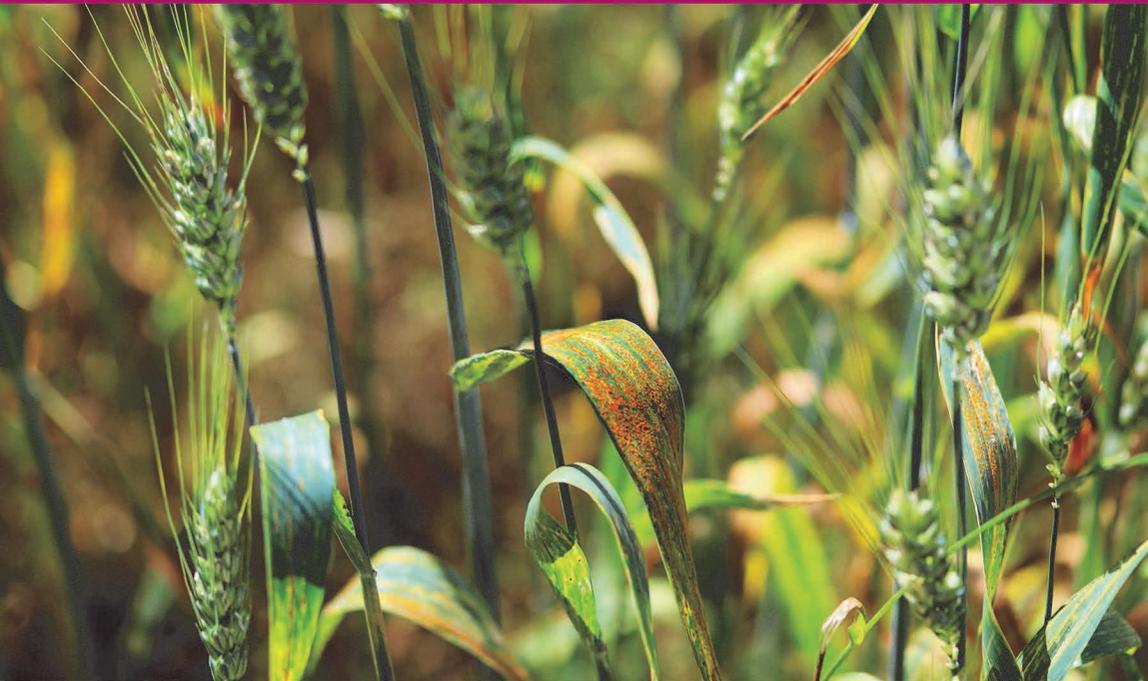


BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Achieving durable disease resistance in cereals

Edited by Professor Richard Oliver, formerly Curtin University,
Australia



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Achieving durable disease resistance in cereals

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Introduction

This volume offers a comprehensive review of research on achieving durable resistance to diseases in cereals. The book opens with a chapter on global patterns in cereals diseases and is then broken down into eight parts. Parts 1 through 6 cover various fungal diseases, such as leaf rust, *Fusarium* head blight, *Septoria tritici* blotch, *Septoria nodorum* blotch and spot blotch, net blotch, and finally, tan spot, blast and *Ramularia*. Chapters in Part 7 of the book focus on barley yellow dwarf virus (BYDV), specifically highlighting the advances in understanding the biology and epidemiology of BYDV and how identifying resistance genes can help breed durable disease-resistant cereals. The final part of the book discusses the regional strategies for breeding durable disease-resistant cereals, focusing on North America, Northwest Europe, North Africa and West Asia.

Chapter 1 sets the scene by highlighting the global patterns of cereal diseases and the impacts of breeding for host plant resistance. Plant breeding for host plant resistance to pathogens brings together different disciplinary domains, especially genetics and plant pathology. The strategies underpinning plant breeding have therefore, logically, been influenced by a number of paradigms that have dominated the field of disease management. The chapter provides a brief overview of these paradigms, where the authors link the implications for plant breeding. It also discusses the meaning of crop losses for plant breeding, then goes on to highlight three paradigms: pathogen elimination and total control, disease management and ecological disease management.

