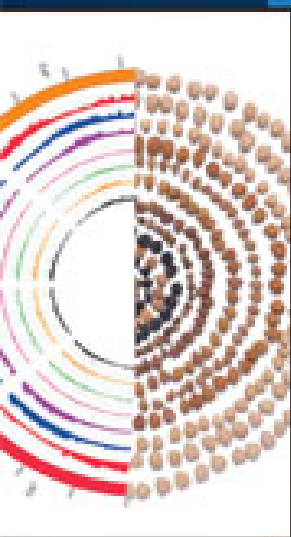


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Translational **G**enomics for **C**rop Breeding

Volume I: Biotic Stress

**Editors: Rajeev K. Varshney
Roberto Tuberosa**



WILEY Blackwell

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Translational Genomics for Crop Breeding, Volume I: Biotic Stress

Edited by

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Foreword

Drs. Rajeev K. Varshney and Roberto Tuberosa have done a great service by bringing out this important book, *Translational Genomics for Crop Breeding, Vol. 1: Biotic Stresses*. This volume deals with the application of genomics in crop breeding for biotic stress tolerance. It will be useful to refer briefly to the transformational role the new genetics based on genomic applications is playing today in improving agriculture, industry, medicine, and environment, following the elucidation of the double-helix structure of the DNA molecule 60 years ago by James Watson, Francis Crick, Maurice Wilkins, and Rosalind Franklin. Their discovery opened up uncommon opportunities for the advancement of science as related to all aspects of life. During recent decades, many Nobel Prizes in Physiology and Medicine have gone to molecular geneticists. At the same time, public concern about the proper measurement of risks and benefits has grown, particularly in the fields of agricultural and food biotechnology. Biotechnology provides an opportunity to convert bioresources into economic wealth. This has to be done in such a manner as to ensure no adverse impact either on the environment or on human and animal health. The bottom line of Indian national agricultural biotechnology policy should be the economic well-being of farm families, food security of the nation, health security of the consumer, protection of the environment, and the security of our national and international trade in farm commodities.

This volume is an epitome of advances in the area of translational genomics application for improving crops with resilience to important components of biotic stress. Integration of high-throughput genotyping with precise

phenotyping is the key for dissecting mechanism of complex traits at the molecular level. There are a number of races and biotypes known for a particular disease and insect, and so it is necessary to have a complete knowledge of the causal organism so that race-specific or biotype-specific resistance can be attained. This encourages optimal and target approach to breeding for the trait of interest. Hence, a more holistic approach and, more importantly, a holistic perspective such as that of systems biology is the need of the hour. The chapters in this volume not only provide in-depth review of the problem at hand but also enlighten readers about the advances and possibility of integrating genomics approach in tackling a research problem. In addition, the successful example and success stories discussed are thought provoking to young plant scientists and make them prepare for the challenges ahead.

New approaches for identifying marker-trait association such as genome-wide and candidate gene association studies are gaining fast acceptance due to advantages such as amenability to phenotype at multi-location for multiple traits and genotyping only once, not at each generation. In addition, marker-trait association is validated simultaneously in order to allow the deployment of markers directly in the breeding program. Another upcoming and promising approach termed as genomic selection is fast gaining importance among the crop specialists. It relies on the genomic-assisted breeding values, rather than phenotypic selection alone, in order to select the lines for crossing and advancing them to next generation. These approaches along with others are covered comprehensively in this book.

I hope this book will be widely read by scientists and scholars, since we must harness the best in the new genetics to overcome the serious threats to human well-being caused by malnutrition, hunger, and disease. The

contents of the book show the ways to enhancing productivity in perpetuity without ecological harm. I congratulate and thank Drs. Varshney and Tuberosa for their labor of love in helping harness the best in modern science for enhancing the quality of human life.



