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# Drought Resistance Improvement in Rice: An Integrated Genetic and Resource Management Strategy

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**Abstract:** Drought is the major constraint to rice production in rainfed areas across Asia and sub-Saharan Africa. In the context of current and predicted water scarcity, increasing irrigation is generally not a viable option for alleviating drought problems in rainfed rice-growing systems. It is therefore critical that genetic management strategies for drought focus on maximum extraction of available soil moisture and its efficient use in crop establishment and growth to maximize biomass and yield. Extensive genetic variation for drought resistance exists in rice germplasm. However, the current challenge is to decipher the complexities of drought resistance in rice and exploit all available genetic resources to produce rice varieties combining drought adaptation with high yield potential, quality, and resistance to biotic stresses. The strategy described here aims at developing a pipeline for elite breeding lines and hybrids that can be integrated with efficient management practices and delivered to rice farmers. This involves the development of high-throughput, high-precision phenotyping systems to allow genes for yield components under stress to be efficiently mapped and their effects assessed on a range of drought-related traits, and then moving the most promising genes into widely grown rice mega-varieties, while scaling up gene detection and delivery for use in marker-aided breeding.

**Key words:** Crop improvement, Drought, Research strategy, Rice.

## 1. Introduction

In the race between increasing world population and food production, the Green Revolution was principally achieved by increasing crop productivity in irrigated ecosystems. However, success has been limited in increasing rice productivity in rainfed systems, which are prone to frequent droughts and other abiotic stresses. Worldwide, drought affects approximately 23 million ha of rainfed rice. Drought is particularly frequent in unbunded uplands, banded uplands, and shallow rainfed lowland fields in many parts of South and Southeast Asia, sub-Saharan Africa, and Latin America. Millions of hectares of mid-lowland rainfed rice areas are also affected by drought in years with very low rainfall. It also affects production on millions of hectares in water-short irrigated areas dependent on surface irrigation, where, in drought years, river flows and water in ponds and reservoirs may be insufficient to supply the crop. These drought vulnerability scenarios are likely to worsen in the future with predicted climate change scenarios (Wassmann et al., 2009a), which will also lead to more complex interactions of drought with

other abiotic and biotic stresses (Wassmann et al., 2009b).

The variation in rice production in areas dependent on rainfall and/or surface irrigation is closely related to total annual rainfall, but, even when total rainfall is adequate, in rainfed areas, shortages at critical periods due to long spells between two rains greatly reduce productivity, resulting in severe economic losses for some of the world's poorest communities. In the eastern Indian states of Jharkhand, Orissa, and Chhattisgarh alone, rice production losses in severe droughts (about one year in five) average about 40% of total production (Pandey and Bhandari, 2009). In the context of current and predicted water-scarcity scenarios, irrigation has only limited potential to alleviate drought problems in rainfed rice-growing systems (O'Toole, 2004). It is therefore critical that both agronomic and genetic management strategies focus on the efficient use of available soil moisture for crop establishment, growth, and yield. Rice yields in drought-prone rainfed systems remain low at 1.0 to 2.5 t ha<sup>-1</sup>, and tend to be unstable because of erratic and unpredictable rainfall. Drought mitigation through improved drought-

resistant rice varieties and complementary practices, such as water conservation, represent an important exit pathway from poverty (Pandey and Bhandari, 2009).

Many of the varieties grown in rainfed ecosystems were originally developed for irrigated ecosystems, without screening for drought tolerance. Although high-yielding, these varieties generally produce poor crops or even fail to produce when exposed to drought (Verulkar et al., 2010). Varieties combining improved drought resistance with high yield under favorable conditions and quality characteristics preferred by farmers are therefore urgently needed. They are likely to be among the most promising and deliverable technologies for alleviating poverty in communities dependent on rainfed rice production, because, if such varieties are truly superior under farmer management, they have the potential to be quickly adopted, because most small farmers generally obtain rice seed from neighbors and relatives, and improved varieties spread rapidly through farmer-to-farmer exchange once farmers are convinced of their superiority.

We have recently reviewed the multiple facets and recent advances in drought resistance improvement research in rice (Bernier et al., 2008; Serraj et al., 2009a). The aims of the present paper are to describe the critical research issues and most important knowledge gaps in drought resistance research, and to present the overall strategy being pursued by IRRI and its NARES partners for the integration of genetic enhancement and management practices for drought resistance improvement in rice.

