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Hidden diversity for abiotic and biotic stress tolerances in the primary gene pool of rice revealed by a large backcross breeding program

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Abstract

Low and unstable rice productivity in many areas of Asia is associated with many abiotic and biotic stresses such as drought, salinity, anaerobic conditions during germination, submergence, phosphorus and zinc deficiency, etc. To develop rice varieties with tolerance to these stresses, we undertook a large backcross (BC) breeding effort for the last 6 years, using three recurrent elite rice lines and 203 diverse donors, which represent a significant portion of the genetic diversity in the primary gene pool of rice. Significant progress has been made in the BC breeding program, which resulted in development of large numbers of introgression lines with improved tolerance to these stresses. Promising lines have been developed with excellent tolerances (extreme phenotypes) to salinity, submergence and zinc deficiency; resistance to brown plant hopper, ability to germinate under the anaerobic condition and low temperature. Our results indicated that there exist tremendous amounts of 'hidden' diversity for abiotic and biotic stress tolerances in the primary gene pool of rice. Furthermore, we demonstrated that despite the complex genetics and diverse physiological mechanisms underlying the abiotic stress tolerances, introgression of genes from a diverse source of donors into elite genetic backgrounds through BC breeding materials for developing new rice cultivars with superior yield and stability by trait/gene pyramiding, but also represent unique genetic stocks for a large-scale discovery of genes/alleles underlying the abiotic and biotic stress tolerances of rice.

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1. Introduction

Rice is the staple food for more than 3 billion people in Asia, where more than 90% of the world's rice is produced and consumed. Rice production in Asia has been more than tripled in the past three decades, resulting primarily from the "Green Revolution" in the irrigated ecosystems (Khush, 2001). However, rainfed lowland rice occupies approximately 28% of the world rice area but contributes only about 16% of total rice production (Garrity et al., 1996). The yield level of rainfed lowland rice is, on average, around 2.3 t ha⁻¹, much lower than that of the irrigated systems of about 4.9 t ha⁻¹, which is due largely to many abiotic stresses such as drought, submergence, salinity, etc. For example, nearly 22 million ha of rice are affected by flash flooding and submergence in Bangladesh, Northeast India, Thailand and South Vietnam

Abbreviations: AG, anaerobic germination; BPHR, brown planthopper resistance; LTG, low temperature germination; ST, salinity tolerance; SUBT, submergence tolerance; ZDT, zinc deficiency tolerance

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(Khush, 1984) and the yield loss can reach nearly 70% from submergence alone, resulting primarily from poor establishment of the crop (Widawsky and O'Toole, 1996). In both South and Southeast Asia, about 90 million ha of land (particularly along the coastal areas of Asia) suited to rice production remain uncultivated due to various soil problems such as salinity, alkalinity, strong acidity or excess organic matter, and of this area, nearly 49 million ha are saline (Poonamperuma and Bandyopadhya, 1980). Rice is very sensitive to salinity at the seedling stage. A low level of salinity with electrical conductivity (EC) of $5-6 \text{ dsm}^{-1}$ can cause significant reduction in height, root growth and dry matter accumulation of susceptible rice lines (Pearson et al., 1966; Akbar and Yabuno, 1974). Saline soils are also commonly associated with many other problems such as mineral deficiencies (Zn, P) and toxicities (Fe, Al and organic acids), submergence, and drought (Gregorio et al., 2002).

