Chapter 2

# Genes and QTLs Resistant to Biotic and Abiotic Stresses from Wild Rice and Their Applications in Cultivar Improvements

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Additional information is available at the end of the chapter

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## 1. Introduction

Rice (*Oryza sativa* L.) is one of the most important food crops for mankind because it feeds more than half the world population, especially in developing countries (Maclean et al. 2002). Although rice production in the world has increased markedly in the past decades, it is still insufficient to cope with the ever-increasing global demands (Sasaki et al. 2000). This is not an easy task in view of the fact that the land available for cultivation is decreasing year by year, especially in Asia where 90 percent of the world's rice is produced and consumed (Khush 1997; Fischer et al. 2005). Meanwhile, since rice is grown worldwide and under a wide range of agro-climatic conditions, its productivity is affected by many abiotic and biotic stresses. Major biotic stresses including insect pests, such as brown planthopper (*Nilaparvata lugens* Stål), green rice leafhopper (*Nephotettix cincticeps*), and stem borer (*Chilo suppressalis*); and diseases, such as sheath blight, bacterial leaf blight, tungro virus; and abiotic stresses including salinity, acidity, drought, cold, and iron toxicity severely affect rice production.

During domestication process from wild species to cultivated rice, selecting desirable-agronomic traits to keep achieving high yield allows many genes to be either directly selected or filtered out, resulting in a significant reduction of genetic diversity in rice gene pool (Brar et al. 2003). Sun et al (2001) revealed that the number of alleles in cultivated rice had been reduced by 50-60% compared to wild rice. Thus, it is necessary to broaden the gene pool in rice breeding from diverse sources, especially from wild rice.

In the genus of Oryza, there are two cultivated species and more than 20 wild species. Both of the cultivated species, O. sativa and O. glaberrima, are diploid (2n = 24) and have the AA genome. Wild species have evolved in a wide range of environments over millions of years

(Stebbins 1981). The wild species have either 2n = 24 or 2n = 48 chromosomes, and seven genomes (AA, BB, CC, BBCC, CCDD, EE, and FF) have so far been designated for 17 species (Vaughan 1994; Brar et al. 1997). Common wild rice (Oryza rufipogon Griff.), due to its long-term growth in the wild conditions, possesses numerous advantages such as genetic diversity, excellent agronomic traits, and resistance against various biotic and abiotic stresses, proved to be an important resource for genetic improvement of rice (Song et al. 2005). Dongxiang wild rice (O. rufipogon Griff.) is in the northern most habitats among O. rufipogon populations to be discovered in the world (Chen et al. 2008; Xie et al. 2010; Figure 1), and displays strong tolerance to low temperature (Figure 2). It is for certain that many valuable traits exist in the wild rice species, but the most challenges to us are how to explore the valuable genes from wild rice and effectively transfer them into the cultivated rice for diversifying genetic basis of cultivated rice. Recently, many genes and QTLs have been mined from the wild rice, which functions include disease and insect resistances, abiotic stress tolerances, high yield, and so on. In this chapter, we will summarize current research progresses in mining elite genes and QTLs from wild rice for cultivar improvement in breeding programs.

**Figure 1.** Dongxiang wild rice (*Oryza rufipogon* Griff.) is a common wild rice located at 28°14′N latitude and 116°30′E longitude in Dongxiang county, Jiangxi province, China, which is considered to be the northernmost region in the world where *O. rufipogon* is found.

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**Figure 2.** Dongxiang wild rice can survive under freezing conditions.

## 2. Disease resistance genes and QTLs in wild rice

Rice diseases such as blast, bacterial blight and sheath blight are major obstacles for achieving optimal yields. To complement conventional breeding method, molecular or transgenic method represents an increasingly important approach for genetic improvement of disease resistance and reduction of pesticide usage. During the past two decades, a wide variety of genes and mechanisms involved in rice defense response have been identified and elucidated. However, most of the cloned genes confer high level of race specific resistance in a gene-for-gene manner, and the resistance is effective against one or a few related races or strains of the pathogens. The resistance is effective for only few years because the pathogen race or strain keeps changing for survival in nature. Therefore, there is an urgent need to broaden the rice gene pool from diverse resources, of which the wild rice is an ideal option.