Part 1 Fungal diseases of cereals: rusts

The first chapter of Part 1 examines advances in understanding the biology and epidemiology of rust diseases in cereals. Chapter 2 provides an overview of the wheat rust pathogen lifecycle that has been critical to the design of effective disease management strategies and discusses recent integration of basic biological knowledge and genomic-led tools within an epidemiological framework. The chapter also includes a case study on the 'field pathogenomics' technique, illustrating the value of genomic-based tools in disease surveillance activities. Bringing together advances in understanding basic pathogen biology, developments in modelling for disease forecasting and identification, alongside genomic-led advances in surveillance and resistance gene cloning, holds great promise for curtailing the threat of these notorious pathogens.

Chapter 3 reviews advances in identifying stripe rust resistance genes in cereals. Stripe rust is one of the most serious wheat diseases of the world, usually resulting in massive loss of grain production. The most effective and environmentally friendly way to control the spread of stripe rust is to plant wheat varieties that carry stripe rust resistance genes. The identification and utilization of stripe rust resistance genes is very important for achieving this goal. The chapter summarises the hazards of stripe rust and the current progress in the discovery of stripe rust resistance genes. It also introduces the advanced methods to identify Yr genes. The chapter also shows the successful application of Yr genes in wheat breeding program in southwestern China, which is the largest epidemic area of stripe rust in the world. The further identification and applications of Yr genes are also discussed.

Part 2 Fungal diseases of cereals: Fusarium head blight

Part 2 opens with a chapter that reviews advances in understanding the epidemiology of *Fusarium* in cereals. Chapter 4 begins by discussing the life cycle of *Fusarium* head blight (FHB) and the factors that can affect the length of the life cycle, including environmental factors and disease management strategies. The chapter then goes on to address mycotoxin production and the influence of environmental factors on disease development, followed by a section on how management practices can influence the risk of disease. The chapter also examines the various methods that can be used to predict FHB epidemics, emphasises the importance of detecting and identifying plant pathogens for disease diagnosis and also provides a discussion on the importance of assessing FHB at the right time.

Moving on to Chapter 5, this chapter focuses on cereal-*Fusarium* interactions. All cereal crop species are vulnerable to root, stem-base and floral diseases caused by various *Fusarium* species. Most problematic is *Fusarium* head blight because grains become contaminated with harmful mycotoxins. Currently, *Fusarium* control using fungicides is only partially effective, whilst cultivars with acceptable resistance levels are scarce. The chapter reviews the recent advances in fundamental knowledge on the cell biology of interactions, the in-planta production of trichothecene mycotoxins, *Fusarium* genomes/pan-genomes, newly discovered *Fusarium* virulence factors, small, secreted effectors, plant defence components and resistance genes underlying major quantitative trait loci. These discoveries are discussed in the context of exploiting new intervention targets to achieve control through genetic modification, gene editing and HIGS. Finally, the chapter explores how to develop a more integrated approach that includes marker assisted selection in breeding programmes, removal of susceptibility loci and the inclusion of new approaches arising from plant defence, virulence and effector studies.

The final chapter of Part 2 of the book examines advances in genetic improvement of durable resistance to *Fusarium* head blight, specifically focusing on wheat. Wheat *Fusarium* head blight is a destructive disease in wheat worldwide. Wheat resistance to FHB is a complex with five types. Each type of resistance is controlled by multiple quantitative trait loci (QTLs) with most having minor effects and being affected by environments. Chapter 6 describes methodologies used for evaluating different types of resistance, consolidates the QTLs for type II and Type III resistance into 26 repeatable QTLs, discusses progresses made in genetics and breeding of wheat FHB resistance, and discusses possible new breeding strategies for FHB resistance improvement. The 26 repeatable QTL were located in ~100 Mb intervals based on IWGSC reference sequence map, which will be critical QTLs for functional marker development and for improvement of FHB resistance in breeding. Genomic selection (GS) together with marker-assisted selection (MAS) coupling with phenotypic selection will facilitate accumulation of multiple QTLs from different sources to create highly resistant cultivars.

Part 3 Fungal diseases of cereals: Septoria tritici blotch

The first chapter of Part 3 examines advances in understanding the epidemiology of *Septoria tritici* blotch in cereals. Chapter 7 begins by discussing the taxonomy of *Zymoseptoria tritici* and how *Septoria tritici* blotch is formed. The chapter then goes on to review the life cycle of *Zymoseptoria tritici* and the modes of nutrition at various stages in its growth cycle. Moving on from this, the chapter reviews the epidemiology of *Septoria tritici* blotch and how diagnosing the disease is important, especially at an early stage in its infection period. It concludes by providing an overview of the steps that need to be taken in order to progress in understanding the biology and epidemiology of *Septoria tritici* blotch.