MS Swaminathan
Founder Chairman
M S Swaminathan
Research Foundation

Chennai
Date: June 15, 2013

Preface

Recent years have witnessed significant progress in the area of crop genomics mainly due to advances in next-generation sequencing and high-throughput genotyping. Such advances are driving genomics-assisted breeding (GAB), a discipline that has grown tremendously during the past decade, particularly for its applications to improve crop productivity and quality. This quantum leap has been possible through the continuous effort and dedication of those engaged in the translation of the findings of genomics research into improved genotypes and populations. As we anticipate a further reduction in genotyping/sequencing cost, translational genomics is expected to become a more integral part of crop breeding.

Biotic stress is one of the major factors behind crop losses. While a number of reports have been available on genomics approaches such as deciphering marker-trait association either through linkage or association mapping, some success stories have also been reported in recent years on translational aspects of this genomics research in crop breeding. However, the ever-changing and dynamic world of causal organisms of diseases and pests pose serious challenges to crop specialists to identify new resistant alleles and to target disease and pest resistance as well as to accelerate development of superior lines with enhanced resistance to biotic stresses. Therefore, there was an urgent need for a book in which translational genomics activities for resistance to key pests and diseases, success stories completed and in progress, and useful take-home messages from GAB efforts in different crops would be compiled. Along these lines, the 16 chapters of *Translational Genomics for Crop Breeding, Volume 1: Biotic Stresses* include not only

details on the aforementioned issues but also address perspectives and challenges in translational genomics for developing superior varieties and lines with enhanced resistance to biotic stresses.

We thank the authors (Appendix I) of different chapters for their commendable effort in summarizing the published and unpublished research and putting all the pieces together in a well-knitted, up-to-date manner, for the benefit of the research challenge in hand. In addition, the cooperation they have extended in terms of timely completion and revision of chapters is greatly appreciated. While editing this book, the strong support received from many other colleagues (Appendix II) willing to review the chapters is equally appreciated. Their constructive comments and suggestions have been instrumental in further improving the contents.

The editors are also grateful to colleagues and staff from their respective laboratories who helped complete the editing of the two volumes in parallel with their demanding responsibilities. In particular, Manish Roorkiwal, B. Manjula, Pawan Khera, and Mahendar Thudi helped RKV with the editorial work. The editors also wish to thank their respective families, as the editorial work for this book took away precious moments they should have spent together with their families. RKV is thankful to his wife Monika for her constant encouragement and support, and to Prakhar (son) and Preksha (daughter) for their love and cooperation. Similarly, RT is equally thankful to his wife Kay for her support and editorial help. RKV would also like to extend his sincerest thanks to Dr. William D. Dar, Director General, ICRISAT, for his guidance and support in completing this book. The cooperation and help received from Justin Jeffryes, Anna Ehlers, Kelvin Matthews, Erin Topp of Wiley Publishers, and Shikha Sharma of Aptara Corp. during various stages of development and completion of this book

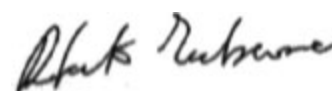
are gratefully acknowledged. RKV would also like to mention that the book was edited during the tenure of RKV as Director, Center of Excellence in Genomics (CEG), ICRISAT, Hyderabad (India), Theme Leader - Comparative and Applied Genomics (CAG), Generation Challenge Programme (GCP) and Adjunct positions at the University of Western Australia, Crops Research Institute of Guangdong Academy of Agricultural Sciences (GAAS), China and BGI-Hongkong Research Institute, China.

We hope that this book will be helpful and useful as a ready guide to students, young researchers, crop specialists, GAB and translational genomics practitioners, and policy makers for developing crops more resilient to biotic stress.



(Rajeev K. Varshney)

Hyderabad, India
June 10, 2013



(Roberto Tuberosa)

Bologna, Italy
June 11, 2013

Chapter 1

Translational Genomics in Crop Breeding for Biotic Stress Resistance: An Introduction

