

Crop Breeding for Sustainable Agriculture, Genomics Interventions in

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Glossary

Association mapping Association mapping is a high-resolution method for mapping quantitative trait loci (QTLs) or gene(s) for traits of interest based on linkage disequilibrium (LD) and holds great promise for the dissection of complex genetic traits.

Back cross (BC) Back cross is a cross of the F_1 with either of the parental genotype and the resultant progeny is called BC_1 . The progeny of the cross between BC_1 and the recurrent parent is called as BC_2 .

Gene pyramiding Gene pyramiding is a process of accumulating the favorable genes/alleles from different genotypes into an elite/commercial cultivar. Gene pyramiding is often performed through marker-assisted selection (MAS).

Genome-wide selection or genomic selection (GS)

Genome-wide selection or genomic selection is a concept for accelerating genetic gain especially for complex traits in elite genotypes by utilizing genomic information and estimating their breeding values in breeding strategies. GS is becoming very popular over marker-assisted selection that was focused on few individual genes or few QTLs to improve genotypes, especially when recent advances in genomic technologies have drastically reduced the cost on marker genotyping.

Genomics-assisted breeding (GAB) Genomics-assisted breeding is a holistic approach, where genomics technologies including molecular markers, transcriptomics, metabolomics, proteomics, bioinformatics, and phenomics are integrated with conventional breeding strategies for breeding crop plants resistant/tolerant to biotic and abiotic stresses or improved for quality and yield.

Haplotype Haplotype is a set of alleles of closely linked loci on a chromosome that tend to be inherited together.

Linkage disequilibrium (LD) Linkage disequilibrium is a nonrandom association of alleles at different loci, describing the condition with non-equal (increased or reduced) frequency of the haplotypes in a population at random combination of alleles at different loci. LD is not the same as linkage, although tight linkage may generate high levels of LD between alleles.

Marker-assisted selection (MAS) Marker-assisted selection is a process of indirect selection for improving the traits of interest by employing morphological, biochemical, or DNA-based markers. DNA-based markers/molecular markers, in the recent past, were proven to be the markers of choice for MAS.

Narrow genetic base Narrow genetic base does frequently exist in modern crop cultivars or breeding lines due to the continuous use of small number of elite genotypes in breeding programs. In fact, it is

a serious obstacle to sustain and improve crop productivity due to rapid vulnerability of genetically uniform cultivars to emerging biotic and abiotic stresses.

Next-generation sequencing (NGS) technologies

Next-generation sequencing (NGS) technologies include various novel sequencing technologies for example 454/FLX (Roche Inc.), ABI SOLiD (Applied Biosystems), Solexa (Illumina Inc.), etc., that have surpassed traditional Sanger sequencing in through-put and in cost-effectiveness for generating large-scale sequence data.

Polygenes Polygenes are a group of non-allelic genes, each having a small quantitative effect, that together produce a wide range of phenotypic variation.

Quantitative trait loci (QTLs) Quantitative trait loci are the loci or regions in the genome that contribute towards conferring tolerance to abiotic stresses (e.g., drought, salinity) or resistance to biotic stresses (e.g., fungal, bacterial, viral diseases) or improving agronomic traits (e.g., yield, quality) which are generally controlled by polygenes and greatly depend on gene \times environmental (G \times E) interactions.

Sustainable agriculture Sustainable agriculture refers to efficient agricultural production while maintaining the environment, farm profitability, and prosperity of farming communities.

Sustainable development Sustainable development is defined as balancing the fulfillment of human needs with the protection of the environment so that these needs can be met not only at the present time, but also in the future.

Definition of the Subject

There has been significant improvement in production and productivity of important cereal crops globally as a consequence of the "Green Revolution" and other initiatives [1]. However, today the stage has reached that the available traditional methods of crop improvement are not sufficient to provide enough and staple food grains to the constantly growing world population [2]. This situation is projected to be worse by the year 2050, especially in context of climate change [3]. In other words, the conventional plant breeding

practices may not be able to achieve the sustainability in today's agriculture.

It is under such circumstances that advances in plant genomics research are opening up a new era in plant breeding, where the linkage of genes to specific traits will lead to more efficient and predictable breeding programs in future. Several initiatives have been started towards use of genomics technologies in number of crop plants to ensure the sustainable production of healthy and safe crops and the results are encouraging. It is therefore expected that the genomics will be the integral part of the agricultural/plant breeding practices in future for improving crop productivity leading to achieve food security and sustainable production.

