
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 Chap-

ter 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 NCI 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 includes sequences of more than 700 candidate resistance genes (McHale et al. 2009), microarray chip with more than 6.5 million feature Affymetrix genechip (Stoffel et al. 2012), and complete genome sequencing of cultivated and wild lettuce (<https://lgr.genomecenter.ucdavis.edu/>; Lavelle et al. 2013), which promises to facilitate faster diagnostics, gene expression analysis, high-throughput genotyping, and cloning of genes.

Improving Disease Resistance in Cassava and Brassica

In addition to the aforementioned cereal, legume, and vegetable crops, Volume I includes GAB activities in cassava and *Brassica*, two other important crops for human diet. Cassava, a starchy root crop, is a major food source for more than 800 million people in Sub-Saharan Africa, Asia, and South America. It is cultivated on more than 20 million hectares, with an annual production of more than 240 million tons (FAO 2011). Cassava suffers from several biotic stresses and is highly vulnerable to viral diseases. Cassava mosaic disease (CMD), caused by cassava mosaic Gemini virus, is one of the major viral diseases of cassava, causing reported yield loss of up to 40% (Taylor et al. 2004). Much success has been achieved in identification of molecular markers for CMD, and MAS for this trait is currently being employed in several popular cul-

tivars of Africa and India. The release in 2010 of cassava cultivar CR41-10 in Nigeria, made possible through the activities of the CGIAR Generation Challenge Program (GCP), is the first example of MAS-derived product in cassava (Ceballos et al. 2012). In Chapter 15, Okogbenin, Moreno, Tomkins, Fauquet, Mkamilo, and Fregene present an informative and critical review of GAB activities in cassava.

The agricultural and horticultural uses of the *Brassica* genus contribute an important part to the human diet and to the global economy. Like with all other crops, a plethora of pests and diseases curtail the yield in *Brassica*. In Chapter 16, Li and McVetty review the recent progress on the genetics and gene mapping for disease resistance in *Brassica* species. Tangible progress has been achieved toward GAB for resistance to blackleg and clubroot. However, the development of MAS of sclerotinia stem rot has seen slower progress, mostly because germplasm accessions with high levels of resistance have yet to be identified.

Summary and Outlook

In summary, this volume presents recent advances, useful insights, and comprehensive reviews for GAB approaches to improve biotic stress tolerance in a range of crops. Although the potential for utilization of GAB in crop improvement programs appears almost endless, its application varies greatly among different crop species, reflecting to a certain extent the state-of-the-art genomics of each single species and their economic importance. In crops such as rice, maize, wheat, and barley, MAS and MABC is already well integrated in breeding programs, whereas in many others, the deployment of molecular breeding activities is under way. Notably, GAB for several traits has recently been initiated in orphan crops.

Thanks to the advent of NGS, it has become possible to generate reference genome sequence data of the main crops and also to (re)sequence several varieties/lines. In parallel, modern genetic mapping approaches such as

genome-wide association studies (GWAS; Rafalski 2010; Hamblin et al. 2011) and nested association mapping (NAM; Yu et al. 2008; McMullen et al. 2009) for trait mapping and modern breeding methodologies like marker-assisted recurrent selection (MARS) (Charmet et al. 1999) and GS (Heffner et al. 2009; Jannink et al. 2010) are being increasingly adopted in several crop species. In addition, molecular breeding decision support tools such as an integrated system for marker-assisted breeding (ISMAB) (<https://www.integratedbreeding.net/ib-tools/breeding-decision/ismab>), OptiMAS (<http://moulon.inra.fr/optimas/index.html>), GS modules (Pérez-Rodríguez et al. 2012; de Los Campos et al. 2013), and platforms like Integrated Breeding Platform (IBP) (<https://www.integratedbreeding.net/>) are being developed. These advances are expected to accelerate GAB for a range of traits, including biotic stress resistance in crop breeding.