Rajeev K. Varshney and Roberto Tuberosa

Abstract

Biotic stresses pose a major threat to crop productivity. Crops are challenged by a plethora of biotic stresses, but only a limited number of key pests and diseases cause the vast majority of economic losses in a particular crop. Plant protection measures such as application of pesticides and deployment of resistant gene(s)/quantitative trait loci (QTLs) into cultivars have so far been quite successful in curtailing the losses; however, these measures have also led to the constant evolution of new biotypes/pathotypes/strains/races of pest and disease organisms. Hence, there is a continuous need to identify genomic regions that can impart resistance against these variants. The availability of large-scale genomic resources in many crop species has enhanced our understanding on the path to developing host-plant resistance. As a result, numerous race-specific gene(s) and QTLs have now been identified and cloned with the help of molecular markers. It is quite exciting that these genomic regions are being introgressed into breeding programs of many crops. The objective of this book is to critically review the current availability and

utilization of genomic tools for major biotic stresses in important cereals, legumes, vegetables, and tuber and oilseed crop. The book also summarizes the success stories achieved through application of genomics-assisted breeding (GAB), as well as the scope for deployment of modern breeding methods such as marker-assisted backcrossing (MABC) and genomic selection in the era of next-generation sequencing (NGS) technologies, which have the potential to advance the genetic gains for enhancing resilience against biotic stress. This chapter summarizes highlights of different chapters included in the book that is expected to be a resource for young researchers, GAB practitioners, and policy makers for employing better strategies toward achieving food security.

Introduction

Several biotic and abiotic stresses challenge crop productivity. Breeders try to develop superior lines by making crosses and selecting the best lines based on their agronomic performance, but the entire process is expensive and takes several years. During the past two decades, remarkable progress in the area of genomics and molecular genetics has greatly improved our basic understanding of resistance to biotic stresses and tolerance of abiotic stresses. Genomics approaches can enhance the precision and efficiency of breeding programs through a better prediction of phenotype from a given genotype – process generally referred to as genomics-assisted breeding (GAB) (Varshney et al. 2005).

Among different GAB approaches, the marker-assisted backcrossing (MABC) approach has been quite successful in transferring the target genomic regions in elite cultivars (Varshney et al. 2012). MABC for gene pyramiding coupled

with selection for the genetic background of the recurrent parent and recombination at the target region(s) could lead to faster and better product delivery, thereby increasing productivity and improving livelihoods of the smallholder farmers (Collard et al. 2008).

Biotic stress caused by pests and diseases continues to pose a significant risk to crop productivity in spite of years of investments in research and development aimed at understanding host-plant interaction and finding more effective methods to control it (Lucas 2011). It has been estimated that even after the deployment of pesticides and improved cultivars in the target environment with resistance to biotic stresses, yield losses resulting from pests and diseases can still reach 20-30% (Oerke 2006). This loss may be attributed to the constant and rapid evolution of new virulent pathogens/pests such as Ug99 for wheat stem rust (Levine and D'Antonio 2003), as well as to their spread to new regions in response to climate change and the adoption of different agricultural practices (e.g., minimum tillage).

Abiotic stresses, such as drought, salinity, cold, submergence, mineral toxicity, and others, also hamper growth, yield, and yield quality of crop plants. In fact, these abiotic stresses represent the main cause of crop failure worldwide, reducing average yields for major crops by more than 50%. Overall, as compared to biotic stresses, abiotic stresses pose more serious constraints to crop production, particularly in view of rapidly deteriorating environmental conditions. Quality traits are the other important class of target traits that breeders select for in order to improve crop productivity as well as nutritional quality.

In recent years, large-scale genomic resources have been developed and are being utilized in breeding programs for several crop species (Varshney et al. 2009; Tuberosa et al. 2011). These advances in genomics research have greatly contributed to the conversion of so-called orphan crops to

genomic resources-rich crops (Varshney et al. 2009, 2010) and to the enhanced precision and speed of breeding programs. In several cases, GAB has delivered superior lines that have been used for developing new varieties or hybrids (Simpson et al. 2003; Sundaram et al. 2008; Ceballos et al. 2012; Singh et al. 2012). However, introgression of QTLs has not always been successful in crop breeding, and even less so for the improvement of tolerance to abiotic stresses (Collins et al. 2008). Therefore, GAB practices have also offered some lessons to the molecular breeding practitioners.