Introduction and Importance of Sustainable Agriculture

The goal of agricultural science is to increase crop productivity coupled with the quality of the products, and maintain the environment [1]. Food security is a growing concern worldwide, and more than 1 billion people are estimated to lack sufficient dietary energy availability [2]. The issue of "food security" has become so important that prominent scientific journals, including *Science*, have also published a special issue on this subject recently (February 12, 2010 issue). With the current rate of growth, the global population is likely to plateau at some 9 billion people by roughly the middle of this century [3]. With this ever-increasing human population and amidst the fear of shrinking resources in terms of cultivable area, irrigation resources, newly emerging insect pests, stagnated yields, etc., it has become difficult to maintain agricultural sustainability. In order to make today's agriculture sustainable, it is necessary that plant breeders adopt innovative technologies that can increase the efficiency of selection with more precision [4]. Under such circumstances, molecular approaches including modern genomics and genetic engineering technologies have emerged as powerful tools to assure rapid and precise selection for the trait(s) of interest. Maintaining effective and environmentally friendly agricultural practices is a necessary prerequisite for maintaining sustainability.

Plant genomics is a rapidly developing field, which is radically improving our understanding of plant biology by making available novel tools for the improvement of plant properties relevant to sustainable agricultural production. Recent advances in high-throughput genomics technologies, including that of next-generation sequencing and high-throughput genotyping, have helped immensely in understanding the functions and regulation of genes in crop plants [5]. The ever-increasing availability of genome sequences in crop plants have facilitated greatly the development of genomic resources that will allow us to address biological functions and a number of basic processes relevant to crop production leading to sustainable agriculture.

One of the myths linked to sustainable agriculture means going back to past techniques/farm practices, which were followed by our ancestors. In fact, sustainable agriculture can be achieved by combining some of the wisdom of past practices with careful use of current technology, including the vast array of information technologies now available. Sustainable agriculture is a key element of sustainable development and is essential to the future well-being of the human race and the planet. A compelling need exists for restorative and sustainable agriculture to help address the pressing trends of population, climate, energy, water, soil, and food. Sustainable agriculture needs to be economically viable, environmentally sound, and socially acceptable. In other words, it is a system of agricultural production that, over the long term, will: (1) satisfy human food, feed, and fiber needs; (2) enhance the environmental quality and the natural resource base upon which the agricultural economy depends; (3) make the most efficient use of available technologies, nonrenewable resources, and on-farm resources, and integrate, where appropriate, natural biological cycles and controls; (4) sustain the economic viability of farm operations; and (5) enhance the quality of life for farmers and society as a whole.

There are various components of sustainable agriculture, which include technological interventions, and environmental and socio-economic factors. As the factors related to socio-economics and environments have been discussed in a number of reviews earlier, in this article, we focus on the interventions of plant genomics technologies in crop breeding.

Contribution of Plant Genomics Technologies to Crop Breeding

Plant genomics technologies have contributed immensely in today's agriculture which has led to better understanding of how plants function, and how they respond to the environment. This has also helped in achieving targeted objectives in breeding programs to improve the performance and productivity of crops. The DNA-based molecular markers have facilitated smarter and knowledge-based breeding, by enabling early-generation selection for key traits, thus reducing the need for extensive field selection. Besides this, the molecular tools can effectively be used for the characterization, conservation, and use of genetic resources.

Recent advances made in the area of molecular biology and bioinformatics offer substantial opportunities for enhancing the effectiveness of classical plant breeding programs. These tools can be integrated into breeding work in order to analyze efficiently high numbers of crosses at the early seedling stage. This approach is known as "genomics-assisted breeding" [6]. Through this approach, both the phenotype and the genotype of new varieties can be analyzed and the performance of new specific introgressed traits can be predicted. The goals of the integration of these technologies in classical breeding are to create genotype-to-phenotype trait knowledge for breeding objectives and to use this knowledge in product development and deployment for the resource poor farmer.