Expanding on topics previously discussed in Chapter 7, Chapter 8 moves on to review plant-pathogen interactions in *Septoria tritici* blotch infection of cereals. The chapter begins by introducing the biology and epidemics of *Zymoseptoria tritici* on wheat, then moves on to discuss *Z. tritici* genomics, focusing specifically on genome characteristics, the *Z. tritici* pangenome, related *Zymoseptoria* species genomics and *Zymoseptoria* transposons. The chapter also discusses the molecular and biological tools available in *Z. tritici* as well as the molecular biology of *Z. tritici* infection, focusing on aspects such as cell biology, transcriptomics of *Z. tritici* infection and secondary metabolism. A section on *Septoria tritici* blotch disease management and control is also provided, before concluding with an overview of why analysing *Z. tritici* infections as a model to study plant-pathogen interactions is important.

The subject of Chapter 9 is advances in understanding breeding techniques for durable *Septoria tritici* blotch resistance in cereals. *Septoria tritici* blotch (STB), caused by the hemibiotrophic fungus *Zymoseptoria tritici*, is one of the most important foliar diseases of winter cereal crops. Recent advances are helping to understand the genetic basis and architecture of resistance to STB. To date, at least 22 genes for qualitative resistance and over 200 quantitative trait loci for quantitative resistance have been identified in cereals. This knowledge is enabling cereal breeding programs to develop varieties with more durable resistance to STB. The chapter reviews recent research on genetic resistance loci and breeding strategies based on both conventional and biotechnology-based breeding approaches (molecular marker/genomic-assisted breeding, genetic transformation, and gene-editing) to achieve achieving durable resistance to STB infection and minimise grain yield losses.

Part 4 Fungal diseases of cereals: *Septoria nodorum* blotch and spot blotch

Part 4 opens with a chapter that examines understanding the plant-pathogen interaction associated with *Septoria nodorum* blotch of wheat. Chapter 10 begins by reviewing the necrotrophic effector-host sensitivity gene interactions in the wheat-*P. nodorum* system. It then reviews the genetic relationship between NE-sensitivity gene interactions and the importance of these interactions in the field. Additional QTL associated with susceptibility/resistance to *P. nodorum* is also discussed, followed by a section on the impact of genome sequencing in characterizing NE-sensitivity gene interactions.

Chapter 11 analyses advances in genetic mapping of *Septoria nodorum* blotch resistance in wheat and applications in resistance breeding. *Septoria nodorum* blotch (SNB) caused by the necrotrophic fungus *Parastagonospora nodorum* is an important wheat disease in many high rainfall areas across the world. It reduces both yield and grain quality by causing symptoms on wheat leaves and glumes and can cause yield losses up to 30% under warm and humid conditions. The chapter gives an update on the recent progress in genetic mapping of SNB resistance in wheat, with focus on adult plant leaf blotch and glume blotch resistance with relevance to resistance breeding. This is followed by a case study on the investigation of the naturally occurring *P. nodorum* population in Norway and mapping of resistance loci in relevant wheat germplasm using multi-parent advanced generation inter-cross (MAGIC) populations and genome-wide association study (GWAS) panels as well as how this information can be used to improve resistance breeding and disease management. The chapter concludes by providing some future perspectives of SNB resistance breeding is provided.

The next chapter focuses on advances in breeding techniques for durable resistance to spot blotch in cereals. Chapter 12 starts by highlighting the spread, economic importance and the disease cycle of spot blotch. The chapter then goes on to examine the diversity of the pathogen and physiological specialization. This is then followed by a discussion on the identification of resistance sources, as well as the histological, biochemical and morphological components of resistance. The chapter also reviews molecular approaches for resistance breeding, specifically focusing on QTL and GWAS. Resistance genes and their possible deployment are also discussed, along with a section on low molecular weight toxins and their possible role in pathogenicity. The chapter also examines necrotrophic effector triggered susceptibility and associated genes and breeding for spot blotch resistance in wheat. Breeding for spot blotch resistance in barley is also discussed, before concluding with a discussion on farmers participatory research in the release of spot blotch resistant varieties.