As mentioned earlier, Volume II of this series documents the application of genomics for abiotic stress tolerance and quality traits in several crops. Therefore, together with Volume I, this volume provides an informative and critical update of genomics applications in crop breeding. We hope these chapters will allow young researchers, including graduate students and postdoctoral scholars, to better appreciate GAB and encourage them to devote their career to this exciting area of crop improvement. Additionally, we hope that GAB practitioners as well as policy makers will find these volumes useful for developing the road map toward a more effective improvement of target crops in their respective geographical areas.

References

- Abu-Salem FM and Abou-Arab EA (2011) Physico-chemical properties of tempeh produced from chickpea seeds. *J Am Sci* 7:107–118.
- Arelli PR and Young LD (2009) JTN-5109 soybean germplasm resistant to nematode population infecting cv. Hartwig. In *Footprints in the Landscape: Sustainability through Plant and Soil Science*. Proceedings of the ASA-CSSA-SSSA Annual Meeting, November 1–5, Pittsburgh, PA. Paper no. 268-18, p. 133.
- Arelli PR, Pantalone VR, Allen FL and Mengistu A (2007) Registration of soybean germplasm JIN-5303. *J Plant Reg* 1:69–70.
- Arelli PR, Young LD and Mengistu A (2006) Registration of high yielding and multiple disease resistant soybean germplasm JTN-5503. *Crop Sci* 46:2723–2724.
- Benson J, Poland J, Stromberg EL and Nelson RJ (2011) Nested association mapping and confirmation of gray leaf spot disease resistance loci. August 6–10, Minneapolis, Minnesota.
- Buerstmayr H, Ban T and Anderson JA (2009) QTL mapping and marker-assisted selection for Fusarium head blight resistance in wheat: a review. *Plant Breed* 128:1–26.
- Ceballos H, Clair H and Luis AB (2012) New Approaches to Cassava Breeding. *Plant Breed Rev* 36:427–504.
- Charmet G, Robert N, Perretant MR, Gay G, Sourdille P, Groos C, Bernard S and Bernard M (1999) Marker-assisted recurrent selection for cumulating additive and interactive QTLs in recombinant inbred lines. *Theor Appl Genet* 99:1143–1148.
- Collard BC Y, Vera Cruz CM, McNally KL, Virk PS and Mackill DJ (2008) Rice molecular breeding laboratories in the genomics era: Current status and future considerations. *Int J Plant Genomics* 2008:524847.
- Collins NC, Tardieu F and Tuberosa R (2008) QTL approaches for improving crop performance under abiotic stress conditions: where do we stand? *Plant Physiol* 147:469–486.
- de Los Campos G, Hickey JM, Pong-Wong R, Daetwyler HD and Calus MP (2013) Whole-genome regression and prediction methods applied to plant and animal breeding. *Genetics* 193:327–345.
- Duncan J (1999) *Phytophthora* – an abiding threat to our crop. *Microbiology Today* 26:114–116.
- Ejeta G (2007) The *Striga* scourge in Africa: A growing pandemic. In: *Integrating New Technologies for Striga Control, Towards Ending the Witch-hunt*. Edited by Ejeta G, Gressel J, pp. 3–15.
- FAO (2011) <http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor>
- Ferreira JJ, Campa A, Pérez-Vega E, Rodríguez-Suárez C and Giraldez R (2012) Introgression and pyramiding into common bean market class fabada of genes conferring resistance to anthracnose and potyvirus. *Theor Appl Genet* 124:777–788.
- Gardner RG and Panthee DR (2010) ‘Plum Regal’ fresh-market plum tomato hybrid and its parents, NC 25P and NC 30P. *Hort Sci* 45:824–825.
- Gopalakrishnan S, Sharma RK, Rajkumar KA, Joseph M, Singh VP, Singh AK, Bhat KV, Singh NK and Mohapatra T (2008) Integrating marker assisted background analysis with foreground selection for identification of superior bacterial blight resistant recombinants in Basmati rice. *Plant Breed* 127:131–139.