### 2.1. Rice blast resistance

Rice blast, caused by pathogen *Xanthomonas oryzae* pv. *oryzae*, is considered as a major disease of rice because of its wide distribution and destructiveness under favorable conditions. Rice blast causes lesion symptoms on leaves, stems, peduncles, panicles, seeds, and even roots. The potential threat for cropping failure makes this disease ranked among the most devastating diseases in rice. It is reported that the rice blast disease can lead to lose one million hectares annually in China alone (Savary et al. 2000; Khush et al. 2009). Exploitation of resistance gene resources for rice breeding is one of the most important ways to control the disease.

*Oryza minuta* J. S. Presl ex C. B. Presl is a tetraploid wild rice, highly resistant to rice blast. By genetic analysis, Amante-Bordeos et al (1992) found that the disease resistance was controlled by a single dominant gene, named *Pi9*. Subsequently, Liu et al (2002) mapped *Pi9* in an approximately 100-kb region on chromosome 6, tightly linked with RFLP markers R2132 and RG6. Finally, this broad-spectrum rice blast resistance gene was cloned using a map-based cloning strategy. It turns out that *Pi9* encodes a nucleotide-binding site-leucine-rich repeat protein, as a member of a multi-gene family in rice (Qu et al. 2006).

Jeung et al (2007) identified a new gene in the introgression line IR65482-4-136-2-2 that has inherited the resistance gene from an EE genome wild *Oryza* species, *O. australiensis* (Acc. 100882). Genetic and molecular analysis localized a major resistance gene, *Pi40*(*t*), on the short arm of chromosome 6, within 70-Kb chromosomal region narrowed by two molecular markers RM3330 and S2539. *Pi40*(*t*) was validated using the most virulent isolates identified in Korea and the Philippines, suggesting a broad resistance spectrum.

Li et al (2009) evaluated blast resistance for 21 progenies from crossing with common wild rice, and obtained three stably resistance progenies. Preliminary analysis showed that the rice blast resistance was controlled by dominant genes. Geng et al (2008) cloned rice blast resistance gene *Pi-ta*$^{+}$ from Jinghong erect type of common wild rice. The *Pi-ta*$^{+}$ coding region shares 99.86% and 98.78% of homologous identity with Japanese waxy cultivar Yashiro-mochi and Yuanjiang type of common wild rice, respectively in the corresponding regions. There are four nucleotides difference in the coding region and six in intron of the cloned *Pi-ta*$^{+}$ gene, compared with *Pi-ta* from Yashiro-mochi. The allele in the Jinghong *Pi-ta*$^{+}$ gene is very rare in nature, because there is an alanine rather than a serine at position 918 within the predicted amino acid sequence of *Pi-ta*$^{+}$. The *Pi-ta*$^{+}$ allele can display disease resistance in response to blast pathogens in rice plant cells.

### 2.2. Bacterial blight resistance

Bacterial blight is caused by *Xanthomonas oryzae* pv. *oryzae*. Yield losses due to bacterial blight are variable, heavily dependent on the cultivar used and the environment. In Japan, yield losses ranged typically between 20% and 30% after distribution of high-yielding dwarf varieties (Mew et al. 1993). Among tropical climates, yield losses up to 75% were reported in Indonesia, India, and the Philippines (Nino-Liu et al. 2006). It is of great importance to explore elite bacterial blight resistance genes in rice. By now, a total of 35 related genes have been reported, and nine of which were from wild rice, i.e. *Xa21*(*t*), *Xa23*(*t*), *Xa27*(*t*), *Xa29*(*t*), *Xa30*(*t*), *Xa32*(*t*), *xa32*(*t*), *Xa35*(*t*) and *Xa36*(*t*).