Part 5 Fungal diseases of cereals: net blotch

Chapter 13 focuses on advances in understanding the epidemiology, molecular biology and control of net blotch and the net blotch barley interaction. Net blotches are the most widely distributed foliar diseases of barley worldwide, causing significant losses in grain yield. They occur as net form net blotch, caused by *Pyrenophora teres* f. *teres* and spot form net blotch caused by *P. teres* f. *maculata*. Both sexual and asexual reproduction play a role in the *P. teres* disease cycles leading to changes in genetic variation of populations. Breeding programs have to keep pace with pathogenic changes and ensure different sources of resistance are present in current barley cultivars. Knowledge of the genetic architecture and genes involved in virulence is thus vital to increase the durability of net blotch resistance in barley cultivars. The chapter explores the molecular biology, lifecycle and epidemiology of the net blotch fungi and discusses the key challenges we are facing in managing the net blotches using both fungicide resistance and breeding strategies to achieve durable disease resistance in barley.

The next chapter discusses understanding plant-pathogen interactions in net blotch infection of cereals. An economically important disease of barley that causes significant yield and quality losses is net blotch caused by the necrotrophic fungal pathogen *Pyrenophora teres*. To reduce the impact of net blotch the research community is engaging in basic and applied research to enhance genetic resistances, as it is the most economic and sustainable management strategy. Durable resistance against *P. teres* will be a major achievement towards the goal of developing widely adapted barley varieties that have high yields and quality across dynamic environments. Chapter 14

focuses on a thorough review of the latest knowledge of both host resistance/susceptibility and pathogen virulence/avirulence in this important pathosystem, and the implications this knowledge will have on deploying sustainable resistances to this destructive pathogen of barley.

The subject of Chapter 15 is breeding barley for durable resistance to net and spot forms of net blotch. It starts by reviewing how *Pyrenophora teres* f. *teres* can cause net form of net blotch. The chapter then goes on to examine the molecular markers that can be identified to provide resistances to net form net blotch. A section on the population dynamics of barley-*P. teres* f. *teres* interactions is also provided. The chapter also reviews how breeding crops with specific genes can help to create durable resistance to net form blotch. It moves on to discuss how *Pyrenophora teres* Drechs. f. *maculata* can cause spot form net blotch and how identifying specific molecular markers can help provide resistance to this form of net blotch. The chapter concludes by highlighting the importance of combining durable resistance to both forms of net blotch.

Part 6 Fungal diseases of cereals: tan spot, blast and Ramularia

The first chapter of Part 6 reviews tan spot disease under the lenses of plant pathologists. Chapter 16 begins by examining the global presence of tan spot. The chapter then goes on to review the fungal and pathogen forms of *Pyrenophora tritici-repentis* (Ptr). A case study on tan spot on the prairies is also provided, focusing specifically on its emergence and agronomic background, the different races of Ptr and the genetic diversity between them, focusing predominantly on ToxA. The chapter also discusses the development of the disease rating system, addressing how early screening for resistance is important for treating diseased crops. The chapter concludes by emphasising how much tan spot disease infection research has changed in the last 90 years.

Chapter 17 examines the development of an early warning system for wheat blast. Wheat blast is caused by the fungus *Pyricularia oryzae* *Triticum* pathotype (PoT). Significantly damaging wheat blast epidemics are sporadic and limited to tropical wheat growing areas in South America. Unexpectedly, wheat blast was reported in Bangladesh and Zambia in 2016 and 2020, respectively. The urgent need to deal with a poorly studied disease has mobilized the scientific community. Original research and reviews have been published in various venues. Nevertheless, disease control is still a difficult task. Much less research has, however, focused on crucially important and complex ecological interactions at the field, landscape, or regional levels. The chapter reviews aspects of the epidemiology of wheat blast, mainly those related to inoculum and its role for the epidemics. It then describes the models that have been developed by the authors as well as the decision support system.

Examples of the implementation of a warning system in Bangladesh and Brazil are also illustrated.

The subject of Chapter 18 is investigating the biology of rice blast disease and prospects for durable resistance. There are important biological processes involved in rice blast disease that are now well-studied during the early events in plant infection which include: the cell biology of appressorium formation, the biology of invasive growth and effector secretion, the two distinct mechanisms of effector secretion, the nature of the plant-pathogen interface, PAMP-triggered immunity modulation by secreted effectors and effector-triggered immunity and blast resistance. The devastating losses caused by the blast fungus have been documented in most grasses, but this chapter discusses the use of major resistance genes to rice blast and wheat blast disease as an emerging threat to global food security. The chapter also highlights an emerging approach to breed for durable resistance to plant pathogens using gene editing technologies with an example: CRISPR-Cas9 mutagenesis of dominant S-genes for disease control.