Rice genotypes are known to vary widely in their responses to these abiotic stresses, and breeding stress tolerant rice cultivars is the most efficient and economical way to overcome the problems, because management strategies to mitigate these stresses are generally beyond reach of the poor farmers in these areas. Unfortunately, breeding efforts to develop high-yielding rice cultivars adapted to the rainfed ecosystems have been less successful than for the irrigated systems. A recent survey indicated that approximately 60% of rice cultivars grown in the rainfed areas of Asia remain traditional landraces, and most modern high-yield semi-dwarf varieties are not adapted to the unfavorable rainfed environments (Pandey, personal communication). There are at least three obvious reasons for slow progress in genetic improvement of rice abiotic stress tolerance. First, past efforts in germplasm screening identified few accessions with high levels of abiotic stress tolerance for use in breeding programs. For instance, two landraces from India, FR13A and Pokkali, are among the few accessions that are highly tolerant to submergence and salinity, respectively. As a result, they have been extensively used as donors for submergence and salt tolerance in breeding programs at IRRI and other Asian countries. However, the poor agronomic performance and narrow adaptability of the two landraces have been formidable obstacles for breeders seeking to combine highvield potential with the good abiotic stress tolerance of these landraces. Similarly, an extensive screening of over 7500 rice germplasm accessions identified only 29 accessions highly resistant to brown plant hopper (BPH) (Pophaly et al., 2001). The rapid evolution of more virulent biotypes of BPH has been a constant challenge to breeders (Ikeda and Kaneda, 1981; Panda and Khush, 1995). Second, rice tolerance to different abiotic stresses is often complex in nature and its genetic basis, as for most quantitative traits, remain poorly understood. Third, in most areas of the rainfed environments, multiple abiotic stresses coexist. For instance, drought and submergence can occur at different times during the same season in certain rainfed environments, and salinity is often accompanied with other soil problems. Thus, desirable rice

varieties for rainfed environments must have tolerances to multiple stresses in addition to good yield potential and acceptable grain quality.

Domestication, artificial selection and intensive breeding of crop varieties by human have resulted in the narrowed genetic base in many crops, which renders modern crop varieties more vulnerable to biotic and abiotic stresses (Tanksley and McCouch, 1997). Base broadening (Simmonds, 1993) or gene pool enrichment has been proposed as an alternative to transfer useful genes from unadapted germplasm into elite backgrounds for developing new cultivars; this has been implemented in maize (Kannenberg and Falk, 1995; Kannenberg, 2001) and barley (Falk, 2001). However, it still remains largely unknown how much useful genetic diversity exists for complex phenotypes in the world's crop germplasm collections. Traditional landraces account for about 70% of the total rice collections in the gene banks worldwide and many of them are known to have different tolerances of abiotic stresses, but plant breeders have been reluctant to utilize these landraces, largely for three reasons (Duvick, 1984, 2002). First, slow but consistent progress can be achieved even within the narrow genetic base of many breeding populations. Secondly, outstanding commercial genotypes tend to be destroyed in crosses involving unadapted exotic parents. Thirdly, selection of germplasm as parents of the breeding programs by breeders has been largely based on the phenotype.

At IRRI, we initiated a large-scale backcross (BC) breeding effort in 1998, as part of the International Rice Molecular Breeding Program (IRMBP), to answer two important questions: (1) whether there is sufficient genetic variation for tolerances of various abiotic and biotic stresses in the primary gene pool of rice; and, if yes, (2) what is the most efficient way to exploit this useful genetic variation. We report here that there is tremendous 'hidden' diversity for abiotic stress tolerances in the primary gene pool of rice and demonstrate that BC breeding and efficient phenotyping are powerful means to exploit this hidden diversity for developing promising lines with significantly improved tolerances to many abiotic stresses.

2. Materials and methods

2.1. Parental lines

Two high-yielding varieties, IR64 (*indica*) and Teqing (*indica*), and a new plant type (NPT or IR68552-55-3-2, tropical *japonica*) breeding line, were used as recurrent parents (RPs). A total of 203 accessions from different parts of the world were used as donors in the BC breeding program (Table 1). Based on an assay with 101 simple sequence repeat (SSR) markers (Yu et al., 2003), 139 of the parents belonged to *indica*, 63 belonged to *japonica*, 2 are of intermediate types derived from *indica/japonica* crosses, and a deep-water rice, 'Jalmagna' from India, forms a single

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