In view of the above, the two volumes on *Translational Genomics for Crop Breeding* compile a number of manuscripts that report on success stories either completed or still in progress, as well as the lessons learned from GAB work on different crops. Volume I compiles 16 chapters that review the current status and recent advances in the application of GAB approaches for biotic stress resistance. Volume II is a compendium of 13 chapters on GAB for enhancing abiotic stress tolerance and improving crop quality.

This introductory chapter of Volume I provides key highlights of GAB applications to enhance biotic stress tolerance. Since the majority (estimated to be ca. 60-70%) of our major caloric intake is obtained directly or indirectly from cereals, the first five chapters summarize the progress on the improvement of biotic stress tolerance in five major cereals, namely rice, maize, wheat, barley, and sorghum. The contribution of legumes to enhancing nutrition in the daily diet has been largely recognized apart from their well-known ability for nitrogen-fixation. The next five chapters deal with GAB applications for important biotic stresses in legumes, namely soybean, peanut, common bean, cowpea, and chickpea. Two additional chapters deal with GAB for enhancing the tolerance of potato and tomato to late blight,

one of the most devastating diseases of these two important vegetable crops. The three final chapters highlight GAB efforts toward improving disease resistance in lettuce, cassava, and *Brassica* species.

Improving Disease Resistance in Cereals

Bacterial blight (BB), effected by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), is a major constraint for rice production, with reported yield losses of up to 50% (Ou 1985). Recently several genes and QTLs have been identified for various virulent strains. Chapter 2 by Kou and Wang provides a comprehensive review of and valuable insights to understanding the interaction between rice and *Xoo* pathogen. This review provides strategies and prior knowledge for effective deployment of resistance genes in target environment against *Xoo* pathogen. Until now, more than 35 BB rice resistance genes have been identified and 7 of these have been isolated. MABC has been quite successful in the case of BB, and various genes such as *Xa4*, *xa5*, *Xa7*, *xa13*, *Xa21*, *Xa23* in single or in pyramided form have been introgressed in popular varieties/parental lines such as, Samba Mahsuri, Pusa Basmati 1, Minghui 63, and have been developed and released in India and China (Gopalakrishnan et al. 2008; Sundaram et al. 2008; Perumalsamy et al. 2010; Huang et al. 2012; Singh et al. 2012).

Chapter 3 by Jamann, Nelson, and Balint-Kurti provides a comprehensive survey of the genetic basis of disease resistance in maize, especially against fungal diseases. In the past, bi-parental linkage mapping was commonly adopted for mapping important genes and QTLs. However, in recent years, modern mapping approaches such as

nested association mapping (NAM), which is an effective combination of linkage and linkage-disequilibrium approaches, are becoming increasingly popular (Yu et al. 2008). The chapter reports on the use of the NAM approach to identify genomic regions responsible for three important diseases in maize, namely southern leaf blight, northern leaf blight, and gray leaf spot (Benson et al. 2011; Kump et al. 2011; Poland et al. 2011). In addition, the authors outline the potential of genomic selection to accelerate the breeding efforts for disease resistance, especially in cases where small-effect and environment-sensitive QTLs are involved, as in *Aspergillus* ear rot and aflatoxin accumulation (Warburton et al. 2009). These genetic studies provide an insight into the disease resistance mechanism, thereby helping molecular breeders understand the genes to be used for their deployment in elite cultivars.

In the case of wheat, among several other diseases, Fusarium head blight (FHB) is an age-old and severe one (Leonard and Bushnell 2003). Importantly, contamination caused by fusarium secondary metabolites, known as mycotoxins, poses a major threat to animal and human health (Van Egmond 2004). Extensive QTL studies for FHB resistance have led to the identification of 19 meta-QTLs spread across wheat chromosomes (Buerstmayr et al. 2009; Liu et al. 2009; Löffler et al. 2009). These GAB efforts for FHB have been summarized in Chapter 4 by Hermann Buerstmayr, Maria Buerstmayr, and Schweiger and Steiner. A closely linked codominant marker is always a prerequisite for making any MABC program a success. In particular, *Umn10*, a PCR-based marker linked to a major gene (*Fhb1*) located on the long arm of chromosome 3B and explaining 40-50% of phenotypic variance (Rosyara et al. 2009), is being used routinely in breeding programs of both hexaploid and tetraploid wheat.