- Haas BJ, Kamoun S, Zody MC, Jiang RHY, Handsaker RE, Cano LM, Grabherr M, Kodira CD, Raffaele S and Torto-Alalibo T (2009) Genome sequence and analysis of the Irish potato famine pathogen *Phytophthora infestans*. *Nature* 461:393–398.
- Hamblin MT, Buckler ES and Jannink JL (2011) Population genetics of genomics-based crop improvement methods. *Trends Genet* 27:98–106.
- Heffner EL, Sorrells ME and Jannink JL (2009) Genomic Selection for Crop Improvement. *Crop Sci* 49:1–12.
- Huang B, Xu JY, Hou MS, Ali J and Mou TM (2012) Introgression of bacterial blight resistance genes *Xa7*, *Xa21*, *Xa22* and *Xa23* into hybrid rice restorer lines by molecular marker-assisted selection. *Euphytica* 187:449–459.
- Jannink JL, Lorenz AJ and Iwata H (2010) Genomic selection in plant breeding: from theory to practice. *Brief Funct Genomics* 9:166–177.
- Koenning SR and Wrather JA (2010) Suppression of soybean yield potential in the continental United States from plant diseases estimated from 2006 to 2009. *Plant Health Progress* doi:10.1094/PHP-2010-1122-01-RS.
- Kump KL, Bradbury PJ, Wissler RJ, Buckler ES, Belcher AR, Oropeza-Rosas MA, Zwonitzer JC, Kresovich S, McMullen MD, Ware D, Balint-Kurti PJ and Holland JB (2011) Genome-wide association study of quantitative resistance to southern leaf blight in the maize nested association mapping population. *Nat Genet* 43:163–168.
- Lavelle D, Reynes-Chin-Wo S, Wang Z, Chi S, Kozik A, Froenicke L, Truco MJ, Beitel C, Xu X, Yang B and Michelmore R (2013) Sequencing the genomes of cultivated *lactuca sativa* and its wild progenitor, *L. serriola*. *Plant & Animal Genome XXI*, San Diego, CA, P0044.
- Leonard KJ and Bushnell WR (2003) *Fusarium head blight of wheat and barley*. American Phytopathological Society (APS Press), St. Paul, Minnesota.
- Levine JM and D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. *Conserv Biol* 17:322–326.
- Liu SY, Hall MD, Griffey CA and McKendry AL (2009) Meta-analysis of QTL associated with Fusarium head blight resistance in wheat. *Crop Sci* 49:1955–1968.
- Löffler M, Schön CC and Miedaner T (2009) Revealing the genetic architecture of FHB resistance in hexaploid wheat (*Triticum aestivum* L.) by QTL meta-analysis. *Mol Breed* 23:473–488.
- Lucas JA (2011) Advances in plant disease and pest management. *J Agri Sci* 149:91–114.
- McHale LK, Truco MJ, Kozik A, Wroblewski T, Ochoa OE, Lahre KA, Knapp SJ and Michelmore RW (2009) The genomic architecture of disease resistance in lettuce. *Theor Appl Genet* 118:565–580.
- McMullen MD, Kresovich S, Villeda HS, Bradbury PJ, Li H, Sun Q, Flint-Garcia S, Thornsberry J, Acharya C, Bottooms C, Brown P, Browne C, Eller M, Guill K, Harjes C, Kroon D, Lepak N, Mitchell SE, Peterson B, Pressoir G, Romero S, Oropeza Rosas M, Salvo S, Yates H, Hanson M, Jones E, Smith S, Glaubitz JC, Goodman M, Ware D, Holland JB and Buckler ES (2009) Genetic properties of the maize nested association mapping population. *Science* 325:737–740.
