medium and long-term priorities for wheat research around a series of core themes and cross-cutting technologies. In late 2016, international researchers reaffirmed the continued relevance of the Agenda. A precis of the Agenda is included in this volume.

The chapters in this volume (*Achieving sustainable cultivation of wheat Volume 1: Breeding, quality traits, pest and diseases*) pick up on the core themes identified in the Wheat Initiative's Strategic Research Agenda:

- Core theme 1: increase wheat yield potential
- Core theme 2: protect yield potential
- Core theme 3: protect the environment and increase the sustainability of wheat production systems
- Core theme 4: ensure the supply of high-quality, safe wheat

This and an accompanying volume (*Achieving sustainable cultivation of wheat Volume 2: Cultivation techniques*) cover key issues such as variety development to improve yields, dealing with biotic and abiotic stresses, improving nutrient use efficiency, enhancing agronomic practices so that wheat crops are more productive and sustainable in the longer term, as well as improving wheat processing and nutritional quality.

Part 1 Wheat physiology and breeding

The importance of wheat to the global food supply means that many institutions across the world hold collections of wheat germplasm to study and preserve wheat genetic material. The use of germplasm has been instrumental in improvements in genetic yield as well as maintaining advances in yields by averting declines due to biotic and abiotic stresses. It is generally agreed that wheat improvement in the future will depend on bringing in new genes through the introgression of novel wheat germplasm, including wide hybridisation.

As Chapter 1 indicates, there are over 80 autonomous *ex situ* germplasm collections holding in excess of an estimated 800,000 accessions. Optimising the use of these collections faces a number of challenges. The first set of challenges relates to how robust and comprehensive collections are. As the chapter argues, regeneration of accessions is probably the single greatest threat to the safety of wheat accessions held in globally important genebanks. Full safety duplication, of at least unique accessions, needs to be the goal of an efficient rationalised global system of collections.

A key issue is estimation of the degree of duplication between collections. In addition, as *in situ* populations of these species become vulnerable, the identification of gaps within the global *ex situ* collection is essential to conserve these threatened sources of wheat-related genetic variability. It is widely agreed that the primary gap is with the wild relatives of wheat in their native environments. Many populations of the annual wild relatives of wheat are under threat because of changing patterns of land use. At the same time, new technologies have made the use of the annual wild relatives as a germplasm source easier, which has generated an interest and need for wild relatives to be maintained in accessible collections. Landrace varieties are also a priority for collection, conservation and documentation because of the increasing threat to their continued existence from the spread of improved modern cultivars.

As Chapter 1 shows, the second set of issues relates to access to collections. A key component of a global system will be linkage of all substantial national, regional and international collections, especially those that contain significant numbers of accessions not

duplicated elsewhere. Key areas to improve linkage relate to access to more information on the collections themselves and tools to facilitate the selection of accessions. Major impediments include:

- Lack of reliable evaluation data on accessions
- Lack of known genetic variability for applied germplasm enhancement for a range of important traits including drought and heat tolerance, Fusarium head blight, crown rot, and *Septoria* blotch and other unspecified diseases
- Intellectual property rights issues, or more often the uncertainty surrounding these.

The development of genebank management software packages such as GRIN-Global will facilitate the secure conservation and use of accessions. A major step in developing an integrated information system for the global system of wheat genetic resources is to ensure adequate information storage and retrieval infrastructure. This will involve, at a minimum:

- Improving the documentation of collections to enhance accessibility and as a tool to assist in the management and rationalisation of collections, using GRIN-Global or other genebank management systems.
- Globally agreed protocols for data ontology and quality.
- Publishing all key accession-level data, such as passport, characterisation, evaluation and other relevant data from individual collections to global portals, such as Genesys, to allow for easy access by all collection holders and the collections' user clientele.

Continued progress in these areas will help breeders to optimise use of genetic resources.

As Chapter 2 indicates, genome sequence information is an essential prerequisite for defining the complete gene catalogue of an organism and it provides a framework for identifying and understanding the function of variants associated with phenotypic traits of interest. For wheat, these traits include disease resistance, crop yield improvement, protein content, quality factors and resistance to abiotic stressors such as drought or poor soils.

The very large size and complexity of the wheat genome has led to it being regarded for many years as 'impossible' to sequence. As a consequence, several projects have focused on sequencing genic sequences or simpler genomes of diploid wheat relatives. Although these earlier initiatives have helped to accelerate marker development and estimate roughly the gene content, these short-read-based assemblies are highly fragmented and do not provide information about the individual gene content per chromosome, nor the order of the genes along the chromosomes.

For these reasons, as Chapter 2 shows, the International Wheat Genome Sequencing Consortium (IWGSC) (www.wheatgenome.org) embarked on a different strategy in 2005. The main objective was to deliver a reference sequence of the bread (hexaploid) wheat genome that contains all of the information necessary to advance agricultural research for wheat production through a better understanding of the molecular basis of agronomic traits. The selection of the hexaploid bread wheat genome was promoted by wheat breeders, seed companies, and growers who wanted to have information about the genome of the species that is grown on more than 90% of the wheat-growing areas. The International Wheat Genome Sequencing Consortium was able to deliver the first reference sequence for wheat in 2017, several years ahead of schedule.

Chapter 2 reviews the challenges posed by the structure and composition of the wheat genome and how they have been addressed through genome sequencing strategies. It also discusses the road map of the IWGSC for the completion of a reference sequence that will meet the needs of breeders and researchers seeking to improve crop varieties and to understand the dynamic genome environment and complexity of the world's most important crop.