## 2. Rice toposequence, drought agroecology, and implications for breeding

The local watersheds in which rainfed rice is grown can be characterized as a *toposequence*, or a series of terraced fields that drain into each other (Homma et al., 2003). Within distances of a few hundred meters, the toposequence may include unbanded upper, drought-prone upper fields that do not retain standing water, well-drained mid-toposequence fields, and poorly drained lower fields in which water can accumulate to depths of 1 m or more during the rainy season. Water-related stresses are variable across years because of variability in the amount and distribution of rainfall (Hijmans and Serraj, 2009), but occur with predictable frequency in a given field based on toposequence position and soil texture. They are most severe in upland fields, at the top of the toposequence (Jongdee et al., 2006). Asia has more than 20 million ha of such lands. Yield variability due to micro-geographic variation in field elevation and levelness can be great even within single fields, resulting in very large estimates of genotype  $\times$  location  $\times$  year interactions and residual error in the analysis of rainfed rice trials, thus complicating the selection of drought-resistant genotypes (Cooper et al., 1999).

Rice yield is linearly related to the number of days in the growing season in which soil is saturated (Boling et al., 2004; Haefele and Bouman, 2009). The ability to maintain biomass accumulation in relatively dry soils is therefore a key feature required in drought-resistant varieties. Intermittent soil drying substantially reduces biomass production and, therefore, total yield potential. However, to a rice farmer, the word “drought” means not only physical water shortage that affects plant growth and development, but a lack of sufficient water to support land preparation, transplanting, fertilizer application, and weed control operations. These operations are dependent on the presence of a standing water layer in the paddy. When the supply of water is delayed or skipped, large yield losses often ensue even though plants have not suffered physiological water stress. Losses from these management disruptions may be as great as those from direct drought damage.

Transplanting is the management step that is most vulnerable to water shortage. Farmers must often delay transplanting until sufficient water accumulates in fields to permit puddling; this may result in transplanting seedlings that are 45 to 60 days old. Transplanting delays of this magnitude result in large yield losses due to reductions in both panicle number and weight. In experiments conducted at IRRI in 2005, transplanting 65-day-old as opposed to 22-day-old seedlings resulted in a yield reduction of more than 50%, averaged across 125 cultivars (Atlin et al., unpublished). Variability for adaptation to delayed transplanting has not been systematically studied, but appears to be large, even in photoperiod-insensitive germplasm, and resistance to delayed transplanting has become an important target of the IRRI drought breeding program. The widespread eastern Indian weed-management practice of *beushening* (also known as *beusani* or *biasi*, among other variants), which consists of cross-ploughing the standing crop about 1 month after direct sowing, followed by re-rooting in field parts with low population density (Singh et al., 1994), cannot be performed without standing water in the field and is also extremely sensitive to drought. Understanding the complexity of rice drought in agroecological terms thus permits the identification of distinct target populations of environments for drought resistance breeding:

### (1) Unbanded upland fields

Upland rice is established via direct seeding in unbanded, unpuddled fields with light soil that never accumulate standing water for even a few hours after cessation of rain. The largest area of drought-prone upland rice is in the eastern Indian plateau region, where 3–5 million ha are grown, but large areas of upland rice production remain in West Africa, Indonesia, and hilly Southeast Asia. In the upland environment, soil water content frequently falls to field capacity or below in the

root zone. Therefore, the ability to root deeply, maintain biomass production in drying soil, and tolerate periods of severe stress throughout the growing season is critical. In direct-sown upland fields, a high degree of seedling vigor to compete with fast-growing upland weeds and resistance to severe drought at any crop stage are of paramount importance. Upland rice yields are closely related to total seasonal rainfall, and are very sensitive to short periods of stress during flowering stage.

### (2) Bunded upper-toposequence lowland fields

Bunded fields at the top of the lowland toposequence accumulate little or no standing water, but are usually either puddled and transplanted or established via beushening. Because these fields can be highly productive in favorable years, combining high yield potential with drought resistance is a prerequisite for varietal adoption. Delayed transplanting, reduced biomass production due to soil drying, and sterility caused by stress around flowering are the major sources of yield loss in these fields. Drought risk could be reduced by developing cultivars that tolerate delayed transplanting, maintain vegetative growth when soil water content drops below field capacity, and tolerate severe stress during flowering and grain-filling. Both transplanting and beushening risk could be avoided by developing cultivars adapted to direct seeding in dry soils. These *aerobic rice* cultivars are an important breeding target at IRRI, since the bunded upper-field target environment occupies millions of hectares across South and Southeast Asia.

These two major target populations of environment require distinctly different types of germplasm, and genetic solutions for one environment are not necessarily effective in the other. This was demonstrated in managed-stress trials at IRRI in the dry season of 2006, in which 64 lines were evaluated under both upland and lowland stress. The genetic correlation between yields in the upland and lowland stress environments was low, indicating that about 10% of the genetic variation for yield under stress was common to the two environments. However, gains made in one environment are likely to generate spillovers and new options in the other. For example, high-yield, drought-resistant aerobic rice performs well when direct-sown in bunded upper fields, opening up new options for reducing transplanting risk.