In 1977, Dr. S. Devadath found that a strain of *Oryza barthii* from Mali is resistant to all the races of bacterial blight in India. Then, Khush et al (1989) found that this strain is akin to *O. longistaminata*, thus crossed it with IR24, which is susceptible to six races of bacterial blight in Philippines. The $F_1$ was resistant to the six races, thereby showing that the resistance of *O. longistaminata* was dominant. They designated this gene as *Xa21*(*t*). By developing nearly isogenic lines of *Xa21*(*t*), Ronald et al (1992) mapped locus *Xa21*(*t*) to a region larger than 270 kb on chromosome 11. By positional cloning, Song et al (1995) isolated *Xa21*(*t*). The sequence of the predicted protein, which carries both a leucine-rich repeat motif and a serine-threonine

kinase-like domain, suggests a role in cell surface recognition of a pathogen ligand and subsequent activation of an intracellular defense response. Furthermore, they demonstrated that the transgenic rice plants carrying the cloned *Xa21*(*t*) gene display high levels of resistance to the pathogen.

*Xa23*(*t*) was first detected from *O. rufipogon* by Zhang (2005), showing resistance to race 6 of bacterial blight in the Philippines. Wang et al (2005) constructed a $F_2$ population of JG30/CBB23 for molecule mapping of the *Xa23*(*t*) in rice. Based on their previous mapping of *Xa23*(*t*) gene, 12 EST markers from Rice Genome Program (RGP) database were surveyed in the susceptible $F_2$ plants and two markers, C189 and CP02662, were found to flank *Xa23*(*t*) gene, with genetic distance of 0.8 cM and 1.3 cM, respectively.

Jin et al (2007) identified a rice bacterial blight resistance germplasm (Y238) from the wild rice species *Oryza rufipogon*, and then they transferred the resistance locus into the cultivated rice to breed near isogenic line. By molecular mapping, the gene *Xa30*(*t*) was mapped on the long arm of rice chromosome 11. Linkage analysis revealed that four molecular markers RM1341, V88, C189 and 03STS located on the same side of *Xa30*(*t*), with genetic distances of 11.4 cM, 11.4 cM, 4.4 cM and 2.0 cM to the candidate gene, respectively.

Gu et al (2004) performed disease evaluation to a *Xa27*(*t*) near-isogenic line, IRBB27 with 35 *Xanthomonas oryzae* pv. *oryzae* strains collected from 11 countries. The *Xa27*(*t*) gene conferred a high level of resistance to 27 strains and moderate resistance to three strains. Resistance of the *Xa27*(*t*) gene was developmentally regulated in IRBB27 and showed semi-dominant or a dosage effect in the cv. CO39 genetic background. Molecular mapping located *Xa27*(*t*) within a genetic interval of 0.052 cM, flanked by markers M964 and M1197 and co-segregated with markers M631, M1230, and M449.

Guo et al (2010) transferred a new rice bacterial blight resistance gene *Xa35*(*t*) from the wild rice species *Oryza minuta* (Acc. No. 101133) into *Oryza sativa* L. (IR24). Through genetic analysis and identification of resistance spectrum, *Xa35*(*t*) showed a high level of resistance to PXO61, PXO112 and PXO339, but was susceptible to PXO86 and PXO99 after inoculation with the five strains of *Xanthomonas oryzae* pv. *oryzae*. With SSR marker analysis, the *Xa35*(*t*) locus was mapped to a 1.80 cM region. This locus was co-segregated with marker RM144, and was 0.7 cM from marker RM6293 on one side and 1.1 cM from marker RM7654 on the other side on rice chromosome 11.