Recent IWGSC activities have continued towards producing a high-quality, ordered sequence that includes annotating and identifying the precise locations of genes, regulatory elements and genetic markers along the chromosomes. Achieving a high-quality annotation will be key to defining the dynamic nature of the wheat genome and its relationship to the adaptation of wheat to different environments, biotic stresses, quality characteristics, and market demands. For each of the A, B, and D genomes that comprise hexaploid wheat, 81-85% of genes look to comprise a core set while the remainder can be considered to be genes located in chromosome regions that are conditionally unstable, namely, units of the genome that enhance plant performance or grain quality in particular environments. Understanding how the genomes are regulated, how they interact, and the role that variation plays in meeting the challenges of environmental and biotic stresses will be fundamental to ensuring our continued ability to adapt and produce grain for a variety of food and non-food products that account for the prominent position of wheat in the modern industrial supply chain. A gold standard sequence of the wheat genome with manual and functional annotation provides a platform for new molecular approaches to wheat breeding.

Since wheat production must be increased to meet growing demand, it is critical to increase the rate of genetic gain in wheat breeding. Chapter 3 provides an authoritative review of the range of existing and emerging techniques in wheat breeding, including those that will benefit from sequencing the wheat genome. As the chapter points out, all methods of wheat breeding operate within the parameters of the breeder's equation. Breeding is targeted at increasing the rate of genetic gain via the components of the equation. Components include increasing selection intensity (the number of individuals selected), selection accuracy (the precision by which individuals are selected), increasing genetic variation and reducing the years required per breeding cycle.

Chapter 3 starts by reviewing the options for improving five conventional methods in wheat breeding:

- pedigree selection and single seed descent (SSD)
- doubled haploids (DH)
- bulk selection and backcross breeding

These five breeding methods are the workhorses of wheat breeding programmes worldwide and have maintained wheat yield increases at a steady rate of approximately 1% per year over a 60-year period. As the chapter points out, in single seed descent (SSD), decoupling inbreeding from selection (in contrast to pedigree selection) means that the development of pure lines can occur more rapidly. Because of this, SSD is the most commonly used method for rapid generation of recombinant inbred lines (RILs) within breeding programmes. With the continued decrease in cost of genotyping and increase in cost of phenotyping, rapid bulk inbreeding (RABID) has been proposed as an alternate method of SSD that allows more crosses to be progressed speculatively.

Doubled haploid (DH) production takes gametes from an F1, culturing them to create haploid individuals which are then chemically treated to double chromosome numbers and create diploid individuals completely homozygous at all loci. These are then multiplied and field tested. There are two notable technologies that would advance the future application of DH in wheat. The first (microspore culture) is well studied, but remains practically difficult, whilst the second is genome elimination, an expanding field of research in model and latterly crop species.

Bulk breeding is a process for inbreeding a segregating population in the absence of selection until the desired level of homozygosity is achieved. This method allows handling of more crosses than is manageable via pedigree selection. Building on the work outlined in Chapter 1, the technique has been used primarily to introgress major genes for disease resistance from unadapted germplasm into elite material.

Whilst techniques such as RABID promise to enhance conventional techniques including SSD, there is a need for novel techniques to achieve more rapid rates of genetic gain, including:

- F1 hybrid breeding
- marker-assisted selection (MAS) and mapping
- genomic selection (GS)
- genetic engineering
- gene and genome editing
- mutation breeding

F1 hybrid breeding is an important inclusion in the development of modern breeding methods. One of the major sticking points in the search for hybrid success in wheat revolves around heterosis: the superior performance of hybrid progeny compared to their parents. This can be highly variable, suggesting the need for a better understanding of the genetic basis of heterosis. Whilst hybrids currently have a predicted yield advantage of around 10% over lines, high seed production costs reduce the absolute advantage.

Numerous molecular markers (MM), that is, randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), sequence tagged site (STS), microsatellites or simple sequence repeats (SSRs) and more recently single nucleotide polymorphisms (SNP) have been developed in wheat. Many of these have been utilised to tag qualitative and quantitative trait loci (QTL) in the genome regions via linkage or linkage disequilibrium (LD) mapping (frequently reported in QTL and association mapping studies), with the ultimate aim of finding markers that tag loci determining traits of interest.

The increasing availability of high densities of genetic markers has opened up new opportunities for marker-assisted breeding. Marker-assisted selection (MAS) provides opportunities for enhancing the selection response in breeding programmes as molecular markers can be applied for selection of plants even at the seedling stage with high precision and at reduced cost. Although applicable for all of the breeding methods described above, MAS has particular potential to improve the efficiency of backcross breeding. Bias and precision are the two major impediments in moving from QTL mapping to MAS in breeding programmes. In an effort to overcome these problems, increasingly sophisticated mapping populations are becoming available for trait dissection and mapping, including, multi-parent advanced generation intercross (MAGIC) populations, nested association mapping (NAM) populations and association mapping (AM) populations.

The ability to combine these genetic regions using MAS in realistically sized breeding programmes remains a challenge. Genomic selection (GS), a form of MAS, is a new molecular breeding approach in which genetic markers covering the whole genome are used to ensure that all quantitative trait loci (QTLs) are in close linkage with at least one marker. GS is a potential solution to this challenge as it removes the burden of phenotyping selection candidates, replacing phenotype with genotype, by exploiting the new availability of high-density genetic marker information. GS is currently used mainly in animal breeding but has great potential in plant breeding. Chapter 3 provides a detailed analysis of the potential and remaining challenges of using GS in hybrid breeding for example.