For successful utilization of genomics-assisted breeding approach in a crop, availability of basic molecular tools, such as molecular markers, genetic maps, etc., is a prerequisite. Among molecular markers, though a variety of molecular markers such as restriction fragment length polymorphism (RFLP), randomly amplified polymorphic DNA (RAPD), microsatellite or simple sequence repeat (SSR), amplified fragment length polymorphism (AFLP), and single nucleotide polymorphism (SNP) markers have been developed in a range of crops, SSR and SNP markers have emerged as the markers of choice [7, 8]. Because of advent of NGS technologies [5] and high-throughput genotyping platforms, SNP marker system and array-based genotyping platforms are becoming more

popular [9, 10]. An overview on availability of genomic resources in some selected important crop species is shown in Table 1. It is evident that cereal crops, especially rice, maize, wheat, barley, etc., are on top in terms of availability of genomic resources (see [11]). Genome sequences have already become available for several crop species, including rice (<http://rgp.dna.affrc.go.jp/IRGSP/>), sorghum [12], and maize (<http://gbrowse.maizedb.org/cgi-bin/gbrowse/maize/>). Recent investments coupled with advances in genomics technologies have contributed towards developing a good resource of genomics tools in legumes as well [13, 14].

Some Modern Breeding Approaches

The availability of genomic resources in almost all important crops combined with information on pedigrees as well as optimized methods of precise phenotyping make it possible to undertake genomics-assisted breeding approaches for crop improvement. In fact, some molecular breeding approaches like advanced backcross QTL (AB-QTL) analysis and marker-assisted selection (MAS) have been successfully employed in several crops, leading to improved cultivars, some other approaches such as marker-assisted recurrent selection (MARS) or genomics selection (GS) are being used in several crops [15, 16].

Marker-Assisted Selection (MAS)

There are three major steps involved in MAS: (1) identification of molecular marker(s) associated with trait(s) of interest to breeders, (2) validation of identified marker(s) in the genetic background of the targeted genotypes to be improved, and (3) marker-assisted backcrossing (MABC) to transfer the QTL/gene from the donor genotype into the targeted genotype. In context of marker-trait association, linkage mapping has been extensively used for identifying the markers associated with a trait of interest in a range of crops including cereals, legumes, horticultural crops, etc. These studies have been reviewed in detail in several reviews [14, 17] and books [18]. Although hundreds of studies have been undertaken, only a few studies were taken further to marker validation and MABC. This may be attributed to (1) identification of few markers associated with small-effect QTLs, (2) non-validation of markers in elite genotypes, and

(3) slow adoption of markers by breeders in their breeding programs. Recent advances in association genetics, however, offer opportunities to overcome the first two constraints.

Association mapping (AM) is considered an alternative strategy to linkage mapping for identifying marker-trait associations and has been used extensively in human and animal systems. AM has a number of advantages over linkage mapping, including the potential for increased QTL resolution and an increased sampling of molecular variation (for reviews see [19, 20]). AM involves studying a natural population rather than the offspring of crosses, and associations in natural populations are typically on a much finer scale because they reflect historical recombination events. Several examples on marker-trait association using AM are available [21]; however, there is a need for optimization of more advanced analytical tools in the area of association genetics [22]. It is anticipated that because of reduction in costs on marker genotyping [10], AM will be extensively used for trait mapping in the future.

Once the markers associated with a trait of interest are identified through linkage mapping or AM, the next step is to use these markers in the breeding programs. In this context, the selection of one or a few genes (QTLs) through molecular markers using backcrossing is a very efficient technique [23, 24]. Important advantages of MAS are that it can be effectively utilized for traits with low heritability; for gene pyramiding, selection can be made at seedling stage; and, above all, there are no issues involving GE crops [25]. Although use of markers in breeding programs through MABC is a common practice in the private sector [26], MAS is in routine use in wheat and barley breeding programs in Australia [8, 27–29] and USA (www.maswheat.ucdavis.edu; <http://barleycap.cfans.umn.edu/>). Nevertheless, there are several success stories in many crops including wheat, rice, barley, maize, soybean, etc., where MAS has successfully been utilized to develop superior lines/varieties/hybrids for improving quality, resistance to diseases or tolerance to abiotic stresses. For example, Gupta et al. [17] has recently summarized success stories of molecular breeding in wheat.