*Xa29*(*t*), which was detected from the wild rice *Oryza officinalis*, has a high resistance to bacterial blight. By molecular mapping, the *Xa29*(*t*) gene was mapped within a 1.3 cM region flanked by RFLP markers C904 and R596 on chromosome 1 (Tan et al. 2004). *Xa32*(*t*), a bacterial blight resistance gene from *Oryzae ustraliensis*, was resistant to *Xanthmonas oryzae* pv. *oryzae* strains P1 (PXO61), P4 (PXO71), P5 (PXO112), P6 (PXO99), P7 (PXO145), P8 (PXO280), P9 (PXO339), and KX085, but susceptible to P2 (PXO86) and P3 (PXO79). *Xa32*(*t*) was mapped within a 2.0 cM interval flanked by two SSR markers RM2064 and RM6293 on the long arm of rice chromosome 11 (Zheng et al. 2009). Miao et al (2010) detected that the rice germplasm C4059 harbored a bacterial blight resistance gene, and designated it tentatively as *Xa36*(*t*). By

analyzing the mapping populations, the gene *Xa36*(*t*) was mapped within a length of 4.5 cM flanked by RM224 and RM2136 on the long arm of rice chromosome 11.

### 2.3. Others

Bacterial leaf streak (BLS) is caused by *Xanthomonas oryzae* pv. *Oryzicola* in rice. BLS occurs in Asia and West Africa, and yield losses are up to 30 percent. The symptoms of BLS include translucent interveinal streaks extending to orange lesions which may kill the leaf. Yellowish bacterial exudates may be seen. Bacteria may enter through small wounds on the leaf surface, including insect damage. Plants are susceptible at all stages, but infection is most damaging at the tillering stage. BLS is often prevalent in the rainy season. In order to determine if the resistance genes to the BLS disease were from Guangxi wild rice in China, Huang et al (2008) screened 1655 accessions of Guangxi *Oryza rufipogon Griss*, and identified 57 (1.87%) accessions to be resistant. In another screening, 15 (48.4%) out of 31 accessions of *O. officinalis* Wall. ex Watt were resistant.

Sheath blight disease, caused by a soilborne necrotrophic fungus *Rhizoctonia solani* Kühn, is one of the most important diseases in cultivated rice. This disease was first reported in Japan in 1910 and subsequently discovered worldwide (Rush et al. 1992). At present, rice sheath blight widely occurs in most rice-growing areas, including temperate, tropical and subtropical regions in diverse rice production systems (Lee et al. 1983). Sheath blight disease causes approximately 50% yield reduction in test plots of susceptible cultivars (Savary et al. 1996). To identify resistant germplasm to sheath blight disease, Prasad et al (2008) reported seven *Oryza spp*. accessions as moderately resistant, three were *O. nivara* accessions (IRGC104705, IRGC100898, and IRGC104443), *O. barthii* (IRGC100223), *O. meridionalis* (IRGC105306), *O. nivara*/*O. sativa* (IRGC100943), and *O. officinalis* (IRGC105979). Greater effort should be paid to search sheath blight resistant germplasm from wild rice and to transfer the resistant genes into the cultivated rice in the future.

## 3. Insect resistance genes and QTLs identified in wild rice

Insects are serious constraints to rice production. In Asia alone, yield loss due to insects has been estimated at about 25% (Savary et al. 2000). Insects not only damage the plant by feeding on its tissue, but also are vectors of devastating rice viruses in many cases. All portions of the plant, from panicle to root, are possibly attacked by various insects. And all growth stages of the rice plant, from the seedling to mature stages, are vulnerable. Even after harvest, the grain in store might face the attack from insects (Cramer et al. 1967). Because the resistance sources in cultivated rice are limited, it is important to keep exploring resistant germplasm from wild rice species for cultivar improvements.

Brown planthopper (BPH) is a destructive insect pest to rice in Asian countries where most rice is produced in the world, including China, India, the Philippines, Japan, Korea, Vietnam, etc (Khush 1984). BPH directly damages the plant phloem by using its piercing-sucking mouthparts, resulting in “hopper burn” in the most serious cases. Furthermore, it is also a

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vector for rice grassy stunt virus and ragged stunt virus, which may cause further yield losses in many Asian countries (Chelliah et al. 1993). Identification and incorporation of new BPH resistance genes from wild rice into modern cultivars are important breeding strategies to control the damage caused by the BPH.