Along with traditional genetic engineering, there is new potential to use biotechnological advances to inactivate genes or promote gene replacement in crop plants. Whilst traditional genetic engineering involves adding specific transgenes to untargeted locations, the ability to modify genetic information to create new traits holds great promise. Gene and genome editing methods offer a means to create new allelic variants for target traits. Finally, although not a new technology, there are emerging methods for using mutagenesis to benefit breeding. Mutations (heritable changes) can occur spontaneously (at very low frequency) or can be artificially induced. The use of artificial mutagenesis via chemical and physical mutagenising agents can be exploited to create new breeding lines and/or varieties using techniques such as TILLING (Targeted Induced Local Lesions in Genomes).

Chapter 3 shows both the challenges and opportunities in improving breeding techniques, from the use of RAPID to improve SSD, the development of MAGIC, NAM and AM populations to improve MAS, the use of MAS to improve backcross breeding, genome elimination to improve DH and GS to improve hybrid breeding. Progress in mapping the wheat genome outlined in Chapter 2 will help to accelerate the use of MAS techniques.

Chapters 4 and 5 show that we still have some way to go in fully understanding, monitoring and improving complex wheat plant functions such as nitrogen assimilation and photosynthetic capacity. Chapter 4 looks at ways of improving the uptake and assimilation of nitrogen in wheat plants. Nitrogen is a critical macro nutrient with a major influence on wheat grain yield and end-use quality. Key challenges are to detect and use genetic variability to breed for more efficient wheat varieties, both improving yields and reducing the need for fertiliser. As Chapter 4 shows, nitrogen uptake is determined by nitrogen capture by the root system, nitrogen assimilation and finally nitrogen remobilisation from source organs to the grain. Direct selection for root architectural traits or other characteristics related to nitrogen use has not taken place because of the difficulty of phenotyping, particularly in the field. There is thus a need to develop new high-throughput phenotyping techniques to better map and understand nitrogen uptake and assimilation by wheat plants in differing conditions, for example by targeting aerial biomass, canopy and root size as well as plant nitrogen content.

Chapter 4 reviews genetics studies to identify genetic variability in root systems and detect the respective chromosomal regions involved. QTL detections based on densely genotyped mapping population or association panels have increased our understanding of the genetic control of different root traits. For example, researchers have detected 29 QTL for root traits and two on chromosomes 2B and 7D which co-localise with grain yield and N uptake QTL. As the chapter indicates, similar advances have been reported for other factors such as N uptake capacity. Nitrogen assimilation depends on factors such as nitrate reduction and biomass accumulation through radiation interception and use. Genes coding nitrate reductase have been identified in bread wheat, and one for nitrite

reductase. Less progress has been made in the area of nitrogen remobilisation. It is clear that more research is needed in mapping QTL associated with these processes. These will then provide the foundation for breeding more efficient plants.

As discussed in Chapter 5, the light-driven assimilation of CO_2 in photosynthesis is the primary determinant of the biomass of wheat. Total biomass achieved is a function of the total photosynthetic activity of the canopy over time. Increasing photosynthesis increases yield, provided that other constraints do not become limiting. Total photosynthetic performance is determined by the ability and duration of the canopy to intercept and convert light energy, CO_2 uptake, photosynthetic efficiency and sink demand. Traits optimising all of these processes can be considered as targets to increase photosynthesis and yield.

Whilst their genetic basis is still poorly described, many photosynthetic component traits are heritable and therefore should be amenable to phenotypic selection. Currently there are still relatively few genetic markers available for individual photosynthetic traits. Selection for variation in photosynthetic traits is thus largely unexploited in wheat breeding, with the exception of a few traits such as canopy architecture and improved transpiration efficiency. A key challenge for breeding is to identify markers for the useful variation in traits that can be combined together to improve photosynthetic performance.

The chapter explores the range of traits that influence photosynthesis. As one example, even a modest increase in the intercellular CO_2 concentration will directly increase photosynthesis and depress photorespiration. Traits that indirectly influence stomatal conductance, such as root architecture to facilitate access to soil moisture, will be beneficial and should be included in breeding programmes, especially for water-limited environments. Similarly, more rapid establishment and early leaf growth enabling the canopy to achieve maximum radiation interception more quickly can extend the effective duration of green leaf area. This trait will be of greatest benefit in warm dry climates.

An example of both challenges and opportunities in this field are the spikes of wheat at the top of the canopy which intercept radiation and undertake photosynthesis to provide photosynthates for grain filling. Understanding factors affecting spike photosynthesis has been challenging due to the multiple complex structures forming the spike and because of the high respiration rates and variable re-fixation of the respired CO_2 within the spikes. However, a recent CIMMYT (International Maize and Wheat Improvement Centre) study has identified a number of molecular markers associated with spike photosynthetic capacity that can now be exploited in order to increase overall canopy photosynthesis and grain yields.

Chapter 6 builds on both Chapters 2 and 5. Starting from models identifying key physiological traits associated with wheat drought adaptation, it reviews photosynthesis-related and stay-green traits, canopy temperature (CT) and canopy temperature depression (CTD), leaf water-holding capacity (with measures such as rate of excised-leaf water loss (REWL) and leaf relative water content (RWC)), accumulation and remobilisation of water soluble carbohydrates (WSC) which can act as potentially powerful indirect selection criteria to guide the breeding of wheat tolerant to drought and heat stresses. Water soluble carbohydrates (WSC) of leaves or stems (culm and leaf sheath), for example, have been considered as important physiological traits indicative of drought and heat tolerance, because of their dual functions of acting in osmotic regulation, as osmolytes, under adverse environmental conditions, and contributing to grain growth and development as the dominant carbon source for grain yield when active photosynthesis is inhibited by drought.