A widely discussed success story of molecular breeding is the introgression of the FR13A *Sub1* locus conferring resistance against submergence in an Asian rice cultivar, Swarna [30, 31] that can confer tolerance

Crop Breeding for Sustainable Agriculture, Genomics Interventions in. Table 1 Genomic resources among selected cereals and legumes

Crop plant	Molecular markers (SSRs and SNPs)	Molecular maps (Genetic/QTL map/ comparative/physical maps)	Transcript data and expression profiling	Genome sequence data
Rice	++++ ^a	++++ ^{b,c}	++++ ^d	++++ ^e
Maize	++++ ^f	++++ ^{b,g,h}	++++ ^d	++++ ⁱ
Wheat	+++ ^j	+++ ^{b,k,l}	+++ ^d	++ ^m
Sorghum	+++ ⁿ	++++ ^{b,o}	+++ ^d	++++ ^p
Barley	+++ ^q	+++ ^r	+++ ^{d,s}	+++ ^t
Soybean	++++ ^{u,v}	+++ ^{w,x,y}	+++ ^z	++++ ^{aa}
Groundnut	++ ^{bb}	+ ^{cc}	+ ^z	
Cowpea	+++ ^{bb}	++ ^{cc}	+ ^z	
Common bean	++ ^{bb}	++ ^{cc}	+ ^z	
Chickpea	+++ ^{bb}	++ ^{cc}	+ ^z	
Pigeonpea	+++ ^{bb}			

+, Very few; ++, Few; +++, Moderate; +++++, Abundant

^a<http://www.gramene.org/markers/index.html>

^b<http://www.gramene.org/cmap/>

^chttp://www.gramene.org/db/qtl/qtl_display?query=&search_field=&species=Oryza+sativa&submit=Submit

^dhttp://www.ncbi.nlm.nih.gov/dbEST/dbEST_summary.html; <http://compbio.dfci.harvard.edu/tgi/plant.html>

^ehttp://www.gramene.org/Oryza_sativa/Info/Index

^f<http://www.maizegdb.org/probe.php>

^g<http://www.maizegdb.org/map.php>

^hhttp://www.gramene.org/db/qtl/qtl_display?query=*&search_field=trait_name&species=Zea+mays+subsp.-mays&submit=Submit

ⁱhttp://www.maizesequence.org/Zea_mays/Info/Index

^j<http://wheat.pw.usda.gov/cgi-bin/graingenes/browse.cgi?class=marker>

^k<http://wheat.pw.usda.gov/GG2/maps.shtml#wheat>

^lhttp://wheat.pw.usda.gov/cgi-bin/graingenes/quickquery.cgi?query=qtl&arg1=*

^m<http://wheat.pw.usda.gov/cgi-bin/graingenes/search.cgi?class=sequence>

ⁿhttp://www.gramene.org/db/markers/marker_view?

[marker_name=*&marker_type_id=&taxonomy=sorghum&action=marker_search&x=0&y=0](http://www.gramene.org/db/markers/marker_view?marker_name=*&marker_type_id=&taxonomy=sorghum&action=marker_search&x=0&y=0)

^ohttp://www.gramene.org/db/cmap/map_set_info?species_acc=sorghum&map_type_acc=-1

^pPaterson et al. [12]

^q<http://wheat.pw.usda.gov/GG2/Barley/>

^r<http://wheat.pw.usda.gov/GG2/maps.shtml#barley>

^shttp://wheat.pw.usda.gov/cgi-bin/graingenes/browse.cgi?class=sequence&query=barley1_*

^t<http://www.public.iastate.edu/~imagefpc/IBSC%20Webpage/IBSC%20Template-home.html>

^u<http://soybeanbreederstoolbox.org/>

^v<http://soybase.org/BARCSOYSSR/index.php>

^w<http://lis.comparative-legumes.org/cgi-bin/cmap/viewer?changeMenu=1>

^xhttp://soybeanbreederstoolbox.org/search/search_results.php?category=QTLName&search_term=

^y<http://soybeanphysicalmap.org/>

^zhttp://lis.comparative-legumes.org/lis/lis_summary.html?page_type=transcript

^{aa}<http://www.phytozome.net/cgi-bin/gbrowse/soybean/?name=Gm09>

^{bb}See Varshney et al. [13]

^{cc}See Varshney et al. [14] marker assisted recurrent selection (MARS) or genomic selection (GS) are being used in several crops [15, 16].

up to 2 weeks of complete submergence. This has offered great relief to the large number of Asian farmers whose rice land is located in deltas and low-lying areas that are at risk from flooding during the monsoon season every year. Some selected examples of molecular breeding in rice and wheat (adopted from [17]) are summarized in Table 2.