The final chapter of Part 6 examines *Ramularia* leaf spot in barley. *Ramularia* leaf spot is an emerging pathogen across barley growing regions of the world. Its rise from minor to major disease has been rapid over the last twenty years. Chapter 19 reviews the latest research into *Ramularia* biology and control and highlights the areas where recent advances have been made. The chapter begins by reviewing how the fungal pathogen *Ramularia collo-cygni* was first reported along with the symptoms that appear in barley crops. It also highlights where *Ramularia* leaf spot first emerged and how it was globally distributed when it was first discovered. The chapter also goes on to analyse the life cycle of the fungus as well as the impact of different environmental factors on disease expression. Sections on genetics of disease resistance, pathogen variability and control of *Ramularia* leaf spot by fungicides are also provided.

Part 7 Barley yellow dwarf virus

Part 7 opens with Chapter 20, which analyses the advances in understanding the biology and epidemiology of Barley yellow dwarf virus. A tri-trophic network of domesticated grasses (host), various aphids (vector) and barley yellow dwarf virus (pathogen) species has been spread by humans from Eurasia to the rest of the world. Understanding how climate, natural and agricultural landscapes challenge pathogens, vectors, and their natural enemies and shape their dynamics is the key to managing this pathosystem. The chapter provides an overview of this complex system and its evolution. The chapter includes a case study of biological control of aphids causing wheat BYDV in Brazil. The current challenge is to create tools that integrate knowledge of this complex

pathosystem and facilitate monitoring and decision making for rational management to reduce the burden of disease.

Moving on from Chapter 20, Chapter 21 focuses on resistance breeding in barley against barley yellow dwarf virus. Barley yellow dwarf is one of the most widespread and damaging viral diseases of grasses and cereal crops worldwide. Due to an increasing risk of food losses e.g. in barley by Barley yellow dwarf virus as a consequence of climate change, associated by a strong demand to decrease the use of chemical insecticides, breeding for BYDV resistance is of prime importance today. The chapter describes the negative impact of BYDV on barley on multiple levels (anatomy, physiology and agronomic traits). It also demonstrates the benefits of BYDV resistance regarding a reduction in yield losses but also a decreased spread of BYDV in the field due to effects on the tritrophic interaction of virus, vector and plant. Until now, several genes and QTL are known that mediate tolerance or resistance against BYDV, respectively. The combination of genomic tools and phenotyping is the basis for the identification of these genes and recent developments facilitate to enhance this process.

Part 8 Fungal diseases of cereals: Regional strategies

The final part of the book begins with a chapter that focuses on the key challenges in breeding durable disease-resistant cereals in North America. Chapter 22 first describes the challenges of diverse climates, diseases, and market classes that face North American small-grain cereal breeders and producers. It discusses the challenges inherent in the complex systems of cereal breeding on the continent, and the changing resistance priorities brought about by shifting pathogen races and production practices. The remainder of the chapter is devoted (in rough order of priority) to the status and prospects for durable resistance to the main pests currently confronting the continent: Fusarium head blight, rusts, powdery mildew, leaf (and glume) blotches, viruses, Hessian fly, and bacterial leaf streak.

The next chapter reviews the achievements in breeding cereals with durable disease resistance in Northwest Europe. Chapter 23 begins by first identifying the main cereals produced in Northwest Europe, then goes on to highlight the additional sources of information about breeding for resistance, such as the AHDB Recommended List. The chapter also examines Plant Breeder's Rights, National List and Recommended List trials and how disease resistances can be rated on a scale of one to nine, one being most susceptible and nine being most immune. A section on the demand for disease resistance in cereals is also provided, emphasising why resistant varieties are needed and the minimum standards that need to be met. The chapter also highlights the use of a Variety Selection Tool. Sections on breeding elite cereal varieties with resistance to

multiple diseases, durable and non-durable resistance are also included. This is then followed by separate sections on resistance to biotrophic fungal diseases, non-biotrophic fungal diseases, viruses and insects. The chapter also examines mitigating trade-offs of disease resistance before highlighting the future disease threats for cereals.

The final chapter of the book reviews the key challenges in breeding durable disease-resistant cereals in North Africa and West Asia. Chapter 24 reviews progress and challenges in breeding disease-resistant cereals in the West Asia and North Africa (WANA) region. It discusses challenges in ensuring durable resistance in the face of constantly-evolving pathogen threats. It includes case studies on progress in combatting rust diseases in Iran and combatting Septoria in North Africa.

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