Recent advances in genetic linkage mapping and association mapping strategies have provided powerful new tools for molecular dissection of drought and heat tolerance. As an example, a large number of photosynthesis-related QTLs have been associated with photosynthesis rate (*P_n*), stomatal conductance (*G_s*), transpiration rate (*E*), chlorophyll content (*Chl*) and chlorophyll fluorescence kinetics under drought or heat stresses, distributed over almost all 21 chromosomes. In a more specific example, single-marker analysis revealed that the SSR markers *Xgwm182* and *Xgwm292* on chromosome 5D and *Xgwm410* on chromosome 5A exhibited significant association with RWC under drought stress, accounting for 21-30% of the phenotypic variation. The marker *Xgwm182* can potentially be used in marker-assisted selection methods to breed drought tolerance in wheat.

The chapter also reviews what we know about specific regulatory and functional/effector genes conferring drought tolerance in wheat. The products of regulatory genes mainly include those involved in signal transduction, such as membrane-localised receptors, calcium sensors, protein kinases, protein phosphatases and transcription factors (TF). Effector genes encode proteins that are likely to function in direct protection, such as key enzymes for osmolyte biosynthesis, scavengers of antioxidants and reactive oxygen species (ROS). As an example, reversible protein phosphorylation has been found to play a role in detecting and responding to environmental stresses, and protein kinase and phosphatase have been found to play pivotal regulatory roles in abiotic stress signalling. The chapter also reviews heat shock transcription factors (HSFs) as central regulators of the expression of heat shock proteins (HSPs).

However, genetic studies of physiological traits have often been too ambitious because of the complexity of the traits themselves and the absence up until now of whole genome data for wheat, a problem addressed by Chapter 2. Improving accuracy requires improvements such as: enlarging population and progeny size or constructing near-isogenic lines, introgression lines, and advanced back-crossing populations in order to fine map QTLs/functional markers using linkage and association mapping strategies; and exploiting QTL hot-spot regions and common QTLs using comparative genomics. As suggested in Chapter 5, most recent research efforts have aimed to characterise individual genes. As cross-talk is a common phenomenon in abiotic stress signalling, and one gene may play different roles in different pathways, the actual function of target genes should be deciphered in networks rather than individually.

Complementing Chapter 6, Chapter 7 summarises and reviews the extensive recent research on understanding the transcriptomic and genetic basis of the wheat plants' response to low, above-freezing temperatures, as well as exposure to subfreezing temperatures. The progression towards completion of vernalisation and development of cold acclimation occur simultaneously and the possible linkage and/or pleiotropy of some of the major genes involved in the two processes has been extensively investigated.

Genes responding at the transcriptomic level can be broadly categorised into three groups; genes encoding structural proteins that may be involved in protecting the cell during low temperature stress; those that regulate gene expression and signal transduction pathways, such as transcription factors, protein kinases, phosphatases, and the enzymes involved in phosphoinositide metabolism; and genes encoding enzymes involved in the biosynthesis of stress response compounds such as osmoprotectants, membrane lipids and antioxidants.

Research has revealed that the transcriptomic response to low, above freezing temperatures involves thousands of genes and that the regulation is highly dependent on

tissue type, growth habit of the plants (spring versus winter), photoperiod, light intensity and the specifics of how the cold temperature was applied (rapid versus slow cooling). The situation is even more complex at freezing temperatures.

Recent efforts to identify molecular markers associated with enhanced freezing tolerance suggests a major chromosomal location affecting cold tolerance of winter wheat is the long arm of chromosome 5A. However, the effectiveness of the 5A QTL region is critically dependent on other regions of the genome. The picture of cold and freezing tolerance of wheat that has emerged is one of complex interaction of many pathways and mechanisms, including transcriptomic changes that occur at above-freezing temperatures, and pathways that may be involved in sensing change in temperature and downstream responses. The chapter also reviews the complex biochemical changes in response to freezing. Studies of freezing tolerance of vegetative and reproductive tissues have so far had little success in identifying levels of resistance that could be used in improvement efforts.

This complexity of the response in wheat may be due, in part, to the complex origin of the allohexaploid genome. The series of responses to low temperature we see in modern-day wheat actually represents a composite response based in the different genomes. Given this level of complexity, it probably should not be considered surprising that improvement of freezing tolerance has so far been elusive. Maximum freezing tolerance will only be obtained in plants in which all of the pathways and interactions function optimally, and defining a genotype where this is the case may require the appropriate combination of many alleles. The recent and current research defining genes and genomic regions that contribute to the survival of wheat following cold stress may ultimately lead to the molecular tools necessary to identify plants carrying these ideal combinations of alleles.

Part 2 Wheat quality traits

Whilst much research has been devoted to improving yields and dealing with biotic stress, it is important not to forget quality issues. As Chapter 8 indicates, quality of wheat is relative to the factors that make a specific genotype or grain lot suitable for the processing of a given end-product. Conventionally, wheat quality has been associated with the functionality of wheat in processing and in creating end-products such as bread with desired attributes. Wheat functionality can be deconstructed into a few broad categories such as grain quality, mechanical properties such as milling performance, and nutritional and other end-product attributes. The chapter reviews the extensive literature on the characteristics and factors affecting these different quality attributes, including the way wheat grain genetics, structure and chemical composition integrate to determine the properties of the grain. It also discusses factors affecting milling performance such as kernel hardness and ways of assessing flour quality.

Wheat quality derives fundamentally from interactions between the components of the kernel. In turn these components are themselves collections of multiple sub-components. The chapter therefore focuses on the three main polymeric components of wheat grain: protein, starch and fibre, as these are arguably the primary contributors to wheat flour functionality. The chapter also summarises the relationship between wheat composition, processing and nutritional quality, including the role of gluten (composed of glutenins and gliadins), as well as factors affecting protein composition such as interactions between the gluten proteins, molecular weight distributions and temperature during grain filling.