In barley, improving virus resistance is one of the top research priorities because it has a serious impact on its production, particularly in Western Europe. Much work has been done in the recent past toward identification of resistance genes for four major viruses affecting barley (Ordon et al. 2009). As a result, molecular markers are now available for fast introgression. In a recent study, improved DH-lines have been developed for Barley Yellow Dwarf Virus through markers (Riedel et al. 2011). Chapter 5 by Ordon and Perovic covers recent advances toward development of genomic tools for transferring virus resistance into elite cultivars via GAB. The authors also highlight the importance and use of allele mining and utilization of high-throughput SNP technologies for carrying out precision breeding activities in barley.

In sorghum, *Striga* is the most damaging obligate parasite pest that leads to yield loss of up to 90% (Ejeta 2007). It is particularly severe in East Africa and some regions in the United States and Asia. Although much progress has been made toward QTL analysis and Marker-assisted selection (MAS) for improving resistance to *Striga*, the molecular mechanisms behind the establishment of parasitism are still not well understood. In Chapter 6, Deshpande, Mohamed, and Hash describe several aspects for elucidating the molecular mechanisms of *Striga* resistance through development of bioassays, exploring the pathway, and identifying the stages as entry points for breeding resistance to *Striga*, as well as GAB approaches to developing sorghum lines with enhanced resistance to *Striga*. The authors also discuss the utility of next-generation sequencing (NGS) technologies for identifying the functional basis of *Striga* resistance.

Improving Disease Resistance in Legumes

Among different legumes, soybean, known for its edible oil and protein content, is an important industry crop. North America and South America are the major production areas, accounting for nearly 86% of total soybean production worldwide (<http://www.soystats.com>). Cyst, root-knot, and reniform nematode are the major pests of soybean, with annual losses of more than \$1 billion (Koenning and Wrather 2010). Chapter 7 by Vuong, Jiao, Shannon, and Nguyen provides a comprehensive review of nematode resistance in soybean. This work highlights the different nematode problems, their biology and candidate genes for host plant response. Notably, the continuous effort toward the identification of genetic markers closely linked to soybean cyst nematode has led to the development and release of three varieties, namely JTN-5503, JTN-5303, and JTN-5109 in the United States, which are essentially gene pyramids of *Rhg1*, *Rhg4*, and *Rhg5* (Arelli et al. 2006, 2007; Arelli and Young 2009).

Grown in more than 100 countries, peanut is one of the most widespread legume crops in the world (Nwokolo 1996). Chapter 8 by Burow, Leal-Bertioli, Simpson, Ozias-Akins, Chu, Denwar, Chagoya, Starr, Moretzsohn, Pandey, Varshney, Holbrook, and Bertioli describes molecular mapping and MAS for several diseases and pest challenges faced by peanut. As to improving the resistance to root knot nematode, a serious problem in the United States caused by *Meloidogyne* species, the effectiveness of MAS has been demonstrated through the development and release of a nematode-resistant variety 'NemaTAM' in the United States (Simpson et al. 2003). With the availability of more than 6,000 SSR markers, extensive studies have also led to the identification of QTLs with high phenotypic variance for

resistance to late leaf spot and rust (Sujay et al. 2012) and tomato spotted wilt virus (Qin et al. 2012). In addition, this chapter presents the prospects and progress of the International Peanut Genome Project toward sequencing the peanut genome, which should help in the identification of candidate genes for stress tolerance and to accelerate GAB in peanut (<http://www.peanutbioscience.com/peanutgenomeproject.html>).

In common bean, the fungal pathogen *Colletotrichum lindemuthianum* (Sacc. & Magnus) causes a devastating disease known as anthracnose. Several resistance genes against race-specific isolates for anthracnose have been reported in the past. Ferreira, Campa, and Kelly in Chapter 9 report on the inheritance pattern of the pathogen and the related allelism tests, and discuss GAB approaches for anthracnose resistance. Furthermore, the authors propose a new system of naming anthracnose resistance gene(s) based on the location on the genetic map. Efforts toward marker-assisted introgression in common bean have led to the release of variety 'USPT-ANT-1' with gene *Co-4²* conferring resistance to anthracnose in the United States (Miklas et al. 2003). Recently, line A3308 carrying genes *Co-2* and *Co-3/9* for anthracnose and bean common mosaic (BCM) resistance by genotype *I + bc-3* has also been developed (Ferreira et al. 2012).