Advanced Backcross QTL (AB-QTL) Analysis

Although MAS has been quite successful, it has always been a difficult task to tackle linkage drag, especially when a QTL or a gene is to be introgressed from wild/exotic species. Furthermore, in MAS, QTL/gene discovery and variety development are two separate processes. To deal with this problem and to harness the potential of the wild/unadapted germplasm in breeding programs, a new approach referred as advanced backcross QTL (AB-QTL) analysis was proposed by Tanksley and Nelson [32]. AB-QTL aims at simultaneous detection and transfer of useful QTLs from the wild/unadapted relatives to a popular cultivar for improvement of a trait. In this context, a superior cultivar/variety is crossed with a wild species leading to the production of a backcross population (BC_2 , BC_3), and molecular markers are used to monitor the transfer of QTLs by conventional backcrossing. The advanced backcross approach has already been successfully utilized in different crops, including tomato [59], rice [60, 61], barley [62], and wheat [63]. It is anticipated that the use of AB-QTL will be accelerated in a range of crops for improving important traits such as disease resistance as well as yield traits.

Marker-Assisted Recurrent Selection (MARS)

In the majority of traits of interest, quantitative variation is controlled by many QTLs, each with minor effect. Moreover, minor QTLs show an inconsistent QTL effect in different environments and over different seasons. Even when the effect of these minor QTLs is consistent, their introgression into the desired genotype through MABC becomes extremely difficult as a larger number of progenies are required to select appropriate lines. In such cases, MARS has been proposed for pyramiding of superior alleles at different loci/QTLs in a single genotype [64, 65].

It was demonstrated in recent studies that the response of MARS is larger when prior knowledge of the QTLs exists and the response decreases as the knowledge of the number of minor QTL associated with the trait decreases [66]. In sweet corn, MARS was employed to fix six marker loci in two different F_2 populations which showed an increase in the frequency of marker allele from 0.50 to 0.80 [64]. Similarly, in a separate study, enrichment of rust resistance gene (*Lr34/Yr18*) with an increase in frequency from 0.25 to 0.60 was reported in wheat BC_1 through MARS [28]. MARS can be utilized effectively for selection of traits associated with multiple QTLs by increasing the frequency of favorable QTLs or marker alleles. Several companies are using MARS in their maize, soybean, etc., breeding programs [66, 67]. Recently, some institutes like International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), the French Centre for International Agricultural Research (CIRAD), and the University of California-Riverside, USA, have also initiated MARS programs in chickpea (PM Gaur, personal communication 2010), sorghum (J-F Rami, personal communication 2010), cowpea (J Ehlers, personal communication 2010), etc., for pyramiding favorable drought-tolerant alleles.

Genome-Wide or Genomic Selection (GS)

Although MAS has been practiced for the improvement of quantitative traits, it has its own limitations. Therefore, in addition to MARS, Genomic Selection can be used to pyramid favorable alleles for minor effect QTLs at the whole genome level [68, 69]. Genomic selection predicts the breeding values of lines in a population by analyzing their phenotypes and high-density marker scores. A key to the success of GS is that, unlike MABC or MARS, it calculates the marker effects across the entire genome that explains the entire phenotypic variation. In simple terms, genome-wide selection refers to marker-based selection without significance testing and without identifying of a subset of markers associated with the trait [68]. The genome-wide marker data (marker loci or haplotypes) available or generated on the progeny lines, therefore, are used to calculate genomic estimated breeding values (GEBV) as the sum of the effects of all QTLs across the genome, thereby potentially exploiting all the genetic variance for a trait [68, 69]. The GEBVs are calculated for every individual

Crop Breeding for Sustainable Agriculture, Genomics Interventions in. Table 2 Some examples of improved cultivars or varieties developed through marker-assisted introgression of important genes/QTLs in rice and wheat