It also covers factors affecting starch composition and quality such as starch synthesis and granule size, amylose to amylopectin ratios, as well as non-starch polysaccharides (NSP) such as dietary fibre and the role of arabinoxylan (AX). Grain composition provides a series of potential targets for breeding.

Building on Chapter 8, Chapter 9 describes the effects of components such as protein and starch on wheat quality and how this affects quality measurement. Traditionally, protein content has been a basic measure of protein quality. For products made from wheat, there is a desired protein range and wheat is graded as suitable for a particular product based primarily on the protein content, for which there are a range of standard methods. These include rheological measurement of doughs, as well as the use of near infrared reflectance (NIR) spectroscopy and near infrared transmittance (NIT). The chapter also reviews standard methods for measuring starch quality as well as variety identification techniques such as high performance liquid chromatography, reversed-phase HPLC (RP-HPLC) and capillary electrophoresis. There are also a number of DNA-based methods, all of which require the extraction of genomic DNA (gDNA) from the sample, amplification of markers, usually by polymerase chain reaction (PCR), followed by analysis of the markers. The chapter also discusses recent developments such as progress in real-time measurement, not only of protein and moisture content, but also of starch damage, ash content and colour.

As Chapter 10 notes, wheat accounts for between 20 and 80% of total food consumption in different regions of the world, providing a key source of carbohydrates, proteins and micronutrients. In addition, current research has also shown that wheat is a source of phytochemicals with nutraceutical value. The chapter describes the content and composition of nutrients and phytochemicals in wheat, and what we know about factors such as variety, genotype, growing environment and seasonal conditions that influence variation in concentrations, as well as the effect of milling on these components.

Carbohydrates are the major components in wheat, of which starch is the largest and a major source of energy. Whole wheat provides substantial amounts of dietary fibre (DF) and is a major contributor to the nutraceutical value of wheat-based products. Important wheat dietary fibre (DF) components include the non-starch polysaccharides (NSP) and arabinoxylan (AX). The chapter also describes the four major types of proteins: albumins, globulins, prolamins (gliadins) and glutelins (glutenin). It shows that protein nutritional quality is the product of several factors, including amino acid composition and the balance of essential amino acids (EAA). Although the concentrations of lipids in wheat are low compared to carbohydrates and proteins, linoleic and linolenic acids in particular are a source of essential fatty acids, tocopherols and pro-vitamin A carotenoids.

As Chapter 10 shows, wheat is also good source of B-vitamins such as thiamine, riboflavin, niacin and pyridoxine. Tocopherols are lipid-soluble antioxidants, also known as vitamin E. They comprise tocopherols and tocotrienols. As antioxidants, they quench free radicals that have been implicated in increased risk of chronic diseases such as cardiovascular disorders and cancer. Wheat is also a rich source of minerals, including macro mineral elements, such as calcium (Ca), magnesium (Mg), potassium (K) and phosphorus (P), and micro mineral elements such as selenium (Se), copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn).

In addition to being a source of nutrients, wheat and other cereals are significant sources of phytochemicals, particularly phenolic compounds and carotenoids. Phenolic compounds are the main phytochemicals found in whole grain wheat and include phenolic acids, flavonoids, anthocyanidins and phytosterols. Cereals such as wheat are also a minor but still significant source of carotenoids in the diet.

Research has shown that milling has both positive and negative effects on the nutritional and nutraceutical value of wheat. It removes the bran and the germ fractions from the starchy endosperm that is ground into refined flour. The bran and germ are fractions where most of the micronutrients and phytochemicals are concentrated. It can also be beneficial in concentrating components such as starch and sugar as well as redistributing nutrients in the different flour/milling fractions. The presence of flavonoids apigenin-C-diglycosides in flour has been attributed to redistribution during milling since these flavonoids are localised only in the germ. The complete benefits of the nutritional and nutraceutical value of wheat can be realised through the use of whole-grains and milling fractions which retain high levels of nutritional and nutraceutical components though there remain processing challenges in achieving this.

Part 3 Wheat diseases, pests and weeds

As Chapter 11 points out, on average about 20% of the global wheat production is lost due to diseases and pests each year. The chapter provides an overview of what we know about the main fungal and viral diseases of wheat. In each case it reviews their mode of infection, effects on wheat plants, distribution and effect on crop yield. It also discusses ways pathogen have been adapting to wheat production systems, including the growing challenge of fungicide resistance.

The chapter starts with an overview of fungal diseases such as leaf rust, stripe rust, stem rust, powdery mildew, *Fusarium* head blight and *Fusarium* crown rot, tan spot, smuts, *Septoria* diseases, blast, spot blotch and eye spot. It then looks at soil-borne viruses including soil-borne wheat mosaic virus, soil-borne cereal mosaic virus, wheat spindle streak mosaic virus and wheat yellow mosaic virus. The chapter also covers insect-transmitted viruses including barley yellow dwarf virus, cereal yellow dwarf virus and wheat dwarf virus before concluding with the key mite-transmitted virus: wheat streak mosaic virus.

The chapter illustrates the dynamic nature of the ongoing battle with disease, for example the potential shift north of insect-transmitted viruses with climate change (a theme also picked up in Chapter 19), or the impact of changes in agricultural practices such as reduced/zero tillage and shorter crop rotations on fungal pathogens like *Fusarium* species (an issue also discussed in Chapter 13). It highlights the continuing need to adapt wheat production systems, develop more integrated disease management strategies, including developing new fungicides and insecticides and, in particular, the development of resistant cultivars which offer the most cost effective and environmental friendly method of plant protection against diseases such as leaf rust, stripe rust, stem rust and powdery mildew.