Ishii et al (1994) found an introgression line from wild species *Oryza australiensis* resistant to three biotypes of BPH, and named the gene *Bph10*(*t*). RFLP analysis resulted in a linkage of the gene *Bph10*(*t*) with RG457 on chromosome 12 at a distance of 3.68 +/- 1.29 cM. A BPH biotype-4 resistance gene *Bph13*(*t*) was identified from *Oryza officinalis* Wall. Using RILs where parents "IR50" (cultivar which is susceptible to BPH Biotype-4) and "IR54745-2-21-12-17-6" (a line with *Oryza officinalis*-derived resistance to BPH biotype-4) are included, *Bph13*(*t*) was located on chromosome 3, linked with a RAPD marker AJ09b with the distance of 1.3 cM (Renganayaki et al. 2002).

Later, Jena et al (2006) identified a major BPH resistance gene *Bph18*(*t*) from an introgression line (IR65482-7-216-1-2) with wild species *Oryza australiensis*. Genetic analysis concluded that *Bph18*(*t*) is a dominant gene located within a 0.843 Mb physical interval flanked by markers R10289S and RM6869 on the long arm of chromosome 12, where three BAC clones are present.,. Subsequently, Jena et al (2010) successful cloned the *Bph18*(*t*) gene. *Bph14* is a BPH resistance gene at seedling and maturity stages. Du et al (2009) cloned *Bph14* gene to encode a coiled-coil, nucleotide-binding, and leucine-rich repeat (CC-NB-LRR) protein. Sequence comparison indicates that *Bph14* carries a unique LRR domain that might function in recognizing the BPH insect invasion and activating the defense response. *Bph14* is predominantly expressed in vascular bundles, the site of BPH feeding. Expression of *Bph14* activates the salicylic acid signaling pathway and induces callose deposition in phloem cells and trypsin inhibitor production after BPH infestation, thus reducing the BPH feeding to yield low growth rate and longevity of BPH insects.

Rahman et al (2009) conducted a genetic analysis of BPH resistance using an $F_2$ population derived from a cross between an introgression line, IR71033-121-15 from *Oryza minuta* (Accession number 101141) and a susceptible Korean *japonica* variety, Junambyeo. Two major QTLs were identified for BPH resistance. One was mapped to 193.4 kb region located on the short arm of chromosome 4, and the other was mapped to a 194.0 kb region on the long arm of chromosome 12.

## 4. Abiotic stress resistance genes and QTLs identified in wild rice

Abiotic stresses including high salinity, drought and flood, high and low temperatures are largely limiting productivity of rice crops in large areas of the world. According to Hossain (1996), abiotic stresses affect rice cultivation more than the biotic stresses. Improving the resistance to abiotic stresses will increase agricultural productivity and extend cultivatable areas of rice. There is, therefore, a strong demand for rice cultivars resistant to abiotic stresses.

Based on physiological studies on stress responses, recent progress in plant molecular biology has enabled discovery of many genes involved in stress tolerance. These genes include

functional genes which protect the cell (e.g., enzymes for generating protective metabolites and proteins), and regulatory genes which regulate stress response (e.g., transcription factors and protein kinases). Wild rice is the ancestor of cultivated rice, having been an important gene pool due to its survival ability in wild conditions and suffering from natural selection. Therefore, it is of great significance to study genetic basis of abiotic stress resistance as well as to explore new related genes in wild rice.

### 4.1. Cold resistance

Cold stress is a common problem for rice cultivation, and is a significant factor affecting global food production since cold stress can cause poor germination, slow growth, withering, and anthers injury on rice plants (Andaya et al. 2007). Annually, about 15 million hectares of rice in the world suffered from cold damage (Zhang et al. 2005). In south Asia, about 7 million hectares cannot be planted timely because of the low temperature stress (Sthapit et al. 1998). Consequently, development of rice cultivars with cold tolerance is recognized as one of the important breeding objectives.