Crop	Genes/QTL introgressed	Function	Variety developed/ released	Reference
Rice	<i>GBSS</i>	Unique cooking and processing quality traits including amylose content	Cadet and Jacinto	[33]
	<i>Xa33t</i>	Bacterial blight resistance	BC ₃ F ₂	[34]
	<i>Xa21</i>	Bacterial blight resistance	Zhongyou 6 and Zhongyou 1176	[35]
	<i>Sub1</i>	Submergence tolerance	BC ₃ F ₂	[30]
	<i>Sub1</i>	Submergence tolerance	Samba Mashuri- <i>Sub1</i>	[36]
			IR64- <i>Sub1</i>	
			TDK1- <i>Sub1</i>	
			CR1009- <i>Sub1</i>	
			BR11- <i>Sub1</i>	
	<i>SUB1QTL</i>	Submergence tolerance	<i>Sub1</i> introgression lines	[37]
	<i>Piz-5+Xa21</i>	Blast and bacterial blight resistance	BC ₄ F ₂	[38]
	<i>Xa4+xa5</i> and <i>Xa4+Xa7</i>	Bacterial blight resistance	Angke and Conde	[39]
	<i>xa7</i> and <i>Xa21</i>	Bacterial blight resistance	Zhenshan97 × Minghui 63	[40]
	<i>xa13</i> and <i>xa21</i>	Bacterial blight resistance, strong aroma	Pusa1460, IET18990	[41]
	<i>xa13</i> and <i>Xa21</i>	Bacterial blight resistance	Improved Pusa RH1	[42]
	<i>xa5, xa13</i> and <i>Xa21</i>	Bacterial blight resistance	Improved PR106	[43]
	<i>Xa5, xa13</i> and <i>xa21</i>	Bacterial blight resistance	BC ₃ F ₂	[44]
	<i>Xa5, Xa13</i> and <i>Xa21</i>	Bacterial blight resistance	IET19046	http://www.drricar.org/four_varieites.htm
	<i>Xa4, xa8, xa13</i> and <i>Xa21</i>	Bacterial blight resistance	BC ₁ F ₃	[45]
	<i>Xa4, Xa5, Xa13</i> and <i>Xa21</i>	Improved bacterial blight resistance	Pusa1526-04-25	http://www.iari.res.in/?q = node/233

Crop Breeding for Sustainable Agriculture, Genomics Interventions in. Table 2 (Continued)

Crop	Genes/QTL introgressed	Function	Variety developed/released	Reference
	–	Bacterial blight resistance	Xieyou218	[46]
	QTL	Drought-tolerant aerobic rice	MAS946-1	www.hindu.com/2007/11/17/stories/2007111752560500.htm
	qSALTOL and qSUB1	Enhanced salt and submergence tolerance	F ₆	http://open.irri.org/sabrao/images/stories/conference/site/papers/apb09final00098.pdf
	QTL	Improved performance under drought	Birsa VikasDhan111 (PY 84)	http://claria13.securesites.net/News/releases/2009/may/26018.htm
Wheat	QPhs.ccsu-3A.1 and Lr24 +Lr28	Preharvest sprouting tolerance and leaf rust resistance	BC ₃ F ₃	[47]
	Lr47	Resistance to leaf rust	BIOINTA2004	[48]
	Gpc-B1	High grain protein content	Lillian	[49]
	Qfhs.ndsu-3AS	Resistance to fusarium head blight	Bena	[50]
	Sm1	Resistance to the insect orange blossom wheat midge	Goodeve	[51]
	Stb4	Resistance to <i>Septoria</i>	Kern	Cited from [17]
	Wsm-1	Resistance to wheat streak mosaic virus (WSMV)	Mace	[52]
	Yr15	Seedling stripe rust	BC ₃ F _{2,3}	[53]
	Qss.msub-3BL	Resistance to wheat stem sawfly	McNeal, Reeder, Hank	http://www.wheatworld.org/pdf/dubcovsky.pdf
	Bdv2	Resistance to yellow dwarf virus	Above, Avalanche, Ankor	http://www.wheatworld.org/pdf/dubcovsky.pdf
	Yr17 and Lr37	Stripe rust and leaf rust resistance	Patwin	[54]
	CreX and CreY	Cyst nematode resistance	F ₃ progenies	[55]
	Yr36 and Gpc-B1	Resistant to stripe rust and high grain protein content	Westmore	[56]
	Yr17 and Yr36	Resistance to stripe rust	Lassik	Cited from [17]
	Lr19 and Sr25	Resistant to stem rust race UG99	UC1113 (PI638741)	[57]
	Yr36 and Gpc-B1	Resistance to stripe rust, high grain protein content	Farnum (WA7975)	http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1671746
	Yr15 and Gpc-B1	Resistance to stripe rust and high grain protein content	Scarlet (WA7994)	http://css.wsu.edu/Proceedings/2005/2005_Proceedings.pdf
	Lr1, Lr9, Lr24, Lr47	Leaf rust resistance	BC ₁ F ₂	[58]

of the progeny based on genotyping data using a model that was “trained” from the individuals of another training populations having both phenotyping and genotyping data. These GEBVs are then used to select the progeny lines for advancement in the breeding cycle. Thus GS provides a strategy for selection of an individual without phenotypic data by using a model to predict the individual’s breeding value [69].