Building on Chapter 11, Chapter 12 provides a comprehensive review of advances in control of wheat rusts with a focus on breeding. The chapter starts by looking at the role of surveillance. Information generated by pathotype surveys allow the identification of the most relevant pathotypes for use in screening and breeding, predictions of the regional effectiveness/ineffectiveness of resistance genes, and have also been used to issue advance warning to growers by identifying new pathotypes that overcome the resistance of cultivars before they reach damaging levels. An example is the Global Cereal Rust Monitoring System (GCRMS), which aims to provide a detailed, online, geo-referenced

information system on where rusts are occurring, their virulence profiles, hot-spots and migration patterns over time.

A second key issue is understanding pathogen biology. Examples are the mechanisms generating variability in rust pathogens such as sexual recombination and ways this can be exploited, for instance by eliminating local sources of initial inoculum so that the rust cannot survive at the uredinal stage year-around due to a lack of host plants. Recognition of increases in virulence can also be important in relation to changes in field responses of resistant cultivars. Molecular genetics is increasingly providing new tools for use in rapid diagnostics, in understanding the population genetics of rust pathogens, and in unravelling how rust pathogens interact with their hosts at the cellular level, including the way pathogens suppress plant natural defences using effector proteins.

Counterbalancing an understanding of pathogen behaviour is understanding mechanisms of plant resistance, including PAMP-triggered immunity (PTI) and Effector-triggered immunity (ETI). As the chapter indicates, currently over 200 genes have been catalogued that provide resistance to one or more of the three rust pathogen species that parasitise wheat. Two distinct categories of rust resistance genes have been identified: all-stage resistance (ASR) genes (previously referred to as seedling resistance genes) and adult plant resistance (APR) genes. Considerable progress has been made towards defining wheat APR genes, with numerous quantitative trait loci (QTL) that provide APR to cereal rusts. These have enabled perfect markers to be produced for these cloned genes which have facilitated disease resistance breeding. A growing number of ASR and APR host genes are being cloned, complemented by non-host resistance genes. Recent major advances in wheat transformation make the possibility of stacking multiple rust resistance genes together at a single transgene locus an attractive proposition.

This knowledge can then be deployed in various methods to transfer resistance genes. Referring back to Chapter 1, one goal should be pre-breeding or germplasm development for the identification and improvement of genetic stocks with resistance to specific races of the pathogen. A second major goal is the deployment of a gene or genes in field-ready cultivars to confer effective and durable resistance to each of the pathogens. Stacking or pyramiding of multiple resistance genes is generally accepted as the preferred strategy to longer-term control of the rusts through resistant cultivars. The chapter looks at challenges and techniques in achieving this through different breeding techniques (as outlined in Chapter 3), including exploiting the broad but partial resistance of APR with effects on multiple rust pathogen species for the efficient incorporation of resistance. It shows, for example, the role of molecular markers in facilitating the stacking of resistance genes. Marker-assisted breeding can be used to enrich the gene frequency of desirable rust resistance alleles. The chapter also identifies the potential of techniques such as genomic selection and gene editing.

Finally, the chapter highlights the problem of recurrent failures in resistance and the need for longer-lasting or more durable resistances through agronomic, epidemiological and breeding strategies. Resistance gene stewardship can be defined as careful and responsible management of resistance genes with the goal that they remain effective for prolonged use. Based on examples such as the Borlaug Global Rust Initiative, several strategies have been proposed including multilines, cultivar mixtures, regional gene deployment, temporal rotation and pyramiding of resistance genes. All of these strategies seek to reduce selection pressure on the pathogen population and increase gene diversity.

Complementing Chapter 12, Chapter 13 reviews advances in tackling *Fusarium* head blight, wheat blast and powdery mildew. After reviewing patterns of disease and crop

losses, the chapter summarises the range of control measures, starting with agronomic practices such as: tillage regime and crop rotation (especially in relation to *Fusarium*), elimination of secondary hosts such as weeds and volunteer plants, the importance of clean seed and seed treatment with a combination of fungicides, varietal diversification, timing of planting, seeding density, fertiliser levels and application. It identifies the limitations of chemical control in the case of *Fusarium* head blight and wheat blast, the potential use of fungal and bacterial biological control agents, as well as the importance of disease forecasting and decision support systems in allowing more targeted site-specific use of fungicides. These control measures are also discussed in Chapter 16 on integrated disease management.

Echoing Chapter 12, it highlights the key role developing resistant varieties plays in integrated disease control, particularly for *Fusarium* and the challenge of creating regionally adapted cultivars that combine high and stable yield and quality performance with resistance to the diseases and pests. As this and previous chapters show, DNA-based markers can be applied to augment conventional breeding, especially for *Fusarium* resistance traits that are difficult or costly to select using conventional methods. Mapping of quantitative trait loci (QTL) either in specifically designed mapping populations or in association mapping panels has led to the discovery of numerous QTL associated with resistance to *Fusarium* and DNA markers linked to these QTL which can be used in marker-assisted breeding. The chapter highlights the potential of genomic selection (GS) to supplement selection for quantitative, multi-genic traits, for which individual QTL are difficult to find and/or validate. The chapter also highlights future challenges such as the need to find out more about the biological function of *Fusarium* resistance genes, better characterisation of APR genes for powdery mildew, as well as the limited genetic resources and lack of genomic knowledge which is hampering resistance breeding to wheat blast.