Various methods have been adapted to improve rice resistance to low temperature stress (Bertin et al. 1997; Takesawa et al. 2002). With increasing emphasis on $F_1$ hybrid rice production in public institutions and private breeding companies, lots of landraces with diversified genetic background continue to decrease, which makes the genetic base of parental materials become more and more narrower. As a result, development of cultivars for strong cold tolerance becomes increasingly difficult using intra-variation. There is thus an urgent need to study the cold-tolerance character and excavate related genes in wild rice to broaden rice gene pool for developing cold tolerance cultivars.

Genetic analysis of cold tolerance at seedling and/or booting stage has resulted in the identification of many QTLs (Lou et al. 2007; Zeng et al. 2009). Zheng et al (2011) constructed chromosome segment substitution line (CSSL) populations using two core accessions of common wild rice (DP15 and DP30) as donor parents and cultivar 9311 as recipient parent. Thus, they identified cold tolerance QTLs effective at the seedling stage. Two donor lines, DP15 and DP30, are different in the number, location and effect of QTLs for cold tolerance. A total of 19 cold tolerance QTLs were detected, and clustered on chromosome 3 and chromosome 8. The survival rates ranged 8 – 74% after cold treatment among the CSSLs. A major QTL *qSCT-3-1* was mapped between SSR markers RM15031 and RM3400, near the centromere of chromosome 3 on the long arm with a distance of 1.8 cM.

Dongxiang wild rice can winter over successful in Wuhan, Hubei province, China, where the lowest temperature can be down to -12C in winter (Liu et al. 2003). In order to transfer cold tolerance gene from Dongxiang wild rice, we have developed introgression lines (ILs) through a backcrossing and single-seed descent program using an elite *indica* restoring cultivar Xieqingzao B (*O. sativa* L.) as recipient and Dongxiang wild rice as donor parent (Jian et al. 2011). Analyzing the introgression lines found that the IL5243 and IL5335 were the best for cold tolerant ability (Chen et al. 2013). Genetic analysis using SSR markers further confirmed that a part of alien DNA has been transferred from the common wild rice into IL5243 and

IL5335. Therefore, IL5243 and IL5335 might be excellent bridging germplasm for breeding programs to improve cultivar tolerance to cold stress.

### 4.2. Soil salinity resistance

Soil salinity is one of the major agricultural problems affecting crop productivity worldwide (Rozema et al. 2008). Of the cereals, rice is one of the most salt-sensitive crops (Shelden et al. 2013). The effects of salinity on rice have been reported to reduce seed germination (Hakim et al. 2010), decrease growth and survival of seedlings (Lutts et al. 1995), damage the structure of chloroplasts (Yamane et al. 2008), reduce photosynthesis (Moradi et al. 2007) and inhibit seed set and grain yield (Asch et al. 2000). Improving evaluation methodologies to identify genetic sources and excavating responsible genes for improving cultivar salt resistance is of continuing importance in rice. *Oryza coaretata* is an Asian wild rice species, occurring mostly in the coastal areas of India. This species is highly resistant to salt because of survival ability in the coastal environments. *O. coarctata* has some special unicellular hairs (trichomes) on the adaxial surface of leaves. The hairs efficiently maintain a low concentration of toxic salts in the plant tissue (Bal et al. 1986).

### 4.3. Low-phosphorus resistance

Phosphorus is one of essential nutritive elements for rice growth and development (Abel et al. 2002). The phosphorus content may be too little in the soil to be able to meet the needs of rice growth. It has been estimated that 5.7 billion hectares of land are deficient in phosphorus worldwide. Phosphorus deficiency is considered as one of the greatest limitations in agricultural production (Schachtman et al. 1998; Lynch et al. 2008).

