Chapter 1

Unraveling the Secrets of Rice Wild Species

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http://dx.doi.org/10.5772/58393

1. Introduction

The world is facing a new challenge with global population predicted to plateau at nine billion people by the middle of this century (Godfray et al. 2010). Increasing food production to feed the world's population is an even greater challenge considering that agriculture is experiencing greater competition for land, water and energy, as well as, the effects of substantial climate change and the unintended effects of crop production on the environment. Part of the solution to increasing food production on the same or less cultivated land lies in exploiting the subset of genes lost during the domestication process and subsequent targeted breeding. Currently, these valuable genes are found only in the progenitor species genepool for crop cultivars. Cultivated plants having desirable genes were utilized in intensive breeding projects focused on increasing yield for particular environments and management systems but this process has narrowed the genetic diversity (Rausher 2001). For cultivated plants, this unexploited genetic material includes both landraces and the more exotic wild relatives. Improving our understanding of this tertiary gene pool and exploiting it for crop improvement is paramount to meeting the challenges of feeding the world in this century through the integration of classical genetics and genomics-enabled research paradigms.

The loss of genetic diversity can be more problematic for self-pollinated plant species where the rate of cross pollination is below five percent, thus making it more difficult to reintroduce the lost diversity. In the case of the two major grain crops, rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.), both self-pollinated, the re-introduction genetic diversity from the wild is central to the continued success of breeding, given that viruses, fungi, and bacteria, three main causal agents of biotic stress, are constantly evolving to cause the breakdown of the host plant's defense mechanisms (Rausher 2001).

Abiotic stress, including salinity, aluminum toxicity and acid sulfate soils, as well as, temperature and drought, complicate the difficulty of improving crop yields, especially in the face of

global warming (Brooker 2006; Tilman and Lehman 2001), which makes modern cultivars even more vulnerable. Genetic sources of resistance or tolerance offer the most promising mechanism to protect plants against these unfavorable conditions. Often wild species are not included as parental lines in cultivar development because it is relatively difficult to harness desirable genes by genetic recombination and many undesirable genes are introgressed from the wild parent resulting in inferior yield, undesirable plant architecture, and/or poor grain quality (Tanksley and McCouch 1997). Recent studies, however, in rice (McCouch et al. 2007) and tomato, *Lycopersicon esculentum* Mill. (Grandillo and Tanksley 2003), have shown that wild species contain genomic components that could result in genetic gains in terms of agronomic performance.

The rapid advancement in molecular technologies allows for genotyping plants much more quickly and inexpensively than ever before. The availability of high resolution genotypic information creates the opportunity to further explore an expanding number of accessions in a greater depth, and harness this information to enhance the efficiency and accuracy of introgression. These developments create opportunities not previously possible, to identify molecular markers associated with desirable traits in wild species and transfer these traits into elite lines and/or varieties, as well as, to unravel multi-genic traits for crop improvement (Tanksley and McCouch 1997; McCouch et al. 2012).

Our main objective is to summarize efforts over the past 15 years to identify useful novel alleles in the *Oryza* species that were lost during evolution and domestication, genetically dissect the traits encoded by these alleles through chromosome mapping, and incorporate these traits or alleles into an agronomically useful genetic background. To do this we will (a) briefly describe the relationships among the species in the genus *Oryza*, (b) describe the types of populations that have been developed for mapping desirable traits identified in the wild *Oryza* species to a chromosome location, and (c) summarize the quantitative trait locus (QTL) studies focused on mapping the useful traits and novel alleles to specific locations in the genomes of *Oryza* species.

2. Phylogeny of the *Oryza* genus

The *Oryza* genus includes two cultivated species, Asian rice, *O. sativa*, which is grown throughout the tropical and temperate climates of the world, and African rice, *O. glaberrima*, which is found in sub-Saharan Africa along the Niger River. The 22 wild species composing the *Oryza* genus are characterized by eleven different genomes identified as the A-, B-, C-, D-, E-, F-, G-, H-, J-, K-and L-genomes and arranged in the following 10 genome types AA, BB, CC, BBCC, CCDD, EE, FF, GG, HHJJ and KKLL. Four of the wild *Oryza* species are tetraploid and the remaining 18 are diploid, as well as, the two cultivated species (Table 1).

http://dx.doi.org/10.5772/58393

Species†	No. of chromo-somes (2n)†	Genome†	Genome size (Mbp)‡	Distribution†
Section Oryza				
Oryza sativa complex				
O. sativa L. (ssp. *japonica*, ssp. *indica*)	24	AA	420, 466	Worldwide
O. nivara Sharma et Shastry	24	AA	448	Tropical and subtropical Asia
O. rufipogon Griff.	24	AA	439, 450	Tropical and subtropical Asia, Tropical Australia
O. glaberrima Steud.	24	A^gA^g	354	West Africa
O. barthii A. Chev.§	24	A^gA^g	411	Africa
O. glumaepatula Steud.	24	$A^{gp}A^{gp}$	464	South and Central America
O. longistaminata A. Chev. et Roehr.	24	A^lA^l	352	Africa
O. meridionalis Ng	24	A^mA^m	435	Tropical Australia
Oryza officinalis complex				
O. punctata Kotschy ex Steud.	24 48	BB, BBCC	423 (BB)	Africa
O. minuta J.S. Presl. ex C.B. Presl.	48	BBCC	1124	Philippines, Papua New Guinea
O. eichingeri A. Peter	24	CC		South Asia and East Africa
O. officinalis Wall ex Watt	24	CC	653	Tropical and subtropical Asia, Tropical Australia
O. rhizomatis Vaughan	24	CC		Sri Lanka
O. alta Swallen	48	CCDD	1124	South and Central America
O. grandiglumis (Doell) Prod.	48	CCDD		South and Central America
O. latifolia Desv.	48	CCDD		South and Central America
O. australiensis Domin.	24	EE	960	Tropical Australia
Section Brachyantha				
O. brachyantha A. Chev. et Roehr.	24	FF	338	Central Africa

Species†	No. of chromo-somes (2n)†	Genome†	Genome size (Mbp)‡	Distribution†
Section Padia				
Oryza granulata complex				
O. granulata Nees et Am. ex Watt	24	GG	862	South and Southeast Asia
O. meyeriana (Zoll. et (Mor. ex Steud.) Baill.)	24	GG		Southeast Asia
Oryza ridleyi complex				
O. longiglumis Jansen	48	HHJJ		Irian Jaya, Indonesia, Papua New Guinea
O. ridleyi Hook. F.	48	HHJJ	1283	South Asia
Oryza schlechteria complex				
O. coarctata Tateoka	48	KKLL	771	Asian coastal area
O. schlerchteri Pilger	48	KKLL		Papua New Guinea

† Classification for species, genome designation and distribution based on Brar and Singh (2011), Lu et al. (2014), Sanchez et al. (2013) and Vaughan (2003). The superscripts for the A-genome indicate a variation of the type of A-genome.

‡ Genome size based on the following: *O. sativa* subsp. *japonica* (Goff et al. 2002), *O. sativa* subsp. *indica* (Yu et al. 2002) and *Oryza* species (Ammiraju et al. 2010).

§*O. barthii* is also classified as *O. breviligulata* A. Chev. et Roehr.

Table 1. Taxonomic classification of *Oryza* species including the chromosome number, genome designation, genome size and distribution for each species.

Rice is the only major cereal found in the ancient lineage of the Bambusoideae and is currently placed in the subfamily Erhartoideae. Historically, the grass family, Poaceae, is thought to have evolved about 70-55 mya (million years ago) with the tribes Oryzeae and Pooideae (wheat and oats) diverging about 35 mya [reviewed by Kellogg (2009) and Vaughan et al. (2008)]. The Oryzinae and Zizaninae subtribes diverged about 20-22 mya and the *Oryza* and *Leersia* genera about 14.2 mya. The genus *Oryza* is divided into three sections: *Padia*, *Brachyantha* and *Oryza*. *Padia* includes the forest-dwelling *Oryza*, which are distributed into the *O. granulata* (GG), *O. ridleyi* (HHJJ) and *O. schlechteria* (KKLL) complexes. The *O. granulata* complex is thought to have diverged from the other *Oryza* species about 8 mya. *O. brachyantha* (FF) is the only species in the section *Brachyantha*. This species is widely distributed across Africa, growing in iron-pan rock pools.

Section *Oryza* consists of two species complexes, the *O. officinalis* complex with the B-, C-, D- and E-genomes and the *O. sativa* complex, which includes all the A-genome species. Within

the *O. officinalis* complex, *O. australiensis* (EE) is the most diverged and *O. eichingeri* (CC) appears to be the most basal of the C-genome species.

The species in the *O. sativa* complex prefer full sun, and grow near lakes, rivers and seasonal pools of water. Molecular data suggests that *O. meridionalis* diverged from the other A-genome species about 2 mya. Also, the perennial African species, *O. longistaminata*, diverged from the Asian A-genome species about the same time period, 2-3 mya. The second divergence between the Asian and African A-genome species, *O. barthii* and *O. glaberrima*, occurred 0.6 to 0.7 mya. More recently, possibly about 0.4 mya (or more than 0.2 mya), the *O. rufipogon* clade(s) that eventually diverged into the *O. sativa* subspecies (subsp.) *Japonica* and *Indica*. Later, the *Indica* subspecies differentiated into the *indica* and *aus* subpopulations and the *Japonica* subspecies into the *aromatic* (Group V), *tropical japonica* and *temperate japonica* subpopulations (Garris et al. 2005, Zhao et al. 2011, Huang et al. 2012). Archaeobotanical evidence from spikelet bases and changes in grain size document this domestication process (Fuller et al. 2010). Recently, based on genome sequences of 446 geographically diverse *O. rufipogon* accessions, Huang et al. (2012) further subdivided *O. rufipogon* accessions into three major *O. rufipogon* clades: one closely aligned with *O. sativa* subsp. *japonica*, one aligned with *O. sativa* subsp. *indica*, and the third clade was independent of *O. sativa*. Furthermore, as part of this study, a neighbor-joining tree constructed from sequence differences of 15 representative A-genome accessions suggested within *Indica*, different *O. rufipogon* clades were associated with the *aus* and *indica* subpopulations, whereas the three *Japonica* subpopulations arose from a single *O. rufipogon* clade. This phylogenetic tree also supported the aforementioned genetic distance between *O. meridionalis*, *O. longistaminata*, *O. barthii* and *O. glaberrima*.

Rice, *O. sativa*, the first monocot plant with a reference genome, is the central comparative genomics model for all grasses, and has been compared to all major cereals. To lay the foundation for interrogating the rice wild relatives, 18 bacterial artificial chromosome (BAC) libraries for 16 different *Oryza* species spanning all 10 *Oryza* genome types including the AA-genome species (*O. nivara*, *O. rufipogon*, *O. glaberrima*, *O. barthii*, *O. glumaepatula*, *O. longistaminata*, *O. meridionalis*), *O. punctata* (BB), *O. officinalis* (CC), *O. minuta* (BBCC), *O. alta* (CCDD), *O. australiensis* (EE), *O. brachyantha* (FF), *O. granulata* (GG), *O. ridleyi* (HHJJ) and *O. coarctata* (HHKK), were generated through the *Oryza* Map Alignment Project (OMAP) as summarized by Ammiraju et al. (2010). Subsequently, the International OMAP consortium was formed in 2007 to (a) generate reference sequences and transcriptome data sets of the eight A-genome species and representative species of the other genome types, (b) generate advanced mapping populations for the A-genome species, and (c) identify naturally occurring populations of the wild *Oryza* species for diversity and evolutionary analyses, as well as, conservation (Jacquemin et al. 2013; Sanchez et al. 2013). The species included in the sequencing effort were A-genome species (*O. nivara*, *O. rufipogon*, *O. barthii*, *O. glaberrima*, *O. glumaepatula*, *O. longistaminata*, *O. meridionalis* and both *O. sativa* subsp. *indica* and subsp. *japonica*), *O. punctata* (BB), C-genome species (*O. officinalis*, *O. eichingeri*, *O. rhizomatis*), *O. australiensis* (EE), *O. brachyantha* (FF), *O. granulata* (GG), and the outgroup, *Leersia perrieri*. To date, the sequencing of nine genomes and *L. perrieri* has been completed, in addition to the established reference sequences for *O. sativa* subsp. *japonica* and subsp. *indica* genomes (Wing 2013). Currently, two additional *O. sativa*

subsp. *indica* cultivars are being sequenced representing the *aus* (DJ123) and *indica* (IR64) subpopulations (McCombie 2013).

3. Methods for developing *Oryza* interspecific mapping populations

Traits are classified as either qualitative or quantitative traits. Qualitative traits are controlled by one or a few genes with major effects while quantitative characters are controlled by many genes with minor effects (Poehlman and Sleper 1994). Identification of genes associated with quantitative traits is always more complicated compared to those involving qualitative traits.