Recently, Wong and Bernardo [70] simulated the comparative responses of phenotypic selection (PS), MARS, and GS with small population sizes in oil palm, and assessed the efficiency of each method in terms of years and cost per unit gain (i.e., the time and cost saved by these different methods over each other for making selection). They used markers significantly associated with the trait to calculate the marker scores in MARS, whereas all markers (without significance tests) to calculate the marker scores in GS. Responses to PS and GS were consistently greater than the response to MARS. Furthermore, with population sizes of $N = 50$ or 70 , responses to GS were 4–25% larger than the corresponding responses to PS, depending on the heritability and number of QTLs. In terms of economics, cost per unit gain was 26–57% lower with GS than with PS when markers cost US \$1.50 per data point, and 35–65% lower when markers cost \$0.15 per data point. Reduction in costs in sequencing and high-throughput marker genotyping may enhance uptake of GS for crop improvement in the future.

Challenges in Adoption of Genomics Technologies

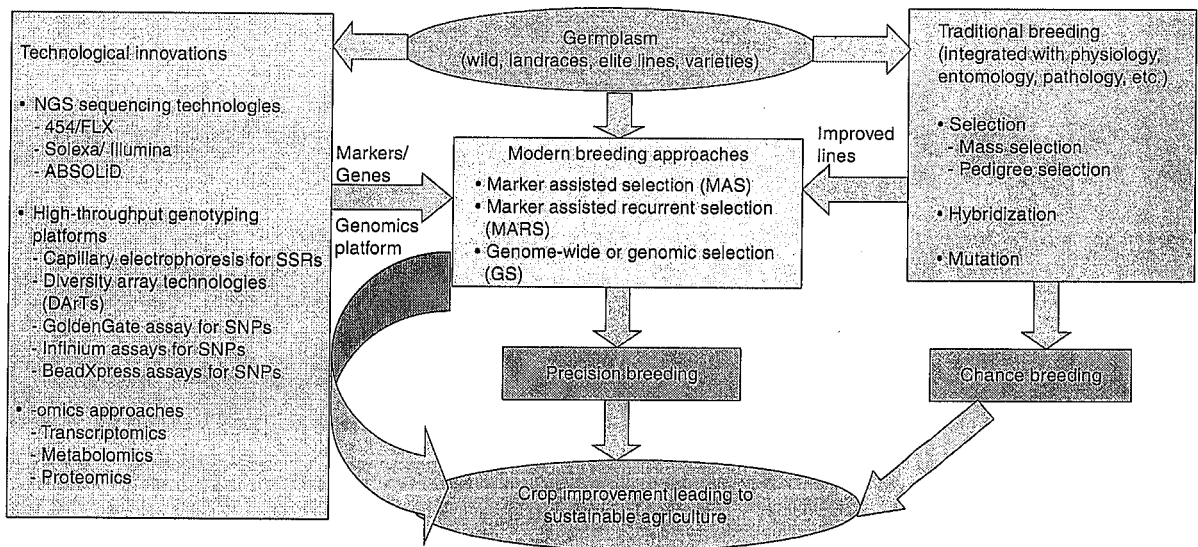
Developing sustainable approaches to agriculture is one of the most difficult challenges facing growers and scientists today. Agricultural sustainability involves successful management of resources for agriculture to satisfy changing human needs, while maintaining or enhancing the quality of the environment and conserving natural resources [71]. However, sustainable production is hampered by the decline in land and soil productivity as a result of inappropriate soil and water management and other agricultural practices, as well as misguided policies and frequent opposition to technological advances that have the potential to improve the quality of life of billions of people worldwide. This is in addition to the postulated challenges of climate change, the number of hazardous chemicals (pesticides and

fungicides) that are constantly being released into the environment and are becoming increasingly toxic to human and animal life [71]. In recent years, the use of promising biotechnology tools like genetic engineering (GE) has offered potential solutions to the above problems. However, the adoption of any new technique, particularly related to genetic engineering, remains a policy matter and as mentioned above faces stiff opposition many a times. In a recent review, Farre et al. [25] addressed several of these issues and advocated to overcome on the major barriers to adoption, which are political rather than technical, for realization of the potential of GE crops in developing countries.