Chen et al (2011) identified the low-phosphorus resistance ability of Dongxiang wild rice at the seedling stage by using the cultivated low-phosphorus sensitive varieties as the control. The results showed that Dongxiang wild rice has strong low-phosphorus resistance ability. And then, they developed BILs by using Dongxiang wild rice as donor parent and the low-phosphorus sensitive variety Xieqingzao B as recurrent parent. By analyzing the morphological indices, they found that the low-phosphorus resistance lines under low-phosphorus stress had higher values of relative leaf age, relative plant height, relative shoot dry mass, and relative soluble content, but low values of relative yellow leaf number and relative malondialdehyde content, suggesting that the low-phosphorus resistance capability of the low-phosphorus resistance lines was mainly attributed to the high phosphorus utilization efficiency of the lines, namely, low-phosphorus resistance lines had stronger capability in synthesizing dry mass with per unit phosphorus uptake (Chen et al. 2011).

### 4.4. Drought resistance

Because of global climate warming and increasing scarcity of water resource, drought stress and water scarcity have severely impacted the security of rice production (Farooq et al. 2009). At least 23 million hectares of rice area in Asia are estimated to be drought-prone (Pandey et al. 2005). To date, however, the major challenge for research communities is the relatively

limited progress achieved in developing high yielding rice cultivars with drought resistance (Rabello et al. 2008). Therefore, the improvement of drought resistance in newly developed cultivars, for the wide adaptability across rice-growing ecologies, has become a major priority in rice breeding programs. Accordingly, identifying genes from new germplasm resources such as wild rice has become extremely important for drought resistance, which will lay the foundation for utilization of drought resistance gene and genetic improvement of drought resistance (Xie et al. 2004).

Our group has already carried out preliminary experiments for many years on characterization of Dongxiang wild rice for genetic differentiation and conservation, and utilization (Xie et al. 2010). We proved that Dongxiang wild rice has strong drought resistance (Figure 3). Subsequently, Hu et al (2013) constructed BIL population using *Indica* restorer line R974 (*Oryza sativa* L.) and Dongxiang wild rice. Using a mixed inheritance model for both major genes and minor genes, they found that the inheritance of drought-resistance at seedling stage was controlled by two independent genes plus polygenes. Therefore, Dongxiang wild rice could be precious resource for genetic improvement of drought resistance in cultivar development.

**Figure 3.** Dongxiang wild rice has strong drought resistance.

## 5. Yield-enhancing QTLs from wild rice

In general, wild rice has smaller seeds and other undesirable traits compared to cultivars, and thus appears not to be appropriate for a donor to enhance yield in cultivars. However, molecular studies have demonstrated that phenotypically poor wild rice contains some genes important for improving cultivar yield (Tanksley et al. 1996). Some wild-QTL alleles

http://dx.doi.org/10.5772/56825

are favorable for some traits, but may be associated with deleterious effects on other traits. The positive QTLs from *O. rufipogon* may be potentially useful for breeding high yield cultivar if the disadvantage linkage drag could be broken through careful selection. In addition, other potentially beneficial QTLs for yield-related traits are often linked to the QTLs conferring negative traits. For example, *gpp1.1* with yield increasing effect is closely linked with a negative QTL to increase plant height because this QTL is closely linked to *sd1* locus (Cho et al. 2003). Brondani et al (2002) detected specific marker regions to strongly associate with multiple yield-related traits including panicle number, spikelets per panicle, seed set percentage, 100-grain weight, grain yield per plant, filled grain number per panicle and grain yield per panicle.

By using a $BC_2F_5$ population derived from the cross between Zhenshan 97 and a wild rice, Wu et al (2012) identified a QTL region flanked by SSR marker RM481 and RM2 on chromosome 7. This QTL has pleiotropic effects on heading date, spikelets per panicle, and grain yield per plant. The alleles from wild rice have increasing effects on these phenotypic traits contributable to grain yield.