- Miklas PN, Delorme R and Riley R (2003) Identification of QTL conditioning resistance to white mold in snap bean. *J Am Soc Hort Sci* 128:564–570.
- Nwokolo E (1996) Peanut (*Arachis hypogaea* L.). In E. Nwokolo and J. Smartt, eds. *Legumes and Oil Seeds in Nutrition*. London: Chapman and Hall pp. 49–63.
- Oerke EC (2006) Crop losses to pests. *J Agri Sci* 144:31–43.
- Ordon F, Habekuss A, Kastirr U, Rabenstein F and Kuhne T (2009) Virus Resistance in Cereals: Sources of Resistance, Genetics and Breeding. *J Phytopath* 157:535–545.
- Ou SH (1985) *Rice diseases*. 2nd ed. Commonwealth Mycological Institute, Kew, Surrey, England.
- Panthee DR and Gardner RG (2010) 'Mountain Merit': A late blight-resistant large-fruited tomato hybrid. *Hort Sci* 45:1547–1548.
- Pérez-Rodríguez P, Gianola D, González-Camacho JM, Crossa J, Manès Y and Dreisigacker (2012) Comparison between linear and non-parametric regression models for genome-enabled prediction in wheat. *G3* 2:1595–1605.
- Perumalsamy S, Bharani M, Sudha M, Nagarajan P, Arul L, Saraswathi R, Balasubramanian P and Ramalingam J (2010) Functional marker-assisted selection for bacterial leaf blight resistance genes in rice (*Oryza sativa* L.). *Plant Breed* 129:400–406.
- Poland JA, Bradbury PJ, Buckler ES and Nelson RJ (2011) Genome-wide nested association mapping of quantitative resistance to northern leaf blight in maize. *Proc Natl Acad Sci USA* 108:6893–6898.
- Qin H, Feng S, Chen C, Guo Y, Knapp S, Culbreath A, He G, Wang M, Zhang X, Holbrook C, Ozias-Akins P and Guo B (2012) An integrated genetic linkage map of cultivated peanut (*Arachis hypogaea* L.) constructed from two RIL populations. *Theor Appl Genet* 124:653–664.
- Rafalski JA (2010) Association genetics in crop improvement. *Curr Opin Plant Biol* 13:174–180.
- Riedel C, Habekuss A, Schliephake E, Niks R, Broer I and Ordon F (2011) Pyramiding of *Ryd2* and *Ryd3* conferring tolerance to a German isolate of *Barley yellow dwarf virus-PAV* (BYDV-PAV-ASL-1) leads to quantitative resistance against this isolate. *Theor Appl Genet* 123:69–76.
- Rosyara UR, Gonzalez-Hernandez JE, Glover KD, Gedye KR and Stein JM (2009) Family-based mapping of quantitative trait loci in plant breeding populations with resistance to Fusarium head blight in wheat as an illustration. *Theor Appl Genet* 118:1617–1631.
- Simpson CE, Starr JL, Church GT, Burrow MD and Paterson AH (2003) Registration of NemaTAM peanut. *Crop Sci* 43:1561.
- Singh BB, Chambliss OL and Sharma B (1997) Recent advances in cowpea breeding. In: Singh BB, Mohan Raj