Interspecific and intergenomic hybridization, hybridization between species with the same or different genomes, have been used to transfer desirable genes or QTL associated with simple or complex traits from wild species into a cultivated genetic background (Brar and Khush 1997; Dalmacio et al. 1995; Tanksley and McCouch 1997). Nevertheless hybridization success can be hindered by genomic incompatibilities and sterility barriers (Ishii et al. 1994; McCouch et al. 2007; Wang et al. 2005). The utilization of embryo rescue and other methods of producing viable and fertile hybrids combined with robust molecular markers and associated computational and statistical analyses, led to the successful generation of interspecific genetic populations that were used to link desirable traits to molecular markers and subsequent identification of the actual genes controlling the traits of interest (Ali et al. 2010; Chen et al. 2010; Ghesquière et al. 1997; Guo et al. 2013; Lexer and Fay 2005; McCouch et al. 2007). Six types of mapping populations are generated from interspecific crosses between *Oryza* species and *O. sativa* including (a) recombinant inbred line (RIL), (b) advanced backcross (AB), (c) backcross inbred line (BIL), (d) chromosome segment substitution line (CSSL), (e) near isogenic line (NIL) and (f) multi-parent advanced generation inter-cross (MAGIC). A discussion of each of these populations follows and examples are included in the third section describing agronomically important traits attributed to the *Oryza* species donor.

3.1. Recombinant Inbred Line (RIL) population

RIL populations have been the most common type of mapping population used in rice genetics and breeding when both parents are *O. sativa* but a limited number of interspecific populations have been reported. To develop a RIL population, two contrasting cultivars or accessions for the trait(s) to be mapped are crossed together to create an F_1 hybrid. By successive self-pollination starting from the F_1 generation, subsequent generations of segregants are produced (up to F_3), representing multiple rounds of recombination and eventually fixation to homozygosity towards either of the parental alleles (Fig. 1). This derived population is advanced for several generations by the single seed descent (SSD) method, where a single F_3 seed from each F_2 plant is planted to produce the F_4 generation, subsequently a single F_4 seed is selected from each line to produce the F_5 generation with the SSD method usually continuing until F_8 seed are produced. At the F_7, the RILs exhibit genetic homogeneity, such that the genomic contribution of each parent is fixed,

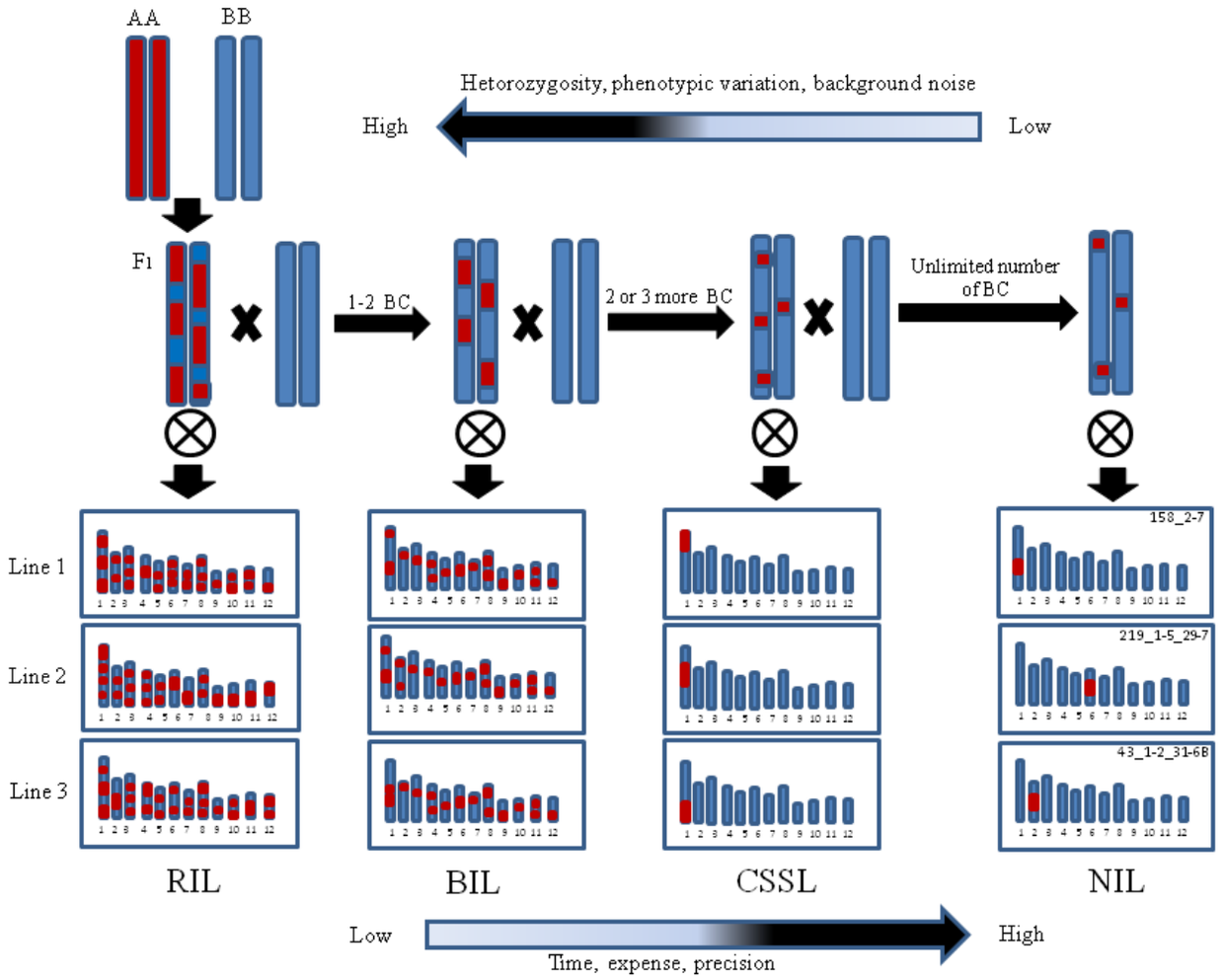

Figure 1. A comparison of the methods for creating primary and advanced bi-parental mapping populations, including recombinant inbred lines (RILs), backcross inbred lines (BILs), chromosome segment substitution lines (CSSLs) and near isogenic lines (NILs) as summarized by Fukuoka et al. (2010). Also shown are the number of backcrosses (BC) required and the genotypes of the lines obtained by each method. Karyotypes of the three CSSLs illustrate how chromosome 1 of the donor can be introgressed into the recurrent parent. The three NIL genotypes are based on the JeffersonNILs, each with a different *O. rufipogon* (IRGC105491) introgression selected for a different yield QTL (Imai et al. 2013).

and together these RILs compose a mapping population. If selections are being made for improved lines with a particular trait(s), this selection often begins in the F_5-F_6 if individual plants can be selected for the trait; otherwise, the selection is postponed to later generations (F_7-F_n) (Nguyen et al. 2003, Poehlman and Sleper 1995). The procedure continues until the superior lines with desirable traits are produced.

The main advantage of the RIL method is that no backcrossing is necessary but when a wild *Oryza* species is a parent, often undesirable traits associated with the wild parent, especially shattering and sterility are problematic, thus it is often necessary to backcross. RIL populations are suitable for identifying major gene(s) or QTL(s), and to detect genetic interactions such as epistasis (Fukuoka et al. 2010). Other advantages are, the individual

RIL may contain more than one introgressed segment in their chromosomes, representing different recombination events and a higher recombination frequency. As a result, fewer progeny lines are required to cover the complete donor genome as compared to other types of bi-parental mapping populations that include a backcross generation. Moreover, epistatic effects can be detected in RILs due to the presence of several introgressed segments in each line (Keurentjes et al. 2007). Because several segments of each parent are present in each individual line composing the population, there is less homogeneity in RIL populations as compared to most other types of populations. This heterogeneity is easy to observe and provides an excellent opportunity for phenotypic evaluation. In summary, the RIL method has proven to be useful when both parents are *O. sativa* but with interspecific and intergenomic crosses, backcrossing is often necessary (Fukuoka et al. 2010).

Commonly used softwares for creating the linkage map from the genotypic (molecular marker) data of the population for QTL analyses include MapMaker-QTL (Lander and Botstein 1989), JoinMap (Van Ooijen 2006) and MapDisto (Lorieux 2012). The possible chromosome location of the QTL for the trait being evaluated is based on the QTL having a significant LOD [logarithm (base 10) of odds] score with the LOD score detecting linkage between the molecular marker and the trait of interest. Several softwares are freely available for conducting the QTL analysis, including MapMaker-QTL (Lander and Botstein 1989), QTLCartographer (Wang et al. 2012), QGene (Joehanes and Nelson 2008), MapDisto (Lorieux 2012) and QTLNetwork (Yang et al. 2008). It is important to confirm that the software being used for QTL analysis can correctly analyze the population type since some cannot be used with BC_2F_2 populations based on differences in fundamental assumptions. Most recent QTL analyses with rice have been performed using either composite interval mapping (CIM) (Zeng 1994) or multiple interval mapping (MIM) (Kao and Zeng 1999) with single point analysis (SPA) (Tanksley et al. 1982), marker regression (Kearsey and Hyne 1994) and interval mapping (IM) (Haley and Knott 1992; Lander and Botstein 1989) being used in earlier analyses.

3.2. Advanced Backcross (AB) population

The advanced backcross (AB)-quantitative trait locus (QTL) analysis is a powerful strategy to map desirable trait(s) discovered in the wild species (Tanksley and Nelson 1996). This method was first applied to QTL mapping in tomato, and subsequently to several other crops, including rice (Grandillo and Tanksley 2003; McCouch et al. 2007). In the process of developing the AB populations used for QTL analysis, plants or lines with unfavorable genes derived from donor parents like sterility and sometimes shattering, are often eliminated from the population after phenotypic and genotypic evaluation. Due to artificial selection in favor of lines with desirable alleles and the genetic background from the recurrent parent, the distribution can be skewed toward the recurrent parent, therefore, after the BC_3 generation, the power of the statistical analysis to detect QTL decreases. Since sequential backcrossing in AB-QTL removes epistatic interactions, the chance of detecting QTLs with epistatic interactions among alleles from the donor parent decreases, while the ability to detect additive QTLs increases (Tanksley and Nelson 1996; Grandillo and Tanksley 2003).

To create an AB mapping population, one parent, usually the wild *Oryza* species, identified as the donor parent, is crossed with the recurrent parent, usually an elite cultivar, which will be crossed with the hybrid parent in subsequent crosses (illustrated in Ali et al. 2010). Often the donor parent is used as a male and the recurrent parent as the female to avoid the cytoplasmic male sterility and because it is usually easier to emasculate the cultivated parent. The F_1 plant(s) is one parent in the second generation and it is crossed with the recurrent parent, which is defined as backcrossing. The resulting first backcross generation (BC_1) may be backcrossed again with the recurrent parent to generate a BC_2 population. If the BC_2 progeny are sterile, it is best to advance the population to the BC_3 generation by crossing the BC_2 plants to the recurrent parent a third time. After the progeny lines are advanced to the BC_2 (or BC_3) generation and allowed to self pollinate, these BC_2F_2 (or BC_3F_2) progeny plants are grown to collect phenotypic and genotypic data for the QTL analysis. After the AB-QTL mapping, the AB population can be advanced by (a) allowing all the progeny lines to self-pollinate and be advanced by SSD for three to four additional generations, thus developing a BIL population or (b) backcrossing the progeny lines additional generations to develop a library of CSSLs or NILs for targeted traits (Fig. 1).

3.3. Backcross Inbred Line (BIL) population

BIL populations are used to introgress desirable traits from the wild *Oryza* species donor into rice with the potential of improving the agronomic performance of elite cultivars and develop mapping populations (Fig. 1). After backcrossing, as described in the aforementioned AB population development, the individual lines, BC_1, BC_2 or BC_3 generation, are self-pollinated for about four generations to the BC_2F_5, as described in the RIL population development. If a specific trait is being selected, the BILs will be screened for that trait and backcrossed as described in the NIL section (Blanco et al. 2003; Fukuoka et al. 2010; Fulton et al. 1997; Bernacchi et al. 1998; Talamè et al. 2004).

The advantages of utilizing BILs are that the method is relatively straightforward and the lines are more homogeneous, having less linkage drag and fewer untargeted segments from the donor parent as compared to RILs. Furthermore, BIL populations can be used to identify major QTLs and single genes, detect QTLs with epistatic or additive effects, as well as, provide an accurate estimation of genotype x environment interactions. It takes more time to develop a BIL population than a RIL population but less time than developing CSSLs and NILs because there are fewer backcrosses to do and less emphasis on targeted segments (Fukuoka et al. 2010; Fulton et al. 1997; Jaquemin et al. 2013). Some disadvantages of this method are the genetic background of the donor parent is higher in the BILs as compared to the CSSLs and NILs, and the lines require more phenotypic evaluation but less genotypic characterization. As a result, mapping in a BIL population is more labor intensive and costly compared to RILs but less costly than NILs and CSSLs. Unfortunately, only limited success has been reported for improving quantitative traits with low heritability and identifying minor QTLs. Also, it is difficult to transfer a relatively large number of genes or QTLs associated with the desirable traits from the wild donor to an elite cultivar using lines selected from a BIL population.