It is thus obvious that the challenges facing agriculture are massive, particularly with the controversies over GE crops world over. It is clear that current methods of food production, in both the developing as well as the developed countries, are neither sufficient nor sustainable [72]. Under these circumstances, genomics interventions have great role to contribute to sustainable agriculture. As mentioned in this article, genomics approaches are very powerful to predict the phenotype, with higher precision and efficiency, based on the genotype. A variety of approaches ranging from MAS to GS are available to become integral part of plant breeding. While in the past, plant breeders were hesitant to use genetic variation existing in wild relatives of crop species in commercial breeding programs due to the long time it takes to recover desired phenotypes because of linkage drag, approaches like AB-QTL, in addition to MAS, can be successfully utilized. Availability of NGS technologies, associated with low costs and high-throughput, offers the opportunity to sequence either entire or major proportion of the germplasm collection for a species present in the gene banks around the world to understand genome variation. In case, the genome variation can be associated with the phenotype, which is not trivial, it will be possible to develop the ideotype, based on haplotype, of the variety to be developed.

Future Directions

While success stories of genomics-assisted breeding are available in several crops, it must also be recognized that much of the genome information generated is not being routinely used by plant breeders, especially in public breeding programs [26]. This may be due to



Crop Breeding for Sustainable Agriculture, Genomics Interventions in. Figure 1

Schematic representation of genomics technologies for crop improvement and sustainable agriculture

In general, traditional crop improvement programs (shown in the box on the right hand side in Fig. 1) employ different breeding strategies integrated with physiology, pathology, entomology, etc., and generate superior lines or improved crop varieties. These approaches, however, take more time, and sometimes such breeding is referred as “chance breeding” due to uncertainty in successes predicted in these approaches. On the other hand, genomics technologies (shown in the box on the left hand side) such as a number of next-generation sequencing (NGS) technologies, availability of high-throughput genotyping such as capillary electrophoresis for large-scale SSR genotyping, microarray-based DArTs, GoldenGate/Infinium/BeadXpress assays for large-scale SNP genotyping, and a range of -omics technologies provide candidate markers, gene(s), and QTLs to be integrated into the breeding programs by using high-throughput genomics platforms. Integrated breeding approaches (shown in the box in the middle) such as marker-assisted selection (MAS), marker-assisted recurrent selection (MARS), and genome-wide selection (GS) offer “precision breeding” with a great potential, versus “chance breeding” to contribute to sustainable crop improvement

shortage of trained personnel, inadequate access to genotyping, inappropriate phenotyping infrastructure, unaffordable bioinformatics systems, and a lack of experience of integrating these new technologies with traditional breeding [4, 26]. However, recently, several international initiatives such as the Integrated Breeding Platform (formerly Molecular Breeding Platform, www.mbp.genertaioncp.org), a joint initiative of The Bill and Melinda Gates Foundation and The Generation Challenge Program, have been started so that plant breeders especially from developing countries can have access to many genotyping, phenotyping, as well as information technologies to integrate their breeding programs with modern genomics approaches.

We believe that integration of modern genomics in combination with other cutting edge technologies in

breeding programs is invaluable for crop improvement (Fig. 1) and will lead to sustainable agriculture for food security, especially in developing countries.

A vital task facing the plant breeding community today is to enhance food security in an environmentally friendly and sustainable manner. Though genomics interventions will not solve all the problems associated with agricultural production leading to sustainability, they have the potential, especially when they are used in an integrated manner as described in Fig. 1, to improve the breeding efficiency to address specific problems. These include increasing crop productivity, diversification of crops, enhancing nutritional value of food (biofortification), and reducing environmental impacts of agricultural production. However, only through judicious, rational, and science- and need-based exploitation

of genetic resources through genomic technologies coupled with conventional plant breeding and genetic engineering will lead to sustainable agriculture.

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