Building on Chapter 13, Chapter 14 provides a detailed case study of breeding for resistance to diseases such as *Fusarium* head blight. The challenge of breeding for resistance to quickly evolving pathogens such as the rusts and powdery mildew and avoiding the 'boom and bust' cycle observed after the deployment of race specific resistance genes can be confronted by greater use of race non-specific genes that have proven more durable. In the case of diseases such as *Fusarium* head blight, the use of screening nurseries and QTL mapping to better understand the genetics of resistance has helped to identify QTL for selection with DNA markers. DNA marker mapping for disease resistance has been largely successful because most plant diseases are controlled by relatively few genes and those genes and the effects of those genes are generally consistent across genetic backgrounds. As an example, the *Fhb1* QTL (syn. *Qfhs.ndsu-3BS*) has been used extensively in marker-assisted breeding programmes worldwide during the past 15 years and has resulted in routine development of *Fusarium*-resistant varieties, reducing disease symptoms by an average of about 25%. With the reduction in sequencing costs, the chapter (like Chapter 13 and other chapters) also highlights the potential of genomic selection in dramatically reducing the size of screening nurseries and allowing breeders to focus resources on characterising breeding lines and parents that have been predicted by genomic selection to have at least moderate resistance. The chapter also assesses the potential of transgenic approaches, for example in the co-introduction of groups of genes to maximise resistance over time, as well as developments in hybrid breeding for resistance.

Plant responses to pathogen infection are mostly initiated through specific recognition of the pathogen followed by signal transmission via plasma membrane-bound receptors. Recent advances in the field of molecular biology and high-throughput technologies have

provided newer tools for understanding these plant-pathogen interactions which then allow more rapid development of agronomically superior and disease-resistant varieties. Chapter 15 discusses some of the most promising of these tools and technologies for the effective management of wheat diseases, for example in boosting effectors-mediated disease resistance as well as transcription factor/peptides-mediated disease resistance.

The chapter reviews novel techniques for developing disease-resistant wheat plants, including the integration of genes involved in expressing *R*-genes, phytoalexins, antimicrobial phenolics/pathogenesis-related (PR) proteins, strengthening of structural barriers, detoxification of pathogen virulence factors and genes involved in host defence-signalling pathways. There is the potential to develop techniques to exploit pathogenesis-related (PR) protein, RNA interference (RNAi), virus-induced gene silencing (VIGS) and genome-editing-mediated disease resistance, as well as systemic acquired resistance (SAR), a secondary resistance response that is activated in whole plant by local defence responses, and induced systemic resistance (ISR) which promotes plant growth promoting rhizobacteria (PGPR) to strengthen plant health and resistance.

In addition to the use of molecular markers in MAS, techniques such as genome selection, TILLING and gene pyramiding have further revolutionised wheat breeding for multiple traits including disease resistance. Genomic selection has made it possible to develop new varieties more rapidly by manipulating several complex traits like disease resistance, drought tolerance and yield together. Finally, the chapter reviews new methods for detecting and modelling plant pathogens, ranging from nucleic-acid-based molecular diagnostic techniques, including DNA/RNA probe technology, PCR, micro-array techniques, real-time and multiplex PCR, to serodiagnostic techniques including enzyme linked immunosorbent assay (ELISA).

Building on Chapter 13, Chapter 16 discusses integrated disease management, which involves combining different approaches to manage plant diseases. Chapter 16 reviews the range of research on the effectiveness of these techniques and how they can best be deployed as well as the synergistic effects of combining techniques in disease control. These tactics include scouting, disease identification and forecasting as well as variety selection. Variety selection uses models such as the NIAB interactive cereal variety Gross Margin Model to factor in the value of selecting for disease resistance compared to other traits. Planting different varieties with varying flowering dates spreads the risk of infection.

Other tactics in integrated disease management include cultural practices, chemical and biological control. In wheat production, the most common cultural practices used to manage diseases include crop rotation (such as use of break crops), residue management, tillage, planting date, nutrient and irrigation management as well as control of volunteer plants and weeds which can serve as hosts for wheat diseases, passing them on from one crop to the next. Tillage and residue management practices can reduce or increase incidence and severity depending on the disease. The chapter reviews the effects of these management practices on four wheat diseases: *Cephalosporium* leaf stripe, tan spot, *Fusarium* head blight and take-all. It compares conventional tillage to reduced/zero tillage practices in relation to the management of crop residues which can harbour residue- and soil-borne diseases. The chapter also reviews studies of the effects of altering planting dates, using as examples root and crown rot fungal diseases, above-ground fungal diseases and viruses. The chapter also shows how insufficient or excessive nutrients can increase susceptibility of plants to diseases such as powdery mildew and stripe rust. Irrigation can also create an environment that is favourable to disease development because moisture is the dominant factor in the development of many plant disease epidemics. To minimise

disease risk, irrigation should be managed such that the wheat crop canopy can dry between irrigations.

Finally, the chapter looks at chemical and biological control, including a detailed review of range of fungicides for seed treatment or foliar application. It also explores the research demonstrating the potential of biological control agents (BCAs) to reduce root, stem base, foliar and head diseases of wheat. As an example, antagonistic activity against *Fusarium* spp. has been demonstrated for bacteria such as *Bacillus* spp. and *Pseudomonas* spp., as well as fungal antagonists such as *Cryptococcus* spp. and *Trichoderma* spp. Further research is needed to develop them to quantities and formulations that can be used on a commercial scale.

The next group of chapters moves from diseases to the main pests of wheat. Chapter 17 focuses on rodent and nematode pests, starting with case studies on mice and vole infestations, their causes and impact. It then surveys different aspects of rodent management, whether chemical methods such as anticoagulant rodenticides or non-chemical approaches, from agronomic practices such as field management to reduce food and habitat opportunities to biological control measures such as encouraging predators. As the chapter indicates, optimal rodent management in wheat should be ecologically based, taking into account the ecology and biology of the target species and effects on non-target species. The chapter also discusses nematode pests with case studies on root-lesion and cereal cyst nematodes. It then reviews the challenges in detecting, sampling and managing nematode pests, including the limitations of nematicides and agronomic practices such as tillage which place the emphasis on the use of wheat cultivars that resist or tolerate nematode attack.