3.4. Chromosome Segment Substitution Line (CSSL) library

A CSSL "library" is a set of near isogenic lines, often ranging from 26 to 80 lines, which cover the entire donor genome when the segments included in each introgression line are in the background of the recurrent parent (Fig. 1; Ali et al. 2010). The concept of CSSL libraries was initially proposed by Eshed and Zamir (1995) as introgression lines and Ghesquière et al. (1997) as contig lines. To develop CSSLs, the initial crossing follows the same scheme as described for AB and BIL populations where the wild, unadapted *Oryza* species is the donor parent and the recurrent parent is usually an elite cultivar. To confirm the entire donor genome is included in the CSSL library, a set of polymorphic markers is often used to assist in selecting lines for each generation, beginning with the BC_1F_1 generation. To develop a CSSL library usually requires backcrossing to the recurrent parent for three to four additional generations (BC_4F_1 or BC_5F_1). The set of polymorphic markers can be used each generation to confirm the targeted segment is present in each line composing the CSSL library as illustrated in Ali et al. (2010). Alternatively, several hundred lines can be backcrossed for 4 to 5 generations and a CSSL library can be selected after genotyping in the BC_4 or BC_5 generation. Once the desired $BC_{4:5}F_1$ lines are selected, the lines are self-pollinated to achieve homozygosity and the lines homozygous for the individual targeted segment are selected from the $BC_{4:5}F_2$ progeny lines. The $BC_{4:5}F_3$ seed is used to establish the CSSL library composed of a set near isogenic lines covering the entire donor genome (Ali et al. 2010; Fukuoka et al. 2010).

A CSSL library has several advantages compared to BILs or an AB mapping population in that it can be used for fine mapping, to identify both major and minor QTLs, and validate genetic interactions. Also, due to the recurrent parent background in CSSLs, linkage drag and its negative effects on the QTL studies are significantly reduced or eliminated. This uniform genetic background enables one to make rapid progress in linkage mapping of targeted QTLs. Lastly, individual CSSLs which carry a specific trait can be used for fine mapping and gene pyramiding (Ali et al. 2010; Fukuoka et al. 2010), as illustrated by the identification of the rice stripe necrosis virus resistance introgression from *O. glaberrima* (Gutiérrez et al. 2010).

The rice universal core genetic map is a set of uniformly distributed polymorphic SSR markers that clearly differentiate *O. sativa* cultivars and wild *Oryza* species accessions, especially within the AA genome (Orjuela et al. 2010). If polymorphic SSR (simple sequence repeat) markers for several different CSSL libraries or other mapping populations are selected from the core map, such that the markers are in approximately the same location, comparisons can be made across several different CSSL libraries or mapping populations. More recently, SNP (single nucleotide polymorphism) markers have been used to genotype the putative lines being selected for the CSSL libraries. For this purpose, several different 384-SNP assays have been used to identify the target donor segment and recurrent parent background (Ali et al. 2010; Tung et al. 2010; McCouch et al. 2010) and most recently a single 6,000 SNP assay is being employed (Zhou et al. 2013; SR McCouch, Cornell University, personal communication).

3.5. Near Isogenic Lines (NILs)

The procedure for developing a set of NILs is similar to CSSLs except the number of backcrosses is unlimited because the focus is on incorporating a single segment with the trait(s) of interest identified in the *Oryza* species donor into the background of the recurrent parent (Fig. 1). With NILs, the focus is on a particular set of lines for the trait(s) of interest, not covering the entire donor genome as with a CSSL library. As with CSSLs, once the targeted segment is introgressed into the recurrent parent background, the pre-NIL lines are allowed to self-pollinate, so that the NILs will be homozygous for the targeted segment. Molecular markers, such as SSRs and SNPs, are used to select for the targeted segment and determine the number of chromosomal segments from the donor parent remaining in the background (Fukuoka et al. 2010).

NILs are often developed to fine map QTLs identified in primary mapping populations, like RIL or BIL, because the QTLs can be mapped precisely as single Mendelian factors (McCouch et al. 2007). Use of NILs, like CSSLs, increases the power to detect small-effect QTL and can overcome or minimize genetic incompatibility, linkage drag, cytoplasmic sterility and epistatic effects, all of which are common obstacles in wide hybridization efforts because the genetic background is more or less uniform. Although developing NILs, like CSSLs, is labor intensive, time consuming, and expensive, NILs are a valuable tool for exploring the genes underlying QTLs because the epistatic effects are removed or minimized making it easier to measure gene expression (Keurentjes et al. 2007). Finally, those NILs with valuable genes introgressed from the wild *Oryza* species donor, can be used as parental lines in breeding programs.

3.6. Multi-parent Advanced Generation Inter-Cross (MAGIC) population

Recently, some efforts have turned to MAGIC populations (Cavanagh et al. 2008; Kover et al. 2009) which can serve the dual purpose of permanent mapping populations for precise QTL mapping, and for direct or indirect use in variety development, especially when the parents used to develop the population are the source of agronomically useful traits (Bandillo et al. 2013). MAGIC populations are developed by systematically crossing several F_1 hybrids involving four to sixteen different parental lines to create a set of double crosses, then systematically crossing the double cross hybrids to create a set of 4-, 8-or 16-way crosses. As the final step, the lines composing the population are advanced four or more generations by single seed descent to obtain a set of advanced intercrossed lines (AILs). Bandillo et al. (2013) reported four different types of MAGIC populations being developed in rice (*O. sativa*) at the International Rice Research Institute (IRRI) which are described as (1) *Indica* MAGIC composed of 1,831 S_8 AILs; (2) MAGIC Plus with 2,214 S_6 AILs; (3) *Japonica* MAGIC with approximately 400 S_6 AILs; and (4) MAGIC Global with 1,402 AILs in the S_5 generation. Currently, a Wild MAGIC population is being developed by a team at IRRI (K. Jena, H. Leung, K. McNally) in collaboration with J. Hibberd (University of Cambridge, U.K.), and I. Mackay (NIAB, Cambridge, U.K.) using multiple accessions of all eight A-genome species (McNally, personnel communication). In most cases, for this population, the initial crosses had *O. sativa* as the female parent, and the goal is to produce 16-way crosses with highly mixed genomes.