- DR, Dashiell KE, Jackai LEN (eds) Advances in cowpea research. IITA and Japan International Research Center for Agricultural Sciences (JIRCAS), Ibadan, Nigeria, pp 30–49.
- Singh KB and Reddy MV (1991) Advances in disease-resistance breeding in chickpea. *Adv Agron* 45:191–222.
- Singh KB and Reddy MV (1996) Improving chickpea yield by incorporating resistance to *Ascochyta* blight. *Theor Appl Genet* 92:509–515.
- Singh VK, Singh A, Singh SP, Ellur RK, Choudhary V, Sarkhel S, Singh D, Gopala Krishnan S, Nagarajan M, Vinod KK, Singh UD, Rathore R, Prasanthi SK, Agrawal PK, Bhatt JC, Mohapatra T, Prabhu KV and Singh AK. (2012) Incorporation of blast resistance into 'PRR78', an elite Basmati rice restorer line, through marker assisted backcross breeding. *Field Crop Res* 128:8–16.
- Stoffel K, Van Leeuwen H, Kozik A, Caldwell D, Ashrafi H, Cui X, Tan X, Hill T, Reyes-Chin-Wo S, Truco M-J, Michelmore R and Van Deynze A (2012) Development and application of a 6.5 million feature affymetrix genechip® for massively parallel discovery of single position polymorphisms in lettuce (*Lactuca* spp.). *BMC Genomics* 13:185.
- Sujay V, Gowda MVC, Pandey MK, Bhat RS, Khedikar YP, Nadaf HL, Gautami B, Sarvamangala C, Lingaraju S, Radhakrishnan T, Knapp SJ and Varshney RK (2012) Quantitative trait locus analysis and construction of consensus genetic map for foliar disease resistance based on two recombinant inbred line populations in cultivated groundnut (*Arachis hypogaea* L.). *Mol Breed* 30:773–788.
- Sundaram RM, Vishnupriya MR, Biradar SK, Laha GS, Reddy GA, Shobha-Rani N, Sarma NP and Sonti RV (2008) Marker assisted introgression of bacterial blight resistance in Samba Mahsuri, an elite *indica* rice variety. *Euphytica* 160:411–422.
- Taylor N, Chavarriaga P, Raemakers K, Siritunga D and Zhang P (2004) Development and application of transgenic technologies in cassava. *Plant Mol Bio* 56:671–688.
- Tomato Genome Consortium (2012) The tomato genome sequence provides insights into fleshy fruit evolution. *Nature* 485:635–641.
- Tuberosa R, Graner A and Varshney RK (2011) Genomics of plant genetic resources: an introduction. *Plant Genetic Resources* 9:151–154.
- Van Egmond HP (2004) Natural toxins: risks, regulations and the analytical situation in Europe. *Anal Bioanal Chem* 378:1152–1160.
- Varshney RK, Close TJ, Singh NK, Hoisington DA and Cook DR (2009) Orphan legume crops enter the genomics era! *Curr Opin Plant Biol* 12: 202–210.
- Varshney RK, Glaszmann J-C, Leung H and Ribaut JM (2010) More genomic resources for less-studied crops. *Trends Biotechnol* 28:452–460.
- Varshney RK, Graner A and Sorrells ME (2005) Genomics-assisted breeding for crop improvement. *Trends Plant Sci* 10:621–630.
- Varshney RK, Mohan SM, Gaur PM, Gangarao NVPR, Pandey MK, Bohra A, Sawargaonkar SL, Gorantla A, Kimurto PK, Janila P, Saxena KB, Fikre A, Sharma M, Rathore A, Pratap A, Tripathi S, Datta S, Chaturvedi SK, Mallikarjuna N, Anuradhā G, Babbar A, Choudhary AK, Mhase MB, Bharadwaj Ch, Mannur DM, Harer PN, Guo B, Liang X, Nadarajan N and Gowda CLL (2013a) Achievements and prospects of genomics-assisted breeding in three legume crops of the semi-arid tropics. *Biotechnol Adv* doi: 10.1016/j.biotechadv.2013.01.001.
- Varshney RK, Ribaut JM, Buckler ES, Tuberosa R, Rafalski JA and Langridge P (2012) Can genomics boost productivity of orphan crops? *Nat Biotechnol* 30:1172–1176.
- Varshney RK, Song C, Saxena RK, Azam S, Yu S, Sharpe AG, Cannon S, Baek J, Rosen BD, Tar'an B, Millan T, Zhang X, Ramsay LD, Iwata A, Wang Y, Nelson W, Farmer AD, Gaur PM, Soderlund C, Penmetra RV, Xu C, Bharti AK, He W, Winter P, Zhao S, Hane JK, Carrasquilla-Garcia N, Condie JA, Upadhyaya HD, Luo M, Thudi M, Gowda CLL, Singh NP, Lichtenzweig J, Gali KK, Rubio J, Nadarajan N, Dolezel J, Bansal KC, Xu X, Edwards D, Zhang G, Kahl G, Gil J, Singh KB, Datta SK, Jackson SA, Wang J and Cook DR (2013b) Draft genome sequence of chickpea (*Cicer arietinum*) provides a resource for trait improvement. *Nat Biotechnol* doi:10.1038/nbt.2491.
- Warburton ML, Brooks TD, Krakowsky MD, Shan XY, Windham GL and Williams WP (2009) Identification and mapping of new sources of resistance to aflatoxin accumulation in maize. *Crop Sci* 49:1403–1408.
- Yu J, Holland JB, McMullen MD and Buckler ES (2008) Genetic design and statistical power of nested association mapping in maize. *Genetics* 178:539–551.