Some of these themes are reflected in Chapter 18, which tackles the major topic of insect pests with representative case studies on the Hessian fly, orange wheat blossom midge, bird cherry oat aphid, greenbug, Russian wheat aphid, Sunn pest, wheat stem sawfly and wheat curl mite. In each case the chapter reviews the insect's life cycle, host plants and status as a wheat pest, ways of understanding plant susceptibility and resistance (including Insect Resistance Management (IRM) to improve and maintain resistance) as well as ways of managing populations (a topic discussed in more detail in Chapter 20 on integrated pest management). Common themes include the limitations of over-reliance on insecticides and the importance of biocontrol methods such as the preservation of natural enemies such as egg-larval parasitoids through conservation agriculture. The chapter also reviews the role of cultural practices such as planting dates, field management techniques such as control of volunteer wheat, the relative merits of conventional versus zero-reduced tillage and the importance of resistant varieties.

Picking up on Chapter 18, Chapter 19 focuses on the ways climate change might affect patterns and severity of insect pest damage to wheat, looking at examples such as cereal aphids, Hessian fly, orange wheat blossom midge, cereal leaf beetle, cotton bollworm and other pest species affecting wheat. These pests can respond to climate variability through changes in the timing and abundance of their annual migrations, which can affect their arrival into fall and spring planted crops, with implications for viral disease epidemiology. The chapter reviews the literature on the potential impact of climate change on the principal insect pests of wheat, the different methods that have been employed to assess likely impacts, and the gaps in knowledge that exist, as well as suggesting a research agenda to address these gaps.

Building on both Chapters 18 and 19, Chapter 20 provides an overview of integrated pest management (IPM) in wheat cultivation. IPM combines chemical with biological and

cultural methods. The chapter reviews the problems in over-reliance on insecticides. These include increasing restrictions on compounds such as neonicotinoids and the emergence of insect strains resistant to insecticides. They also include the fact that insecticides (whether broad-spectrum or more selective) can result in the development of secondary pest outbreaks (e.g. due to loss of predator species).

IPM in grain crops has benefited considerably from the increased availability and adoption of biopesticides as well as biological control agents, whether resident (ground-dwelling) or transient (foliar-foraging) predators and parasitoids. Cultural measures include variety selection, avoiding large-scale monocropping in favour of crop rotations, timing of planting, tillage practices (including stubble management) and nutrient management, as well as leaving unsprayed strips and planting field margins with appropriate year-round plants as a refuge for predator species. A key issue is the knowledge and motivation to adopt IPM practices in a flexible way that suits individual farm conditions. The chapter includes a case study of a participatory IPM project in New Zealand which shows both its effectiveness and how direct access to experts by farmers is critical for the successful adoption of IPM.

The final chapter in the book is on integrated weed management (IWM) and picks up a similar theme to Chapter 20 by showing that overuse of herbicides has led to weed resistance to herbicides and the need for alternative weed control strategies that will preserve herbicide efficacy as well as agricultural and environmental sustainability. The focus of the chapter is on cultural strategies that can be used as part of an IWM strategy with the aim of promoting wheat plant growth and canopy closure to outcompete weeds. Cultural practices that improve wheat plant health whilst inhibiting weeds include diverse crop rotations, the proper placement and timing of balanced nutrients, no-till and direct seeding. Practices that promote wheat canopy closure include growing competitive cultivars, cultivar mixtures, seeding date, increasing wheat density, decreasing wheat row spacing, planting wheat in uniform patterns, and intercropping. Combining several of these cultural practices is more likely to lead to successful IWM than focusing on any single practice. Integrating cultural, herbicidal, physical and biological weed control methods into economically feasible and regionally adapted cropping systems is an urgent activity for researchers, agronomists and growers interested in sustainable agriculture and the preservation of valuable herbicide tools.

Summary

Written by some of the world's leading experts in their subjects, these chapters provide an authoritative review of the state of the art in key areas of wheat research. They both reflect and make a contribution to the priorities set out in the cross-cutting themes identified in the Wheat Initiative's Strategic Research Agenda:

- enabling technologies and shared resources
- knowledge exchange and education

Chapters show the importance of identifying gaps in germplasm coverage, for example in dealing with wheat blast as well as the huge potential of mapping the wheat genome achieved by the International Wheat Genome Sequencing Consortium, and through

analysing gene networks involved in more complex physiological processes such as response to abiotic stresses.

Chapters show the current constraints and potential to improve current breeding techniques as well as develop new ones, such as the strides made in deploying marker-assisted selection (MAS), especially in areas such as disease resistance, as well as the potential of techniques such as genomic selection (GS) able to manipulate complex traits such as drought resistance. The chapters also demonstrate the current limits in our knowledge, for example the need to know more about plant physiology and to measure complex processes such as nitrogen assimilation, photosynthetic capacity, drought resistance and cold tolerance. They also show the complexity of pathogen–plant interactions and behaviour as well as how this understanding can be used in future to disrupt pathogens and enhance plant defence mechanisms.

The chapters show both the importance of breeding in such areas as insect and disease resistance and integrating developments in breeding with agronomic practices, as well as ensuring that agronomic practices such as zero/reduced tillage are compatible with and support integrated insect and disease management strategies. A truly sustainable future lies in a coordinated and synergistic combination of approaches from pre-breeding to harvest and beyond.

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