4. Useful agronomic traits mapped in *Oryza* species and transferred into cultivated rice

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	Reference
Vegetative Growth Stages								
Days to flowering	*O. australiensis*	IRGC100882	IR31917-45-3-2	IL		10	RFLP	Ishii et al. (1994)
Days to heading	*O. glaberrima*		IR64	BC_2F_3	SPA	2, 10	SSR, STS	Bimpong et al. (2011)
	O. glaberrima	IRGC103544	Milyang 23	BC_3F_2	SPA	1, 4, 7, 8	SSR	Suh et al. (2005)
	O. glumaepatula		Taichung 65	BC_4F_2		7	RFLP	Sanchez et al. (2003)
	O. grandiglumis	IRGC101154	Hwaseongbyeo	AB-QTL	SPA	6	SSR	Yoon et al. (2006)
	O. meyeriana	Y73	IR24	RIL	CIM	6, 7, 8, 11	SSR, STS	Chen et al. (2012)
	O. nivara	IRGC100898	Bengal	AB-QTL	MIM	3, 6	SSR	Eizenga et al. (2013)
	O. nivara	IRGC100898	Bengal	AB-QTL	MIM	3, 4, 6, 8	SSR	Eizenga et al. (2013)
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	3, 8	SSR	Eizenga et al. (accepted)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	1, 2, 3, 4, 10	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	2, 7	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	6, 12	RFLP	Xiao et al. (1998)
	O. rufipogon	IRGC105491	Hwaseongbyeo	AB-QTL, NIL	SPA, IM, ANOVA	6, 9	SSR	Jin et al. (2009), Xie et al. (2008)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	3	SSR	Wickneswari et al. (2012)
	O. rufipogon	W1944	Hwayeongbyeo	IL	SPA, IM	1	SPA, IM	Yuan et al. (2009)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	Reference
Days to maturity	*O. rufipogon*	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	4, 7, 8	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	6, 12	RFLP	Xiao et al. (1998)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	4, 6	SSR	Wickneswari et al. (2012)
Seedling height	*O. rufipogon*	W1944	Hwayeongbyeo	RIL	SPA, CIM	1	SSR	Lee et al. (2005)
Culm length	*O. glaberrima*	IRGC103544	Milyang 23	BC_3F_2	SPA	2, 10	SSR	Suh et al. (2005)
	O. grandiglumis	IRGC101154	Hwaseongbyeo	AB-QTL	SPA	1, 4	SSR	Yoon et al. (2006)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	6, 7, 12	SSR, STS	Rahman et al. (2007)
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	1, 6	SSR	Lee et al. (2005)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	1, 3, 9	SSR	Wickneswari et al. (2012)
	O. rufipogon	W1944	Hwayeongbyeo	IL	SPA, IM,	1, 12	SPA, IM	Yuan et al. (2009)
Plant height	*O. glaberrima*		IR64	BC_2F_3	SPA	1	SSR, STS	Bimpong et al. (2011)
	O. longistaminata		RD23	BC_7F_2	CIM	1	SSR	Chen et al. (2009)
	O. nivara	IRGC100898	Bengal	AB-QTL	MIM	1	SSR	Eizenga et al. (2013)
	O. nivara	IRGC104705	Bengal	AB-QTL	MIM	1, 12	SSR	Eizenga et al. (2013)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	1	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	1, 4, 10, 11	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	Hwaseongbyeo	AB-QTL, NIL	SPA, IM, ANOVA	7, 9	SSR	Jin et al. (2009), Xie et al. (2008)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	Reference
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	1, 3, 9	SSR	Wickneswari et al. (2012)
	O. rufipogon	IC22015	IR 58025A	AB-QTL	IM, CIM	1	SSR	Marri et al. (2005)
Plant type (Culm habit or tiller angle)	*O. nivara*	IRGC100898	Bengal	AB-QTL	MIM	9	SSR	Eizenga et al. (2013)
	O. nivara	IRGC104705	Bengal	AB-QTL	MIM	9	SSR	Eizenga et al. (2013)
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	9	SSR	Eizenga et al. (accepted)
Flag leaf length	*O. minuta*	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	8, 9	SSR, STS	Rahman et al. (2007)
Third node width	*O. rufipogon*	W1944	Hwayeongbyeo	RIL	SPA, CIM	1	SSR	Lee et al. (2005)
Tiller number	*O. glaberrima*		IR64	BC_2F_3	SPA	2, 7	SSR, STS	Bimpong et al. (2011)
	O. glumaepatula	RS-16	BG90-2	BC_2F_2	SPA, IM	4, 5, 7, 8, 11	SSR, STS	Brondani et al. (2002)
	O. glumaepatula	RS-16	Cica8	$BC_2F_{2\text{-}9}$	CIM	7, 11	SSR	Rangel et al. (2013)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	3	SSR, STS	Rahman et al. (2007)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	2, 5, 8	SSR	Wickneswari et al. (2012)
Panicle Development								
Panicle exsertion	*O. rufipogon*	W1944	Hwayeongbyeo	RIL	SPA, CIM	1	SSR	Lee et al. (2005)
Panicle density	*O. rufipogon*	IRGC 105491	Hwaseongbyeo	NIL	ANOVA	9	SSR	Xie et al. (2008)
Panicle number	*O. glaberrima*	IRGC103544	Milyang 23	BC_3F_2	SPA	4	SSR	Suh et al. (2005)
	O. glumaepatula	RS-16	BG90-2	BC_2F_2	SPA, IM	5, 8, 11	SSR, STS	Brondani et al. (2002)
	O. glumaepatula	RS-16	Cica8	$BC_2F_{2\text{-}9}$	CIM	7, 11	SSR	Rangel et al. (2013)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	Reference
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	4	SSR, STS	Rahman et al. (2007)
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	7	SSR	Eizenga et al. (accepted)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	3, 7	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	2	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	1, 2	RFLP	Xiao et al. (1998)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	2, 8	SSR	Wickneswari et al. (2012)
	O. rufipogon	IC22015	IR58025A	AB-QTL	IM, CIM	2	SSR	Marri et al. (2005)
	O. rufipogon	W1944	Hwayeongbyeo	RIL, IL	SPA, IM, CIM	1, 7, 12	SSR	Lee et al. (2004), Yuan et al. (2009)
	O. rufipogon	YJCW	93-11	AB-QTL	SPA, IM, CIM	1, 2, 7, 8, 11	SSR	Fu et al. (2010)
Panicle length	*O. glaberrima*	IRGC103544	Milyang 23	BC_3F_2	SPA	2, 5, 6, 10, 12	SSR	Suh et al. (2005)
	O. meyeriana	Y73	IR24	RIL	CIM	1, 2	SSR, STS	Chen et al. (2012)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	6, 7, 8	SSR, STS	Rahman et al. (2007)
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL	SPA, IM, ANOVA	9	SSR	Xie et al. (2008)
	O. rufipogon	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	1, 9, 10	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	1, 2, 4, 9, 12	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC2	ANOVA	1, 2, 4, 8, 9, 12	RFLP	Xiao et al. (1998)
	O. rufipogon	IC22015	IR 58025A	AB-QTL	IM, CIM	2, 5, 9	SSR	Marri et al. (2005)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping popu-lation†	QTL mapping analysis‡	Chromo-some location§	Type of mark-er¶	Reference
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	1	SSR	Lee et al. (2005)
	O. rufipogon	W1944	Hwayeongbyeo	IL	SPA, IM,	1, 2	SPA, IM	Yuan et al. (2009)
Primary branches per panicle	*O. minuta*	IRGC101144	Hwaseongbyeo	NIL		7	SSR	Balkunde et al. (2013)
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	1	SSR	Lee et al. (2005)
Secondary branches per panicle	*O. rufipogon*	IRGC105491	Hwaseongbyeo	AB-QTL	SPA, IM	6, 8	SSR	Jin et al. (2009)
	O. rufipogon	W1944	Hwayeongbyeo	RIL, IL	SPA, IM, CIM	1, 2, 9	SSR	Lee et al. (2005), Yuan et al. (2009)
Reproductive Growth Stages								
Pollen (male) sterility	*O. glumaepatula*	IRGC105688	Taichung 65	BC_4F_2		2, 7	RFLP	Sobrizal et al. (2000a, 2000b)
	O. longistaminata		RD23	BC_7F_2	CIM	6	SSR	Win et al. (2009; 2011)
	O. nivara	IRGC105444	Taichung 65	IL-BC_4F_1		4, 8, 12	RFLP, SSR, SNP	Chen et al. (2009)
Hybrid breakdown locus	*O. nivara*	IRGC105444	Koshihikari	BC_4F_3		2	SSR, SNP	Miura et al. (2008)
Panicle fertility	*O. glaberrima*		IR64	BC_2F_3	SPA	2, 10	SSR, STS	Bimpong et al. (2011)
Productive panicle number	*O. rufipogon*	G52-9	Yuexiangzhan	AB-QTL	CIM	2, 3, 7	SSR	Jing et al. (2010)
Spikelets per plant	*O. minuta*	IRGC101144	Hwaseongbyeo	NIL		7	SSR	Balkunde et al. (2013)
	O. rufipogon	G52-9	Yuexiangzhan	AB-QTL	CIM	2	SSR	Jing et al. (2010)
	O. rufipogon	IC 22015	IR 58025A	AB-QTL	IM, CIM	2, 5	SSR	Marri et al. (2005)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	Reference
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	1	RFLP	Xiao et al. (1998)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	1	SSR	Wickneswari et al. (2012)
Spikelets per panicle	*O. glaberrima*	IRGC103544	Milyang 23	BC_3F_2	SPA	3	SSR	Suh et al. (2005)
	O. grandiglumis	IRGC101144	Hwaseongbyeo	AB-QTL	SPA	2, 3, 4, 11	SSR	Yoon et al. (2006)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	6	SSR, STS	Rahman et al. (2007)
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL, AB-QTL	SPA, IM, ANOVA	8, 9	SSR	Xie et al. (2008), Jin et al. (2009)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	2, 3, 9	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	1, 9	RFLP	Xiao et al. (1998)
	O. rufipogon	W1944	Hwayeongbyeo	IL, RIL	SPA, IM, CIM	1	SSR	Yuan et al. (2009), Lee et al. (2005)
	O. rufipogon	YJCW	93-11	AB-QTL	SPA, IM, CIM	3	SSR	Fu et al. (2010)
	O. glaberrima		Milyang 23	BC_2F_5		2	SSR	Kang et al. (2008)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	3	SSR	Wickneswari et al. (2012)
	O. minuta	IRGC101144	Hwaseongbyeo	NIL		7	SSR	Balkunde et al. (2013)
Spikelet fertility	*O. glaberrima*	IRGC103544	Milyang 23	BC_3F_2	SPA	2, 4, 8	SSR	Suh et al. (2005)
	O. longistaminata		RD23	BC_7F_2	CIM	6	SSR	Chen et al. (2009)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	6	SSR, STS	Rahman et al. (2007)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping popu-lation†	QTL mapping analysis‡	Chromo-some location§	Type of mark-er¶	Reference
Shattering	*O. rufipogon*	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	8	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	1, 3, 6	SSR	Lee et al. (2005)
	O. rufipogon	W1944	Hwayeongbyeo	IL, RIL	SPA, IM, CIM	1, 4, 5	SSR	Yuan et al. (2009), Lee et al. (2005)
Grains per panicle	*O. minuta*	IRGC101144	Hwaseongbyeo	NIL		7	SSR	Balkunde et al. (2013)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	2, 3, 8, 9	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	1, 8, 12	RFLP	Xiao et al. (1998)
	O. rufipogon	IRGC105491	Hwaseongbyeo	AB-QTL, NIL	SPA, IM, ANOVA	8, 9	SSR	Jin et al. (2009), Xie et al. (2008)
	O. rufipogon	IC22015	IR 58025A	AB-QTL	IM, CIM	2, 5	SSR	Marri et al. (2005)
	O. rufipogon	G52-9	Yuexiangzhan	AB-QTL	CIM	4, 10, 11	SSR	Jing et al. (2010)
	O. rufipogon	YJCW	93-11	AB-QTL	SPA, IM, CIM	1, 3	SSR	Fu et al. (2010)
Percent seed set	*O. meyeriana*	Y73	IR24	RIL	CIM	8	SSR, STS	Chen et al. (2012)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	3	SSR	Wickneswari et al. (2012)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	2, 4	RFLP	Xiao et al. (1998)
	O. rufipogon	W1944	Hwayeongbyeo	IL, RIL	SPA, IM, CIM	10	SSR	Lee et al. (2005)
Awn length	*O. minuta*	IRGC101144	Hwayeongbyeo	AB-QTL	SPA, CIM	6, 9	SSR	Linh et al. (2004)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	5, 9	SSR, STS	Rahman et al. (2007)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	Reference
	O. rufipogon	IRGC105491	Hwaseongbyeo	AB-QTL	SPA, IM	8	SSR	Jin et al. (2009)
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	8, 11	SSR	Lee et al. (2005)
	O. rufipogon	W1944	Hwayeongbyeo	IL	SPA, IM,	1, 8, 11, 12	SPA, IM	Yuan et al. (2009)
Grain (kernel) Traits								
Grain (kernel) length	*O. grandiglumis*	IRGC101154	Hwaseongbyeo	AB-QTL	SPA	11	SSR	Yoon et al. (2006)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	3, 5, 6, 7, 9	SSR, STS	Rahman et al. (2007)
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	1	SSR	Eizenga et al. (accepted)
	O. nivara	IRGC100898, IRGC104705	Bengal	AB-QTL	MIM	1, 9	SSR	Eizenga et al. (2013)
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL	SPA, IM, ANOVA	8	SSR	Xie et al. (2006)
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	1, 2, 3, 5, 6	SSR	Lee et al. (2005)
Grain (kernel) width	*O. glaberrima*	IRGC103544	V20A	AB-QTL	SPA, IM, CIM	10, 11	RFLP, SSR	Li et al. (2004)
	O. nivara	IRGC81848	Swarna	BC_2F_2	IM, CIM	3, 6	SSR	Swamy et al. (2012)
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL	SPA, IM, ANOVA	8	SSR	Xie et al. (2006)
Grain (kernel) length to width ratio	*O. glaberrima*	IRGC103544	Caiapó	BC_3F_1	IM, CIM	1	SSR	Aluko et al. (2004)
	O. glaberrima	IRGC103544	V20A	AB-QTL	SPA, IM, CIM	12	RFLP, SSR	Li et al. (2004)
	O. grandiglumis	IRGC101154	Hwaseongbyeo	AB-QTL	SPA	2, 11	SSR	Yoon et al. (2006)
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	1, 2, 5	SSR	Lee et al. (2005)
	O. minuta	IR71033-121-15	Junambyeo	$F_{2:3}$	SPA, IM	2, 3, 5	SSR, STS	Rahman et al. (2007)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping popu-lation†	QTL mapping analysis‡	Chromo-some location§	Type of mark-er¶	Reference
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	1, 5	SSR	Eizenga et al. (accepted)
	O. nivara	IRGC81848	Swarna	BC_2F_2	IM, CIM	12	SSR	Swamy et al. (2012)
Grain thickness	*O. grandiglumis*	IRGC101154	Hwaseongbyeo	AB-QTL	SPA	6, 11	SSR	Yoon et al. (2006)
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL	SPA, IM, ANOVA	8	SSR	Xie et al. (2006)
	O. rufipogon	W1944	Hwayeongbyeo	RIL	SPA, CIM	1, 12	SSR	Lee et al. (2005)
Pericarp color	*O. rufipogon*	IRGC105491	Ce64, Caiapó, Hwacheong, Jefferson, IR64	AB-QTL	IM, CIM	7	SSR	McCouch et al. (2007)
	O. rufipogon	W1944	Hwayeongbyeo	IL	SPA, IM,	1, 7	SPA, IM	Yuan et al. (2009)
Yield Traits								
Grain weight	*O. glaberrima*	IRGC103544	Milyang 23	BC_3F_2	SPA	2, 3	SSR	Suh et al. (2005)
	O. grandiglumis	IRGC101154	Hwaseongbyeo	AB-QTL	SPA	3, 6, 8, 11	SSR	Yoon et al. (2006)
	O. meyeriana	Y73	IR24	RIL	CIM	3, 9, 11	SSR, STS	Chen et al. (2012)
	O. minuta	IR71033-121 -15	Junambyeo	$F_{2:3}$	SPA, IM	3, 7, 11	SSR, STS	Rahman et al. (2007)
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	10	SSR	Eizenga et al. (accepted)
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL	SPA, IM, ANOVA	8	SSR	Xie et al. (2006)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	1, 5	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	1, 3	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	4, 8, 9, 11, 12	RFLP	Xiao et al. (1998)
	O. rufipogon	IRGC105491	MR219	AB-QTL	CIM	6	SSR	Wickneswari et al. (2012)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping popu-lation†	QTL mapping analysis‡	Chromo-some location§	Type of mark-er¶	Reference
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL	ANOVA	9	SSR	Xie et al. (2008)
	O. rufipogon	IRGC105491	Hwaseongbyeo	AB-QTL	SPA, IM	8	SSR	Jin et al. (2009)
	O. rufipogon	IRGC105491	Ce64&V20A, Caiapó, Hwacheong, Jefferson, IR64	AB-QTL	IM, CIM	3	SSR	McCouch et al. (2007)
	O. rufipogon	IC22015	IR 58025A	AB-QTL	IM, CIM	2, 9	SSR	Marri et al. (2005)
	O. rufipogon	W1944	Hwayeongbyeo	IL	SPA, IM	1	SPA, IM	Yuan et al. (2009)
	O. rufipogon	YJCW	93-11	AB-QTL	SPA, IM, CIM	1	SSR	Fu et al. (2010)
Brown rice yield	*O. glaberrima*	IRGC103544	V20A	AB-QTL	SPA, IM, CIM	12	RFLP, SSR	Li et al. (2004)
Grain yield per plant	*O. glaberrima*		IR64	BC_2F_3	SPA	2, 6, 8, 9	SSR, STS	Bimpong et al. (2011)
	O. glaberrima	IRGC103544	V20A	AB-QTL	SPA, IM, CIM	12	RFLP, SSR	Li et al. (2004)
	O. rufipogon		MR219	AB-QTL		1	SSR	Bhuiyan et al. (2011)
	O. rufipogon	G52-9	Yuexiangzhan	AB-QTL	CIM	1, 2, 3		Jing et al. (2010)
	O. rufipogon	IC22015	IR 58025A	AB-QTL	IM, CIM	2, 9	SSR	Marri et al. (2005)
	O. rufipogon	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	1	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	Hwaseongbyeo	NIL	ANOVA	9	SSR	Xie et al. (2008)
	O. rufipogon	IRGC 105491	V20A, V20B	BC_2	ANOVA	1, 2, 8	RFLP	Xiao et al. (1998)
Yield	*O. glaberrima*	IRGC103544	Milyang 23	BC_3F_2	SPA	2, 3, 4, 6, 8	SSR	Suh et al. (2005)
	O. glaberrima	IRGC103544	Milyang 23	BC_2F_5		2	SSR	Kang et al. (2008)

Trait	Donor species	Donor accession	Recurrent parent(s)	Type of mapping popu-lation†	QTL mapping analysis‡	Chromo-some location§	Type of mark-er¶	Reference
	O. grandiglumis	IRGC101154	Hwaseongbyeo	AB-QTL	SPA	2	SSR	Yoon et al. (2006)
	O. minuta	IRGC101144	Hwaseongbyeo	NIL		7	SSR	Balkunde et al. (2013)
	O. meyeriana	Y73	IR24	RIL	CIM	6	SSR, STS	Chen et al. (2012)
	O. rufipogon		MR219	AB-QTL		4	SSR	Bhuiyan et al. (2011)
	O. rufipogon	IC22015	IR58025A	AB-QTL	IM, CIM	1, 2, 8	SSR	Marri et al. (2005)
	O. rufipogon	IRGC105491	Jefferson	AB-QTL	SPA, IM, CIM	2, 3, 6, 9	RFLP, SSR	Thomson et al. (2003)
	O. rufipogon	IRGC105491	IR64	AB-QTL	SPA, IM, CIM	1	RFLP, SSR	Septiningsih et al. (2003)
	O. rufipogon	IRGC105491	V20A, V20B	BC_2	ANOVA	1, 2, 8, 12	RFLP	Xiao et al. (1998)
	O. rufipogon	IRGC105491	Hwaseongbyeo	AB-QTL	SPA, IM	8	SSR	Jin et al. (2009)
	O. rufipogon	YJCW	93-11	AB-QTL	SPA, IM, CIM	1	SSR	Fu et al. (2010)
Harvest index	*O. glaberrima*		IR64	BC_2F_3	SPA	2, 7	SSR, STS	Bimpong et al. (2011)
	O. rufipogon	IC22015	IR58025A	AB-QTL	IM, CIM	2	SSR	Marri et al. (2005)

† Abbreviations for mapping population types are: AB-QTL, advanced backcross-quantitative trait locus; IL, inbred line; NIL, near isogenic line; RIL, recombinant inbred line.