Fu et al (2010) developed an advanced backcross population by using an accession of common wild rice collected from Yuanjiang County, Yunnan Province, China, as the donor and an elite cultivar 9311 as the recurrent parent. From this population, several QTLs originating from *O. rufipogon* display beneficial effects for yield-related traits in the 9311 genetic background. In addition, five QTLs controlling yield and its components are newly identified, and they are potentially novel alleles in Yuanjiang common wild rice. Three regions underling significant QTLs for several yield-related traits are detected on chromosome 1 (RM212-RM5362), 7 (RM125-RM1135) and 12 (RM7003-RM277).

Xiao et al (1998) identified two yield-enhancing QTLs, *yld1.1* and *yld2.1*, from *O. rufipogon* using $BC_2$ populations. QTLs *yld1.1* and *yld2.1* have been transferred to the elite restorer lines Ce64-7, 9311 and Minghui63 by marker-assisted selection (MAS), and they are confirmed to produce significant yield-enhancing effects in field tests. Xie et al (2006) fine mapped a yield-enhancing QTL cluster using a $BC_3F_4$ population derived from a cross between the Korean *japonica* cultivar Hwaseongbyeo and *O. rufipogon.* The cluster contained seven QTLs for 1000-grain weight, spikelets per panicle, grains per panicle, panicle length, spikelet density, heading date and plant height. The alleles from the low-yielding *O. rufipogon* parent are beneficial in the Hwaseongbyeo background.

## 6. Present problems and future directions

As the wild relatives and ancestor of cultivated rice, wild rice carries various characteristics resistant to biotic and abiotic stresses, beneficial agronomic traits, and abundant genetic diversity, which have been lost in the cultivated rice due to breeding activities (Sakai et al. 2010). Thus, it is an extremely important resource for improving important traits in cultivated rice (Xie et al. 2004). However, loss of wild rice genetic diversity was sped up

by increasing deterioration of original habitat. For example, the Dongxiang wild rice was sharply reduced from nine populations in nine isolated areas in 1978 to three in 1995 (Hu et al. 2011). The dramatic reduction makes the unique gene pool endangered. Therefore, it is necessary to accelerate a rational conservation for effective utilization of these survived genetic resources.

Breeders have long recognized the intrinsic value of wild rice for improving the traits of modern cultivars. The most successful examples to utilize wild rice in the history of rice breeding include the use of *Oryza nivara* genes to provide long-lasting resistance to grassy stunt virus (Plucknett et al. 1987), and the use of *O. spontanea* as a source of wild abortive cytoplasmic male sterility, which has made a cornerstone for today's hybrid rice (Li et al. 1988). However, despite these successes, it is still difficult to utilize wild rice for the improvement of quantitatively inherited traits. Great progress of molecular markers and maps makes it possible to identify individual QTL associated with elite traits from wild rice, which will help transfer the valuable QTLs into modern cultivars to improve their qualities (Tanksley et al. 1996).

Nowadays, QTL studies for mining favorable genes from wild rice species are receiving more and more attentions in global rice community. Several studies have successfully identified and introduced the QTL enhancing alleles from wild rice for yield-related traits into high-yielding elite cultivars (He et al. 2006; Deng et al. 2007; Tan et al. 2008). In addition, some QTLs related to rice quality traits were also detected using wild rice introgression lines (Hao et al. 2006; Garcia-Oliveira et al. 2009). Molecular mapping of these good genes will help discover and make full use of the elite resources of wild species to broaden the genetic base of modern cultivars. However, only a few genes have been cloned from wild rice, and the mechanism for those excellent traits from wild rice are far from being clarified. Cloning more genes from wild rice should be emphasized in the future, which will help make full use of these elite resources more effectively.

In summary, as a rare germplasm resource, wild rice is of great significance to our agricultural heritage and biodiversity protection. Research reveals that wild rice not only has many elite genes which have lost in cultivated rice, but also maintains a greater genetic diversity than cultivated rice. We should use the wild rice to broaden genetic diversity of cultivated rice, by which new cultivars could withstand biotic and abiotic stresses. This is of great significance to assure both high yield and quality in rice production.

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