Cowpea is an important leguminous crop in the tropical and subtropical areas, especially in Latin America, Asia, and Sub-Saharan Africa (Singh et al. 1997). Recent advances in the development of genomic tools in cowpea have enabled the identification of molecular markers for resistance to critical biotic stresses. This notwithstanding, application of modern breeding approaches is still in its infancy. In Chapter 10, Huynh, Ehlers, Close, Cissé, Drabo, Boukar, Lucas, Wanamaker, Pottorf, and Roberts review initial MABC

work for various disease resistance and genomic resources available for carrying out GAB in cowpea. The transgenic approach has also been discussed as an option to increase resistance to pod borer and cowpea weevil, as the level of resistance to these pests in the available germplasm is negligible.

Chickpea is another important leguminous crop, mainly grown in Asia and the Mediterranean regions of the world, which is highly nutritious and rich in protein, carbohydrates, and vitamins (Abu-Salem and Abou-Arab 2011). India is the largest producer of chickpea in the world, accounting for more than 65% of global production (FAO 2011). Among important biotic stresses, *Fusarium* wilt and *Ascochyta* blight can cause yield losses of more than 90% (Singh and Reddy 1991, 1996). Efforts to develop genomic resources have led to the identification of molecular markers for agronomic as well as biotic stress, paving the way for GAB activities in this crop (Varshney et al. 2013a). In Chapter 11, Millan, Madrid, Imtiaz, Kharrat, and Chen extensively review disease resistance aspects in chickpea. Furthermore, as genome sequencing of 90 chickpea lines is now available, molecular breeding efforts can now be accelerated to develop tolerant lines for disease resistance (Varshney et al. 2013b).

Improving Disease Resistance in Vegetables

Potato is one of the major staple and vegetable crops, covering more than 100 countries, with an annual production of more than 300 million tons (FAO 2011). *Phytophthora infestans*, which causes late blight, is the main, devastating disease in potato, with an annual yield loss of more than \$3 billion (Duncan 1999). Chapter 12 by

Śliwka and Zimnoch-Guzowska discusses recent advances in discovering, identifying, mapping, and cloning the resistance genes in potato. This information could be quite useful for the deployment of race-specific resistance in improved lines for target environments.

Tomato is another major vegetable crop for which late blight is a major devastating disease causing vast yield loss. In Chapter 13, Nowicki, Kozik, and Foolad make a special emphasis on late blight resistance in tomato. The chapter provides comprehensive insight into the disease, its chemical control, and GAB aspects. Furthermore, the recently sequenced tomato genome (Tomato Genome Consortium 2012) and *Phytophthora* genome (Haas et al. 2009) provide much-needed understanding of *R-Avr* interaction for late blight. Molecular breeding activities have been quite successful in imparting resilience against late blight, and several varieties such as NC1 CELBR, NC2 CELBR, Mountain Magic, and Mountain Merit have been developed by stacking two genes (*Ph-2* + *Ph-3*) and released in the United States (Gardner and Panthee 2010; Panthee and Gardner 2010).

Lettuce, one of the most commercially important leafy vegetables, has an annual production of more than 23 million tons (FAO 2011). The crop is grown for a variety of purposes such as salad, stem, and oilseed. The crop is challenged by many biotic stresses leading to huge economic losses. In Chapter 14, Simko reviews recent developments in MAS for resistance to downy mildew, corky root, lettuce mosaic, and lettuce dieback. To achieve these traits, both public and private sectors are routinely utilizing allele-specific assays in their breeding programs. Furthermore, details and current status regarding mapping efforts for other important traits are discussed. Important progress has been made in generating large-scale genomic resources/platforms in lettuce, such as an EST database that