‡ Abbreviations for QTL analysis method are: ANOVA, analysis of variance; CIM, composite interval mapping; IM, interval mapping; MIM, multiple interval mapping; SPA, single point analysis.

§ Only the chromosomes where the QTL increase is attributed to the wild parent are listed.

Abbreviations for types of markers are: RAPD, random amplified polymorphic DNA; RFLP, restriction fragment length polymorphism; SNP, single nucleotide polymorphism; SSR, simple sequence repeat; STS, sequence-tagged site.

Table 2. Summary of QTLs for improved yield and yield components attributed to the non-*O. sativa* parent.

4.1. Yield enhancing QTL from exotic *Oryza* genomes

Several plant traits directly or indirectly affect rice grain yield including days to heading and maturity; plant height; panicle length; number of panicles per plant, spikelets per panicle and

http://dx.doi.org/10.5772/58393

grains per panicle; seed set; grain weight; grain size and shape; and shattering (Table 2). The most important yield components in rice are the number of panicles per plant, number of grains per panicle, and grain weight (Chen et al. 2012; Lee et al. 2004; Septiningsih et al. 2003; Thomson et al. 2003). Yield improvement can be achieved as a result of the vast allelic diversity for these traits found in interspecific populations, especially number of grains per panicle which has proven to have the greatest relevance for rice breeding programs (Li et al. 1998; Liu et al. 2008; Tian et al. 2006).

Modern rice varieties are developed after an extensive selection process to improve a few targeted traits related to cultivation and end-use quality but primarily those associated with yield components, such as resistance to shattering, compact growth habit and improved seed germination (Tanksley and McCouch 1997). This prolonged breeding procedure can lead to a reduction in the genetic variability found in modern cultivated rice (Rangel et al. 2008), thus identifying genetic sources for agronomically important traits from wild *Oryza* species and introgressing them into cultivated rice is desirable and necessary. Although wild *Oryza* species are inferior in grain yield, especially when compared to cultivated rice, transgressive segregation resulting from a cross between cultivated rice and a wild *Oryza* species, especially the ancestral species, *O. rufipogon* and *O. nivara*, revealed the presence of favorable alleles from the wild parent that can increase yield in the genetic background of cultivated rice (Brar and Singh 2011). Xiao et al. (1996) developed a genetic population by initially crossing the cytoplasmic male sterile parent, V20A, with *O. rufipogon* (IRGC105491), the donor, as male parent. Subsequently, F_1 plants and later BC_1 plants selected for vigor, plant type, maturity and fertility, were backcrossed to V20B (maintainer line of V20A). A selected subset of 300 BC_2F_1 lines was crossed with Ce64 to create the genotype of the Chinese hybrid rice variety V/64, developed from V20A x Ce64. Xiao et al. (1996) reported that 15% of the testcross families outperformed the recurrent parent, 14% of the yield improvement was related to grains per plant and 56% was related to 1000-grain weight. Subsequently, Xiao et al. (1998) identified 35 QTLs associated with yield improvement, 19 of which, including *yld1.1* and *yld 2.1*, were located on chromosomes 1 and 2, respectively. They also observed no undesirable alleles causing negative effects on yield components, thus the presence of alleles in wild *O. rufipogon* can improve rice yields.

Other AB-QTL populations developed using the same *O. rufipogon* (IRGC105491) donor parent with recurrent parents representing various *O. sativa* subpopulations including *indica* with IR64 (Septiningsih et al. (2003), upland *tropical japonica* with Caiapó (Moncada et al. 2001), irrigated *tropical japonica* with Jefferson (Thomas et al. 2003), and *temperate japonica* with Hwaseongbyeo (Xie et al. 2006 & 2008), revealed enhanced yield and yield components attributed to the *O. rufipogon* donor parent. Selected progeny lines were advanced to BILs or NILs and this yield enhancement was confirmed in field studies with the recurrent parents IR64 (Cheema et al. 2008a), Jefferson (Imai et al. 2013), and Hwaseongbyeo (Jin et al. 2011). Also, an epistatic interaction was noted between the QTLs for grain weight on chromosomes 8 and 9 in the Hwaseongbyeo background (Jin et al. 2011).

Tian et al. (2006) selected an introgression line, SIL040, from the BC_4F_4 lines of *O. rufipogon* (Dongxiang) x Guichao 2, an *indica* rice cultivar. High resolution QTL mapping and analysis

in the SIL040 x Guichao 2 F_2 progeny for yield components revealed *gpa7* (grains per panicle) on the short arm of chromosome 7. This QTL contained five putative genes associated with five panicle traits: panicle length, number of primary and secondary branches per panicle, and number of grains on primary and secondary branches, in the same region. These findings supported the importance of *gpa7* in rice domestication and yield enhancement.

Two AB-QTL populations were developed using the *O. rufipogon* identified as YJCWR (collected from Yuanjiang County, Yunnan Province, P.R. China) as a donor, and TeQing, a popular *indica* cultivar (Tan et al. 2008) and 93-11, a two-line elite *indica* restorer (Fu et al. 2010), as the recurrent parents. Both studies revealed QTL attributed to *O. rufipogon* having a beneficial effect on yield related traits. A CSSL library of 120 lines selected from the TeQing AB-QTL population and evaluated at two locations confirmed a yield advantage associated with *O. rufipogon* alleles for all traits evaluated except 1000-grain weight (Tan et al. 2007).

Similarly, a CSSL library composed of 133 lines selected from an AB-QTL population with an *O. rufipogon* collected in Hainan Province, P.R. China, as the donor, and TeQing as the recurrent parent was used to identify *spd6*, a gene on chromosome 6 responsible for the small panicle and dwarf traits (Shan et al. 2009). This gene, *spd6*, had pleiotropic effects on panicle number per plant, grain size, grain weight, grain number per panicle and plant height, suggesting it may have played a role in the domestication of rice.

To identify the genetic potential of *O. glumaepatula* ($A^{gp}A^{gp}$ genome) as a genetic resource for cultivar improvement, Brondani et al. (2002) developed an AB-QTL population using RS-16, an accession of the Amazonian native rice wild species, *O. glumaepatula*, as the donor parent, and BG90-2, a Latin American *indica* rice, as the recurrent parent. QTL analysis of 96 BC_2F_2 progenies for eleven agronomic traits with *O. glumaepatula* alleles revealed none were positively associated with yield traits. However, several BC_2F_2 lines indicated the presence of introgressed alleles related to yield improvement which were not detected in the QTL analysis. Later, Rangel et al. (2008) evaluated the agronomic performance of 35 BC_2F_8 ILs selected from this population over two years and in multiple locations by measuring grain yield and grain quality traits. The six highest yielding ILs had the highest percentage of recurrent parent genomic background. One of the six ILs, CNAi 9930, was recommended for cultivar release due to its good cooking and milling qualities, and high yield stability. Also, all six ILs contained novel alleles, thus were incorporated as parents in the breeding program for developing high yielding cultivars.

BILs in the $BC_5F_{5:6}$ were derived from *O. grandiglumis* (IRGC101154; CCDD) as the donor parent, and Hwaseongbyeo (Yoon et al. 2006). One BIL, HG101, was backcrossed, and evaluation of the targeted IL, CR1242, revealed the beneficial effect of the *O. grandiglumis* allele on yield and yield components. Further analysis of the QTL, *tgw11*, on chromosome 11 associated with 1000-grain weight showed that a single gene in this QTL controls three grain traits: grain weight, grain width and grain thickness (Oh et al. 2011).

To evaluate the effect of *O. minuta* (IRGC101141) with a BBCC genome on yield components, a single plant, WH79006, was selected from the Hwaseongbyeo x *O. minuta* BC_5F_3 families and selfed (Jin et al. 2004). QTL analysis of Hwaseongbyeo x WH79006 $F_{2:3}$ progeny identified four

QTLs, *sw7* (seed width), *sl11* (seed length), *tsw7* (1000-seed weight) and *lw10* (seed length to width ratio). Similarly, WH29001 was selected from the BC_5F_3 families, selfed and by QTL analysis the co-located QTLs for days to heading, *dth6* and *dth8*, and awn length, *awn6* and *awn8*, were identified on chromosomes 6 and 8, respectively (Linh et al. 2006). Subsequently, a new QTL, *spp7*, for spikelets per panicle, was detected on the long arm of chromosome 7 with the allele attributed to the *O. minuta* parent and validated in the F_3 and F_4 progeny (Linh et al. 2008). Similarly the introgression line IR71033-121-15 was selected from the BC_3 progeny of the same *O. minuta* (IRGC101141) x *indica* cultivar, IR31917. To introgress the *O. minuta* genome into *japonica*, IR71033-121-15 was crossed with Junambyeo, a Korean *japonica* cultivar, and QTL analysis of F_2 progeny identified 14 QTLs associated with agronomic traits reported in previous studies and 22 novel QTLs related to yield components (Rahman et al. 2007).

Awns are an important trait in wild rice species because it protects the seeds from birds and other animals. By contrast, the majority of modern rice cultivars have short awns so that it is easier to harvest the seed. This trait is reported to be controlled by several genes located in different chromosomes, including *An-1* on chromosome 3, *An-2* and *an-5(t)* on chromosome 4, and *An-3* on chromosome 5 (Hu et al. 2011; Nagao and Takahashi 1963; Takamure and Kinoshita 1991). *O. meridionalis* has long awns, ranging in length from 7.8-10.3 cm (Vaughan 1994) and two genes, *An7* and *An8*, associated with the trait, were identified on chromosomes 5 and 4, respectively (Kurakazu et al. 2001). Analysis of *O. meridionalis* x *O. sativa* $BC_4F_{2:6}$ and $BC_4F_{2:8}$ revealed the presence of two dominant genes at different locations on chromosome 1, *An9* and *An10*, and a new allele, *An6-mer* on chromosome 6 (Matsushita et al. 2003a). Another study of an *O. sativa* x *O. glumaepatula* population also identified new alleles, *An7* and *An8* (Matsushita et al. 2003b), thus confirming awn length is controlled by several genes.

A doubled haploid (DH) population was developed from Caiapó (*tropical japonica*, recurrent parent) x *O. glaberrima* (donor parent, IRGC103544, MG12) BC_3F_1 progeny (Aluko et al. 2004). This population was evaluated for agronomic traits including yield and yield components in Colombia and Louisiana, USA (Gutiérrez et al. 2010). Strong segregation distortion was found on chromosomes 3 and 6 indicating the presence of interspecific sterility genes. Evaluation of the phenotypic data revealed transgressive segregation for several traits. A set of 34 CSSLs was selected from Koshihikari, an elite *temperate japonica* rice cultivar (recurrent parent) x *O. glaberrima* (donor parent, IRGC104038) BC_5F_1 progeny, advanced to the F_7 generation, and genotyped with 142 SNP markers (Shim et al. 2010). QTL analysis of phenotypic data from field grown plants revealed 105 putative QTL of which 84 were positive with 64 being related to grain yield components, suggesting the possible use of favorable alleles in *O. glaberrima* for improvement of cultivated rice.

These studies give several examples of QTL or genes for yield and yield components being attributed to the wild donor parent not only the ancestral A-genome species, *O. rufipogon* or *O. nivara*, but also in the more distant tetraploid *O. minuta* with a BBCC genome. These observations confirm that not only single genes and alleles are affecting these traits but there are epistatic interactions and epigenetic interactions, as well as environmental factors affecting many of these traits, resulting in the phenomenon often described as transgressive variation. Currently, six CSSL libraries are under development with three different *O. rufipogon*/*O.*

nivara donor accessions, representing the *Indica*, *Japonica* and independent groups of *O. rufipogon* (Huang et al. 2012), and two recurrent parents, IR64, an *indica* representing the *Indica* subspecies, and Cybonnet, a U.S. *tropical japonica*, representing the *Japonica* subspecies to further explore these interactions resulting in transgressive variation (Tung et al. 2010; SR McCouch, Cornell University and GC Eizenga, personal communication).

4.2. Genes for sterility

Reproductive barriers, such as crossability, hybrid seed inviability, hybrid sterility and hybrid breakdown, have significantly limited the success of interspecific hybridization between *O. sativa* and non-A genome *Oryza* species. Several studies reported the production of F_1 seeds by crossing male sterile lines and *Oryza* species (Huang et al. 2001; Luo et al. 2000). The crossability rate between *O. sativa* and other *Oryza* species vary; however, the rate of crossability between A-genome and non-A genome diploid *Oryza* species is higher than with tetraploid *Oryza* species, none of which has an A-genome (Jena and Khush 1989 & 1990; Yasui and Iwata 1991).

The phenomenon of transmission ratio distortion (TRD) where one allele is transmitted more frequently than the opposite allele in interspecific and intraspecific hybrids has been discovered in a broad range of organisms and is often a reproductive barrier (Koide et al. 2012). Recently, Koide et al. (2012) identified a unique sex-independent TRD (*si*TRD) where one allele is preferentially transmitted through both the male and female parent derived from *O. rufipogon* (W593). This research showed the S_6 allele on chromosome 6 is responsible for the *si*TRD allele and influenced by other unlinked modifiers. The locus, *sa1*, conferring pollen sterility was found in *O. glaberrima* (W025) x T65*wx* progeny (Sano 1990) where T65*wx* is an NIL derived from Taichung 65 (*japonica* rice) x Peiku (*indica* rice) with a Taichung 65 background and the Peiku *waxy* gene on chromosome 6. Other studies identified several pollen sterility loci, *S-1, S3, S18, S19, S20, S21, s25, s27, S29, S29(t)* and *s36*, in populations resulting from interspecific hybridizations between various *O. sativa* cultivars and the *Oryza* species, *O. glumaepatula*, *O. glaberrima* and *O. nivara* (Doi et al. 1998 & 1999; Hu et al. 2006, Sano 1983 & 1986; Taguchi et al. 1999; Win et al. 2009). To overcome such barriers, several methods have been suggested including anther culture, backcrossing, marker-assisted selection (MAS) and asymmetric somatic hybridization, (Fu et al. 2008; Sarla et al. 2005). Also, Deng et al. (2010) demonstrated the fertility in *O. glaberrima* x *O. sativa* crosses could be improved by using an *O. sativa* bridging parent. The bridging parent had the *O. glaberrima* sterility gene, *S1-g* on chromosome 6, introgressed into the particular *O. sativa* cultivar background.

4.3. Grain quality traits

Acceptable rice grain quality is a major goal of rice breeding programs worldwide because it determines the acceptability of cooked rice to the consumer. Grain quality is a combination of several components including milling efficiency, physical appearance, cooking and eating characteristics, and nutritional quality (Aluko et al. 2004; Li et al. 2004). A few interspecific populations were evaluated for grain quality traits (Table 3). These studies showed the *Oryza* parent affects the apparent amylose content, alkali spreading value, protein content, rice bran

percentage, milled rice percentage and seed size. What is desirable for these traits is determined for the most part, by consumer preference and marketing classes. When selecting for these traits, often the grain quality of the recurrent parent is preferred.

Most interesting was the BC_3F_1 progeny of the Caiapó x *O. glaberrima* (IRGC103544, MG12) doubled haploid population (Aluko et al. 2004). For this population, the QTL analysis revealed 27 QTLs associated with rice quality of which seven QTLs including percent rice bran, percent milled rice, alkali spreading value (inversely related to gelatinization temperature), percent protein and grain dimensions (length to width ratio), were traced to alleles originating from the *O. glaberrima* parent.

Trait	Donor species	Donor accession	Recurrent parent(s)	Mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	References
Grain Quality								
Apparent amylose content	*O. glaberrima*	IRGC103544	V20A	AB-QTL	SPA, IM, CIM	6, 12	RFLP, SSR	Li et al. (2004)
	O. grandiglumis	IRGC101154	Hwaseong-byeo	AB-QTL	SPA	3, 5, 7	SSR	Yoon et al. (2006)
	O. nivara	IRGC81848	Swarna	BC_2F_2	IM, CIM	2	SSR	Swamy et al. (2012)
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	6	SSR	Eizenga et al (accepted)
	O. rufipogon	IRGC105491	IR64	AB-QTL	IM, CIM	6	RFLP, SSR	Septiningsih et al. (2003b)
Alkali spreading value (ASV) or gel consistency	*O. glaberrima*	IRGC103544	Caiapó	BC_3F_1	IM, CIM	6	SSR	Aluko et al. (2004)
	O. glaberrima	IRGC103544	V20A	AB-QTL	SPA, IM, CIM	12	RFLP, SSR	Li et al. (2004)
	O. nivara	IRGC100195	M-202	AB-QTL	MIM	6	SSR	Eizenga et al. (accepted)
	O. rufipogon	IRGC105491	IR64	AB-QTL	IM, CIM	6	RFLP, SSR	Septiningsih et al. (2003b)
Kernel elongation	*O. glaberrima*	IRGC 103544	V20A	AB-QTL	SPA, IM, CIM	3	RFLP, SSR	Li et al. (2004)
Protein	*O. glaberrima*	IRGC103544	Caiapó	BC_3F_1	IM, CIM	2, 6	SSR	Aluko et al. (2004)
	O. glaberrima	IRGC103544	V20A	AB-QTL	SPA, IM, CIM	8	RFLP, SSR	Li et al. (2004)

Trait	Donor species	Donor accession	Recurrent parent(s)	Mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	References
Percent rice bran	*O. glaberrima*	IRGC103544	Caiapó	BC_3F_1	IM, CIM	4, 7	SSR	Aluko et al. (2004)
Percent milled rice	*O. glaberrima*	IRGC103544	Caiapó	BC_3F_1	IM, CIM	5	SSR	Aluko et al. (2004)
	O. nivara	IRGC81848	Swarna	BC_2F_2	IM, CIM	1	SSR	Swamy et al. (2012)
Biotic Stress-Diseases								
Bacterial blight	*O. australiensis*		IR31917-45-3-2	MAAL		12		Multani et al. (1994)
	O. brachyantha O. longistaminata O. officinalis			AIL		5, 6, 8, 11	SSR	Hechanova et al. (2008)
	O. latifolia	IRGC100914	IR31917-45-3-2	AIL	ANOVA	12, others	SSR, SNP, STS, InDel	Angeles-Shim et al. (accepted)
	O. longistaminata	WLO2	BS125	NIL		11	RFLP, RAPD	Ronald et al. (1992)
	O. longistaminata		IR24			11		Khush et al. (1990)
	O. meyeriana	Y73	IR24	RIL	CIM	1, 3, 5, 10, 11	SSR, STS	Chen et al. (2012)
	O. minuta	78-1-5	IR24	F_2- BC_1		6	RAPD, AFLP	Gu et al. (2004)
	O. nivara	IRGC81825	PR114	RIL, BIL, IL	SMA-IM	4	SSR, STS	Cheema et al. (2008)
Blast disease	*O. australiensis*	IRGC100882	Lijiangxintuan-heigu			6	CAPS, SSR, STS	Jeung et al. (2007)
	O. minuta	IRGC101141	IR31917	F_2		6	RAPD	Liu et al. (2002)
	O. nivara	IRGC100898	Bengal	AB-QTL	MIM	8	SSR	Eizenga et al. (2013)
	O. nivara	IRGC104705	Bengal	AB-QTL	MIM	8, 12	SSR	Eizenga et al. (2013)

Trait	Donor species	Donor accession	Recurrent parent(s)	Mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	References
	O. rufipogon	IRGC104812	Koshihikari	IL		3, 11		Hirabayashi et al. (2010); Sobrizal et al. (1999)
	O. rufipogon	IRGC104814	Koshihikari	IL		3, 5, 6		Hirabayashi et al. (2010)
Sheath blight disease	*O. nivara*	IRGC100898	Bengal	AB-QTL	MIM	6	SSR	Eizenga et al. (2013)
	O. nivara	IRGC104705	Bengal	AB-QTL	MIM	3, 6	SSR	Eizenga et al. (2013)
Stem rot	*O. rufipogon*	IRGC100912 (87-Y-550)	L-201 (long grain-breeding lines)	F_2	SPA	2, 3	AFLP	Ni et al. (2001)
Grassy stunt virus	*O. nivara*	IRGC101508	IR8, IR20, IR22, IR24, IR773A-1-3	F_2				Nuque et al. (1982)
Rice stripe necrosis resistance	*O. glaberrima*	IRGC103544	Caiapó	CSSL	IM, CIM	11	SSR	Gutiérrez et al. (2010)
Biotic Stress-Insects								
Brown planthopper	*O. australiensis*	IRGC100882	IR31917-45-3-2	IL		12	RFLP	Ishii et al. (1994)
	O. australiensis	IR65482-7-216-1-2	Jinbubyeo	F_2, BC_2F_2	ANOVA	12	SSR, STS	Jena et al. (2006)
	O. australiensis		IR31917-45-3-2	MAAL		12		Multani et al. (1994)
	O. eichingeri	IRGC105159	2428	F_2, BC_1F_1		2	RFLP, SSR	Guoqing et al. (2001)
	O. latifolia	B14	Taichung	RIL		4	SSR, RFLP	Yang et al. (2002)
	O. minuta	101141	Junambyeo	F_3		4, 12	SSR, STS	Rahman et al. (2009)
	O. officinalis	IRGC100878, IRGC100896, IRGC101150,	IR31917-45-3, IR25587-109-3	BC_2F_8		4, 10, 12	RFLP	Jena et al. (1992)

Trait	Donor species	Donor accession	Recurrent parent(s)	Mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	References
		IRGC101412, IRGC102385						
	O. officinalis	IR54745-2-21-12-17-6	IR50			3	RAPD, STS	Renganayaki et al. (2002)
	O. officinalis	B5	1826, 93-11			3, 4	SSR	Li et al. (2006)
	O. officinalis	IRGC100896	IR31917-45-3-2	F_2		11	RAPD	Jena et al. (2002)
	O. officinalis					3	RFLP	Hirabayshi et al. (1998)
	O. officinalis	IR54745-2-21-12-17-6	IR50	RIL		3	RAPD	Renganayaki et al. (2002)
	O. officinalis	B5	Minghui 63	F_2		3	RFLP	Huang et al. (2001)
	O. officinalis	B5		RIL		4	AFLP, RFLP, SSR	Yang et al. (2004)
	O. rufipogon	WBO1	Minghui 63	F_2		4, 8	SSR	Hou et al. (2011)
Green rice leafhopper	*O. glaberrima*	IRGC104038	Taichung 65	NIL	IM, CIM	3, 7, 9, 10	SSR	Fujita et al. (2010)
	O. rufipogon	W1962	Taichung 65	NIL, BC_4F_2		8	SSR	Fujita et al. (2006)
White-backed planthopper	*O. officinalis*	B5	Minghui 63	RIL		3, 4	SSR	Tan et al. (2006b)
	O. rufipogon	BILs-DWR/Dingxiang	XieqingzaoB	BIL	CIM, MIM	2, 5, 9	SSR	Chen et al. (2010)
Abiotic stress								
Aluminum tolerance	*O. rufipogon*	IRGC106424	IR64	RIL	IM	1, 3, 9 (2, 7, 8)	RFLP	Nguyen et al. (2003)
Drought tolerance	*O. rufipogon*		Guichao 2	IL	SMR	2, 12	SSR	Zhang et al. (2006)
	O. rufipogon	W630	Nipponbare	BIL	IM	1, 5	SSR	Thanh et al. (2011)

Trait	Donor species	Donor accession	Recurrent parent(s)	Mapping population†	QTL mapping analysis‡	Chromosome location§	Type of marker¶	References
Heat tolerance	*O. rufipogon*	YJCWR	TeQing	IL	CIM	1	SSR	Lei et al. (2013)
Low temperature tolerance	*O. nivara*	IRGC100195	M-202	AB-QTL	MIM	5	SSR	Eizenga et al. (accepted)
	O. rufipogon	W1943	Guang-lu-ai 4	BC_4F_2	IM, CIM	3, 11	SNP	Koseki et al. (2010)
	O. rufipogon	Dongxiang	Nanjing11	BC_2F_1	CIM	10	SSR	Xia et al. (2010)
	O. rufipogon	W1944	Hwayeong-byeo	RIL	SPA, CIM	2, 5	SSR	Lee et al. (2005)
Salt tolerance	*O. rufipogon*		TeQing	IL	SPA	1, 2, 3, 6, 7, 10	SSR	Tian et al. (2011)
Submergence stress	*O. rufipogon*					9		Li et al. (2011)
Biomass	*O. glaberrima*		IR64	BC_2F_3	SPA	1, 2, 3, 6, 10	SSR, STS	Bimpong et al. (2011)

† Abbreviations for mapping population types are: AB-QTL, advanced backcross-quantitative trait locus; AIL, alien introgression line; BIL, backcrossed inbred line; CSSL, chromosome segment substitution line; IL, inbred line; MAAL, monosomic alien addition line; NIL, near isogenic line; RIL, recombinant inbred line.

‡ Abbreviations for QTL analysis method are: ANOVA, analysis of variance; CIM, composite interval mapping; IM, interval mapping; MIM, multiple interval mapping; SMR, single marker analysis; SPA, single point analysis.

§ Only the chromosomes where the QTL increase is attributed to the wild parent are listed.

Abbreviations for types of markers are: AFLP, amplified fragment length polymorphism; CAPS, cleaved amplified polymorphic sequence, InDel, insertion-deletion polymorphism, RAPD, random amplified polymorphic DNA; RFLP, restriction fragment length polymorphism; SNP, single nucleotide polymorphism; SSR, simple sequence repeat; STS, sequence-tagged site.

Table 3. Summary of QTLs for grain quality, biotic stress tolerance, abiotic stress tolerance and biomass attributed to the non-*O.sativa* parent.

4.4. Resistance to biotic stress

4.4.1. Disease resistance

Pathogenic microorganisms, such as fungi, oomycetes, viruses and bacteria, and pests, such as insect herbivores, significantly reduce rice seed yield and quality. The most destructive rice diseases include bacterial blight caused by *Xanthomonas oryzae* pv. *oryzae* Ishiyama Dye (Cheema et al. 2008), blast caused by the fungus *Magnaporthe oryzae* B. Couch (Couch and Kohn 2002), and sheath blight caused by the soil-borne fungus *Rhizoctonia solani* Kühn (Zhang 2007). The first reported successful introduction of an agronomically important trait from a

wild *Oryza* species was the introgression of grassy stunt virus resistance from the AA-genome species *O. nivara* into the cultivated *O. sativa* genetic background (Khush et al. 1977). The resistance mechanism was subsequently introduced into several other rice cultivars (Sanchez et al. 2013). Since this first introduction, wild *Oryza* accessions have been screened as a potential source of resistance genes to biotic and abiotic stresses, as well as, yield and yield components, as previously discussed. These screening efforts, including successful introduction of stress resistance genes from *Oryza* species were recently summarized by Ali et al. (2010), Brar and Singh (2011) and Sanchez et al. (2013). Table 3 summarizes the efforts to identify the chromosome location of stress resistance genes introduced from the wild *Oryza* species by QTL and fine mapping analyses.

Seed yield losses due to bacterial blight were reported to be up to 75% in India, Indonesia, and the Philippines, and 20 to 30% in Japan (Mew et al. 1993; Nino-Liu et al. 2006). Thus far 31 bacterial blight resistance genes have been reported and six of these were identified in species other than *O. sativa*. These resistance genes were identified in several wild *Oryza* species, including *Xa21* in *O. longistaminata*, *Xa23* in *O. rufipogon*, *Xa27* in *O. minuta* (IRGC101141), *Xa29*(t) in *O. officinalis* (B5), and *Xa30*(t) in *O. nivara* (IRGC81825) (Brar and Singh 2011; Cheema et al. 2008b; Gu et al. 2004; Khush et al. 1990; Tan et al. 2004; Zhang et al. 1998). Most recently, *Xa34*(t) exhibiting broad spectrum resistance, was identified in *O. brachyantha* (IRGC101232) as a single dominant gene after examining the crossed progeny of two resistant introgression lines derived from IR56 (recurrent parent) and *O. brachyantha* (Ram et al. 2010a).

Both bacterial blight and blast resistance were identified in the tetraploid CCDD genome species, *O. minuta* (IRGC101141). To transfer these resistance genes into the background of diploid, cultivated rice, Amante-Bordeos (1992) used embryo rescue and backcrossing to produce interspecific hybrids between the elite *O. sativa* line, IR31917-45-3-2 (recurrent parent) and *O. minuta* (donor parent).

Lastly, the line Y73 was selected for a high level of bacterial blight resistance from the hybrid progeny of an asymmetric somatic hybridization between a resistant *O. meyeriana* and a *O. sativa* subsp. *japonica* cultivar (Yan et al. 2004). Subsequently, Chen et al. (2012) developed a RIL population from Y73 x IR24 (*O. sativa*) and identified five QTLs, two were major QTLs located on chromosomes 1 and 5, and three were minor QTLs on chromosomes 3, 10 and 11. They also mapped 21 additional QTLs related to yield components and yield.

Blast is considered the most destructive fungal disease in irrigated rice. The symptoms include lesions on leaves, stems, peduncles, panicles, seeds and roots (Savary and Willocquet 2000; Khush et al. 2009). To date, 41 blast resistance genes have been reported; however, there are only two genes, *Pi9* and *Pi40(t)*, that have been identified in wild *Oryza* species, *O. minuta* and *O. australiensis*, respectively. *Pi40(t),* which confers broad spectrum of blast resistance, was introgressed into the elite breeding line, IR65482-4-136-2-2 (Liu et al. 2002; Jeung et al. 2007). Qu et al. (2006) cloned the *Pi9* gene via a positional (map-based) cloning technique and found the gene is a member of a group of six resistance-like genes, which encodes a nucleotide-binding site (NBS) and leucine-rich repeats (LRRs). Silué et al. (1992) screened 99 *O. glaberrima* accessions for blast resistance by inoculating with ten *M. oryzae* strains from Cote d'Ivoire. The results revealed that nine accessions were resistant to all *M. oryzae* strains and 32 accessions

were moderately resistant, suggesting these accessions may be the source of novel resistance genes. Eizenga et al. (2009) identified resistance to U.S. blast races in some *Oryza* species but no accession exhibited resistance to all races. Subsequently, two AB-QTL populations with two different resistant *O. nivara* (IRGC100898; IRGC104705) accessions as donor parents x Bengal, a U.S. medium grain *tropical japonica*, as recurrent parent were evaluated for reaction to two U.S. blast races. QTL analysis of these populations mapped resistance to U.S. leaf blast races *IB1* and *IB49* to chromosomes 8 and 12 (Eizenga et al. 2013).

Rice sheath blight, *Rhizoctonia solani* Kühn, was reported for the first time in Japan in 1910 and since then, it has spread to many rice growing areas worldwide (Lee and Rush 1983; Savary et al. 2000). To date, no major resistance gene(s) that confers complete resistance to sheath blight has been discovered, only genes conferring partial resistance (Pinson et al. 2005; Jia et al. 2009). Several *Oryza* species accessions were screened for sheath blight resistance at the International Rice Research Institute (IRRI) in the Philippines with resistance being identified in accessions of *O. minuta* and *O. rufipogon* (Amante et al. 1990), and a resistant *O. officinalis* accession being the donor of sheath blight resistance genes in *O. sativa* introgression lines (Lakshmanan, 1991). Prasad and Eizenga (2008) screened a collection of 73 *Oryza* species accessions using three different methods and identified seven accessions with moderate resistance including three *O. nivara* accessions and one each of *O. barthii*, *O. meridionalis*, *O. nivara*/*O. sativa* hybrid, and *O. officinalis*. Based on these results, Eizenga et al. (2013) developed two AB-QTL populations using two of these *O. nivara* accessions (IRGC100898; IRGC104705) as the donor parents, and Bengal as the recurrent parent for both populations. QTL analysis identified a major QTL, *qShB6*, associated with sheath blight attributed to the wild rice parent. Two other minor QTLs, *qShB1* and *qShB3*, were identified but not attributed to the *O. nivara* parent in all sheath blight tests. A third AB-QTL population with the more distant A-genome species, *O. meridionalis* (IRGC105306), as the donor parent, and Lemont, a U.S. long grain *tropical japonica*, as the recurrent parent, was evaluated for reaction to sheath blight disease and the QTL analysis is currently underway (Eizenga, unpublished data).

Stem rot, a fungal disease caused by *Sclerotium oryzae* Catt., causes yield losses by reduced tillering, more unfilled grains per panicle, chalky grain, lower milling yields and increased lodging (Ou 1985). The germplasm line 87-Y-550 (PI566666) was derived from a cross between the stem rot resistant *O. rufipogon* (IRGC100912) and L-201, a long grain California (USA) *temperate japonica* cultivar (Tseng and Oster 1994). To identify the location of this resistance gene and associated molecular markers, Ni et al. (2001) developed four RIL populations from crosses between 87-Y-550 and four susceptible long grain *O. sativa* breeding lines. Following the bulk segregant analysis method, QTLs revealed an association between the AFLP marker, TAA/GTA167, on chromosome 2 and SSR marker, RM232, on chromosome 3.

African cultivated rice, *O. glaberrima*, is an excellent, potential donor of genes to improve the tolerance of Asian cultivated rice, *O. sativa*, to biotic stresses, including bacterial blight, rice blast, rice stripe necrosis virus (RSNV), nematodes (*Meloidogyne graminicola* Golden and Birchfield) and especially rice yellow mottle virus, RYMV (Djedatin et al. 2011; Gutiérrez et al. 2010; Ndjiondjop and Alber 1999; Plowright et al. 1999; Silue et al. 1992; Thiémélé et al. 2010). A set of 64 CSSLs selected from a Caiapó x *O. glaberrima* (IRGC103544) DH, BC_3F_1 population

was used to identify a major QTL controlling RSNV resistance on chromosome 11 (Gutiérrez et al. 2010). RYMV is one of the most destructive rice viral diseases. Few RYMV resistance genes have been found in *O. sativa* accessions, but 8% of the *O. glaberrima* accessions that were screened exhibited resistant to the virus with three recessive resistance alleles *rymv1-3*, *rymv1-4*, and *rymv1-5* and one dominant resistance allele, *RYMV1*, were identified. Three lines, TOG5681, TOG5672 and TOG7291 initially derived from the wild *Oryza glaberrima* showed resistance to RYMV, blast, and lodging (Futakuchi et al. 2008; Sié et al. 2002; Thiémélé et al. 2010).

4.4.2. Insect resistance

Genetic resistance is an effective method of protecting rice from insect pests in Asia and the Americas (Kiritani 1979; Way 1990) and avoids the possible environmental contamination associated with chemical control (Zhang 2007). The brown planthopper, *Nilaparvata lugens* (Stål), one of the most devastating herbivores of rice in Asia, causes damage by feeding on rice plants and transmitting two viruses, rice ragged stunt virus and rice grassy stunt virus. A total of 26 brown leafhopper resistance genes have been reported, of which 10 genes are recessive and 18 are dominant. Of the 26 genes, 12 genes, *Bph1, bph2, Bph3, bph4*, *bph5*, *Bph6*, *bph7*, *bph8*, *Bph9*, *bph19, Bph25* and *Bph26,* are found in *O. sativa;* two genes, *Bph10* and *Bph18,* are found in *O. australiensis;* seven genes, *Bph11*, *bph11, bph12, Bph14, Bph15, bph16* and *Bph17,* in *O. officinalis;* one gene, *Bph13*, in *O. eichingeri;* one gene, *Bph17*, in *O. latifolia*; two genes, *Bph20(t)* and *Bph21(t)*, in *O. minuta*; one gene, *bph22(t)* in *O. glaberrima*; and three genes, *Bph22(t), Bph23(t)* and *Bph24(t),* in *O. rufipogon* (Deen et al. 2010; Jena 2010; Oryzabase 2014; Ram et al. 2010, Zhang 2007).

Early efforts to evaluate the *Oryza* species accessions as a source of brown planthopper resistance and incorporation of this resistance into *O. sativa* were in a large part due to the efforts at IRRI. Early reports include introgression of resistance from *O. australiensis* through backcrossing into an *O. sativa* background and using RFLP markers to resolve the position of the gene in chromosome 12 (Ishii et al. 1993). Introgression of resistance to three brown planthopper biotypes from five different *O. officinalis* accessions into cultivated *O. sativa* breeding lines resulted in 52 BC_2F_8 ILs (Jena and Khush 1990; Jena et al. 1992). Genotyping of these lines with RFLP markers showed *O. officinalis* introgressions in 11 of the 12 rice chromosomes with markers on chromosomes 4, 10 and 12 appearing to be associated with BPH resistance but not unequivocally. More recently, a single dominant gene, *bph22(t)*, was discovered in *O. glaberrima* and transferred into *O. sativa* (Ram et al. 2010).

The white-backed planthopper, *Sogatella furcifera* (Horvath), is another serious insect pest of rice in Asia (Chen et al. 2010). Six major QTLs, *Wbp1, Wbp2, Wbp3, wbh4*, *Wbp5* and *Wbp6*, have been identified (Angeles et al. 1981; Hernandez and Khush 1981; Oryzabase 2014; Ravindar et al. 1982; Sidhu and Khush 1979; Min et al. 1991; Wu and Khush 1985). *O. officinalis* has been reported as a source of resistance to both white-backed and brown planthoppers. Further study identified two QTLs, *Wph8(t)* and *Bph15* on chromosome 4, with *wph7*(t) and *Bph14* on chromosome 3 (Huang et al. 2001; Oryzabase 2014; Tan et al. 2004). Chen et al. (2010) developed a BIL population derived from *O. sativa* x *O. rufipogon* and found three QTLs from wild *Oryza*

including *qWph2* on the short arm of chromosome 2, *qWph5* on the long arm of chromosome 5, and *qWph9*, which confers high resistance on the long arm of chromosome 9. In addition, these wild alleles reduced the rate of seedling mortality.

Guo et al. (2013) analyzed 131 BC_4F_2 ILs resulting from a cross between *O. minuta* (IRGC101133) x IR24 (*O. sativa*) by using 164 SSR markers, and estimated the average length of introgressed segments to be 14.78 cM. They observed a range of morphological and yield traits, as well as, resistance to bacterial blight, brown planthopper, and white-backed planthopper among the populations.

Rice monosomic alien addition lines (MAALs) contain the complete *O. sativa* chromosome complement ($2n=24_{AA}$) plus an additional, unpaired chromosome from a wild *Oryza* (alien) donor, thus the designation $2n=24_{AA}+1_{alien}$ (Jena 2010). MAALs have been used to identify important genes conferring resistance to biotic stresses, such as bacterial blight, brown planthopper and white-backed planthopper, from *O. australiensis* (EE) and *O. latifolia* (CCDD) into cultivated *O. sativa* (Multani et al. 1994 & 2003). Recently, Angeles-Shim (accepted) evaluated a set of 27 alien introgression lines developed from the *O. sativa* breeding line IR31917-45-3-2 x *O. latifolia* (IRGC100194) MAALs and identified putative QTLs for resistance to four Philippine races of bacterial blight, as well as, yield components and stem strength.

Green leafhopper [*Nephotettix virescens* (Distant)] is an insect found in wetlands including irrigated and rainfed environments. Six resistance loci, *Grh1, Grh2, Grh3, Grh4, Grh5* and *Grh6*, and one QTL, *qGRH4*, conferring resistance to green leafhopper have been reported. *Grh5* was identified in the wild rice, *O. rufipogon*, for the first time. *Ghr6* was identified in both cultivated rice and *O. nivara* (Fujita et al. 2003, 2004 & 2010; Fukuta et al. 1998; Saka et al. 1997; Tamura et al. 1999; Yasui and Yoshimura 1999; Yazawa et al. 1998).

The wild *Oryza* species have been used successfully as a source of novel alleles conferring resistance to both rice diseases and insect pests because in many instances these alleles could be transferred to *O. sativa* by backcrossing and screening the progeny. In fact, several of these alleles were successfully transferred even before the advent of molecular markers. With molecular markers, it is now possible to expedite the introduction of these novel alleles because marker-assisted breeding techniques can be used. With the molecular tools currently available, it should be possible to unravel those resistances which are quantitatively inherited like sheath blight.

4.5. Genes for abiotic stress

Abiotic stresses, including drought and flood, high and low temperatures, high salinity, high aluminum and acid sulfate soils, have a negative impact on rice productivity worldwide. Rice, like other plant species, has evolved to adapt to different environmental stresses using different mechanisms and strategies with multiple sensors. When the sensors identify a stress, a signal transduction pathway is invoked, which activates genes conferring the initial response for short term or long term tolerance to the stress (Grennan 2006; Lexer and Fay 2005). Recent studies identified many genes involved in plant tolerance to abiotic stress, which are classified into two groups based on their products. The first group includes genes that protect the cells

via synthesis of chaperones, a group of proteins that help non-covalent folding and unfolding of other proteins in the cell under stress conditions, and enzymes for protecting metabolites and proteins. The second group includes those genes that regulate stress responses acting as transcriptional factors to control stress genes or by producing hormones (Grennan 2006).

4.5.1. Tolerance to drought and heat

Drought reduces grain yield and affects yield stability in many rainfed regions by decreasing the number of tillers per plant, plant height, number of leaves and leaf width; and delaying anthesis and maturity as shown by Ndjiondjop et al. (2010) using 202 BILs derived from WAB56-104 (*O. sativa*) x CG14 (*O. glaberrima*) to identify the effect of drought on rice agronomic traits. Despite the fact that African rice (*O. glaberrima*) has low productivity and grain yield, it is an excellent source of genes associated with drought tolerance (Blum 1998; Hanamaratti et al. 2008; Manneh et al. 2007; Ndjiondjop et al. 2010).

Bocco et al. (2012) evaluated the morphological and agronomical traits of 60 genotypes including 54 BC_3F_6 introgression lines from IR64 (recurrent parent, elite *indica* cultivar) x TOG5681 (*O. glaberrima*), two parents (IR64 and TOG5681) and four NERICA-L cultivars derived from the same parents, for comparison as controls. These genotypes were evaluated in two time periods corresponding to the dry season under irrigated (control) and drought conditions to identify the most drought tolerance introgression lines. Plant height, spikelet fertility, grain yield and leaf area at harvesting were consistently reduced by drought and values for leaf temperature, leaf rolling, leaf tip drying, leaf blast disease, days to flowering and days to maturity were increased under drought conditions. From this evaluation, five BC_3F_6 lines were identified that out yielded the four NERICA-L cultivars described as drought tolerant.

Several accessions of *O. barthii*, *O. meridionalis* and *O. australiensis* were screened for heat and drought tolerance at the University of Arizona, which is located in a desert environment at Tuscon, Arizona, USA (Sanchez et al. 2013). One of the most tolerant *O. meridionalis* accessions was crossed with M-202, a California (USA) medium grain, *temperate japonica* cultivar. From the backcross progeny, two heat-tolerant advanced backcross lines resembling the M-202 parent were selected for variety release as 'Arizona Rice-1' and 'Arizona Rice-2'.

4.5.2. Tolerance to low temperatures

Low temperatures during the rice growing season causes poor germination, slow growth, withering and anther injury (Andaya et al. 2007; Hu et al. 2008). To cope with cold stress, many plant species including rice have developed several physiological and biochemical pathways for surviving and adapting to stress conditions (Ingram and Bartels 1996; Pastori and Foyer 2002; Hu et al. 2008). Rice is predominately grown in tropical and sub-tropical regions; therefore, many cultivars are sensitive to cold temperature especially during the seedling stage. The optimum temperature range for germination and early seedling growth is 25-30^{o}C, and temperatures below 15-17^{o}C during this period delay plant establishment, reduce plant competitive ability against weeds, delay plant maturity, and decrease grain yield. Improving

cold tolerance at this stage is one of the most effective ways to achieve yield stability and genetic tolerance is the most promising strategy (Andaya and Mackill 2003; Fujino et al. 2004; Koseki et al. 2009). Overall, the *Indica* subspecies is more sensitive to cold stress than *Japonica* rice. Several QTLs associated with cold tolerance have been identified, especially in populations derived from crosses between *Japonica* and *Indica* cultivars (Lu et al. 2007; Zhang et al. 2005).

Wild rice species, such as *O. rufipogon*, contain QTLs that can be integrated into cultivated rice to improve cold tolerance (Koseki et al. 2010). Lee et al. (2005) constructed a RIL population consisting of 120 BC_1F_7 lines derived from a cross between the *japonica* cultivar, Hwayeongbyeo and *O. rufipogon* (W1944). The population was genotyped with 124 SSR markers and evaluated for 20 agronomic traits including leaf discoloration which is associated with cold stress. Of the 63 QTLs identified, there were two QTLs for decreased leaf discoloration, in other words, increased cold tolerance, attributed to the *O. rufipogon* parent. These QTLs, *dc2* located on chromosome 2 and *dc5* on chromosome 5, accounted for 11.2% and 11.1% of the phenotypic variation, respectively. The *O. rufipogon* parent also contributed favorable alleles to panicle length, spikelets per panicle and days to heading.

Koseki et al. (2010) analyzed 184 F_2 introgression lines from crosses of Guang-lu-ai 4 (cold sensitive, *indica* cultivar) x W1943 (cold tolerant, *O. rufipogon*) for cold tolerance at the seedling stage (CTSS). Three *Ctss*-QTLs were detected with those on chromosomes 3 (*qCtss 3*) and 11 (*qCtss*11) attributed to the *O. rufipogon* parent, and on chromosome 10 (*qCtss10*) to Guang-lu-ai 4. The major QTL, *qCtss11*, explained 40% of the phenotypic variation and using backcross progenies, it was fine-mapped to a 60kb candidate region defined by markers AK24 and GP0030 with Os11g0615600 and/or Os11g0615900 hypothesized as the causal gene(s) for cold tolerance.

Seedling cold tolerance was measured in the M-202 (medium grain, U.S. *temperate japonica*) x *O. nivara* (IRGC100195) AB-QTL population using a slant board method [Jones and Petersen 1976; Eizenga et al. (accepted)]. In this study, QTLs for increasing coleoptile length and shoot length were identified in the same region on chromosome 5 and attributed to the *O. nivara* parent. QTLs for increased shoot length and root length were found on chromosome 8 and 6, respectively, and attributed to the M-202 parent.

4.5.3. Tolerance to aluminum and acid soils

Aluminum toxicity is another abiotic stress that causes grain yield reduction especially when rice is grown in an acidic soil (IRRI 1978). If the soil pH falls below 5.5, aluminum will more likely separate from the soil colloids and come into a solution phase. Aluminum at toxic levels slows root development, reduces the plant's ability to take up water and nutrients, and decreases plant growth, consequently reducing grain yield and grain quality (Foy 1992). Application of lime to the soil, reduces soil acidity and improves soil fertility but the results have showed limited success in overcoming the effects of aluminum toxicity. Aluminum tolerance is a quantitative trait and varies among rice species. Both additive and dominance effects contribute to the genetic heritability of aluminum tolerance as documented by the

importance of both general combining ability and specific combining ability (Howeler and Cadavid 1976; Wu et al. 1997).

In the past decade, one *O. rufipogon* (IRGC106424) accession found growing in an acid sulfate soil in Vietnam (Sanchez et al. 2013) has proven to be valuable for improving tolerance to both aluminum and acid sulfate soils in cultivated rice. Initially, Nguyen et al. (2003) evaluated 171 F_6 RILs derived from IR64 (*indica*, susceptible) x *O. rufipogon* (IRGC106424, tolerant) for aluminum tolerance. QTL analysis revealed QTLs for root length under stress conditions attributed to the *O. rufipogon* parent in six different chromosomal regions on chromosomes 1, 2, 3, 7, 8 and 9 that individually explained 9.0–24.9% of the phenotypic variation and were controlled by additive effects. The major QTL on chromosome 3, explaining 24.9% of the variation, was found to be conserved across cereal species. During the same time period, the tolerance to acid sulfate soils identified in this *O. rufipogon* accession was introgressed into the IR64 background through breeding efforts. The selected introgression line, IR73678-6-9-B, was released by IRRI as variety AS996 (Sanchez et al. 2013). AS996 is currently grown on 100,000 ha in the Mekong Delta and described as moderately tolerant to acid sulfate soils and tolerant to brown planthopper and blast.

Even though traits associated with abiotic stress are more difficult to evaluate because of environmental effects and interactions between genes, the development of the AS996 variety is an exciting success story. The release of Arizona-1 and Arizona-2 could make significant contributions to improving rice yields in areas where high temperatures routinely lower yield. With the improved molecular techniques for dissecting these traits and the gene functions related to abiotic stress, more significant advances should be made in the near future, especially as the scientific community provides the tools for rice producers to deal with global climate change.

5. Conclusions

The repositories of *Oryza* species accessions found around the world are a storehouse of novel alleles and traits lost during the evolution and domestication of cultivated rice as we know it today. The fact that introgression lines derived from crosses between Asian rice and it's ancestral species, *O. rufipogon* and *O. nivara*, exhibited notable improvement in yield and yield components through the phenomenon known as transgressive variation, was surprising and unexpected. The identification of novel alleles related to biotic stress, especially insect pests like brown planthopper and bacterial leaf blight, and more recently abiotic stresses like acid sulfate soils and drought, underscore the importance of mining these collections. The advent of molecular marker technology and development of mapping populations, especially AB-QTL and CSSL, have made it possible to map many of these alleles to chromosome location and begin to dissect the interactions between various genes. The fact that high quality genome sequences are now available or will soon be available, make it possible to interrogate the wild *Oryza* species accessions at a level that was not possible before. These resources will allow us

to move swiftly beyond the first step of QTL identification to fine mapping traits of interest; introgressing desirable traits into elite breeding lines using markers within the gene, thus decreasing linkage drag; identifying genotype by environment interactions; determining the effect of epistasis (non-allelic genes) on traits of interest; discovering epigenetic effects such as histone modification or DNA methylation; and finally unraveling other genetic phenomenon like gene silencing. In summary, the interspecific and intergenomic mapping populations available or soon to be available, and the increased availability of SNP data, resequencing data and advanced statistical software, create even more opportunities to investigate novel alleles for agronomically important traits discovered in the *Oryza* species and increase our understanding of the mechanisms underlying these traits to deal with the challenges of climate change and feeding nine billion people.

Acknowledgements

The support of National Science Foundation-Plant Genome Project: "The Genetic Basis of Transgressive Variation in Rice" (Award no. 1026555) to Ehsan Shakiba is gratefully acknowledged. Dr. Paul L. Sanchez and Dr. Benildo G. de los Reyes are acknowledged for their critical reading of this manuscript.

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