### (3) Bunded mid-toposequence lowland fields

In the rainfed ecosystems of South and Southeast Asia and sub-Saharan Africa, the largest area consists of mid-toposequence lowland fields. Farmers cultivate rice mostly by transplanting or beushening (e.g. in Eastern India). In the event of failure of rain for a few days, these bunded fields can escape drought because they accumulate water. However, failure of rain for 2 weeks or more at any stage of the rice crop has adverse effects on grain yield, although this effect may not be visible to the farmer. The effect is

more severe in case of early withdrawal of rain when the crop is around or at flowering. Developing high-yielding and drought-resistant lowland cultivars that can withstand delayed transplanting, maintain vegetative growth when soil water content drops below field capacity, and tolerate stress during flowering could be an efficient strategy for reducing drought risk in this target population of environment. Cultivars with better ability to penetrate the hardpan layer formed by puddling and extract water from soil more efficiently would be more suitable for tolerating water shortages in this target population of environment (Samson et al., 2002). Developing drought-resistant lowland cultivars has been an important objective of IRRI's drought breeding program. However, in the event of high rainfall, mid-toposequence rainfed lowland rice fields are often subjected to short periods of submergence. This has been witnessed the most in the rainfed areas of eastern Uttar Pradesh and Bihar of eastern India. Developing high-yielding cultivars that combine drought and submergence tolerance could be the best alternative. IRRI has started drought and submergence breeding programs to develop germplasm for this target population of environment (Kumar et al., 2008; Septiningsih et al., 2009).

The discussion above indicates that there are four critical entry points to the development of varieties with reduced risk and greater productivity in drought-prone fields:

- Improved maintenance of biomass production in drying soils (for both bunded and unbunded target environments)
- Resistance to severe stress during the critical reproductive stage (for both bunded and unbunded target environments)
- Adaptation to direct seeding in dry soil (for bunded and unbunded target environments)
- Tolerance of delayed transplanting (for bunded target environments only)

### 3. Old challenges and recent breakthroughs

Progress in developing drought-resistant rice varieties has been slow, despite considerable past efforts (Fukai and Cooper, 1995; Lafitte et al., 2004; O'Toole, 2004). Drought resistance is a difficult trait to evaluate because of the unpredictable occurrence of natural droughts and lack of information on effective screening techniques. Consequently, few national programs have systematically incorporated drought resistance as a breeding objective, e.g., in the Mekong region (Fukai et al., 2009). Biotechnological approaches have also had little impact on the development of improved cultivars, largely because the key mechanisms conferring improved drought resistance have not been clearly identified and few highly resistant donor varieties have been identified. Recently, however, research breakthroughs have revived interest in drought

resistance breeding and the use of new genomics tools to enhance crop water productivity. In rice, these breakthroughs include particularly

- Sequencing of the rice genome and the development of new genomics and post-genomics tools for detecting genetic polymorphisms, discovering genes, and functionally analyzing stress-related genes and mechanisms (IRGSP, 2005; McNally et al., 2009).
- The development of repeatable and predictive field screening methods suitable for use in breeding programs, and the prospects for new high-throughput and precise phenotyping under drought (Campos et al., 2004; Granier et al., 2006; Serraj and Cairns, 2006).
- Proof of concept that conventional breeding based on direct selection for yield under artificially imposed drought stress can result in actual gains in drought resistance (Venuprasad et al., 2007; Kumar et al., 2008; Lafitte et al. 2006; Jongdee et al., 2006).
- Identification of varieties and breeding lines with high drought resistance for use as donors in breeding and gene discovery (Verulkar et al. 2010; Ouk et al., 2006; Toojinda et al., 2005; <http://koios.generationcp.org/drought>).
- Localization of quantitative trait loci (QTLs) with large effects on yield under drought stress that may be useful in marker-aided backcrossing (Bernier et al., 2007; Venuprasad et al., 2009; Yue et al., 2005), and the development of near-isogenic genetic stocks that could be used to dissect the physiological and molecular mechanisms of drought resistance (Li et al., 2005; Lafitte et al., 2006; Bernier et al., 2009).
- Identification of genes and transcription factors from other plant species that may potentially improve drought resistance, if transferred to rice (see Yamaguchi-Shinozaki and Shinozaki, 2006 for a review).

These advances have set the stage for the development of varieties that can double the yield of current widely grown rainfed rice varieties such as IR64, IR36, Swarna, and Sambha Mahsuri under severe drought stress, but also have equivalent yield potential in high-rainfall years. Such varieties would have large effects on poverty alleviation by protecting food supply and income in drought years. Because of the reduction in risk of crop failure that would result from their adoption, they would also increase productivity and income in favorable years by encouraging farmers to increase investment in yield-enhancing inputs. In addition, any development of drought-adapted rice varieties for South and Southeast Asia will also affect rice production in sub-Saharan Africa, where rice consumption is growing faster than anywhere else in the world, and where government policies are moving the continent rapidly away from imports and toward self-sufficiency.

Thus, rice cultivars combining improved drought resistance with responsiveness to favorable conditions are among the most promising and deliverable technologies for alleviating poverty.

#### 4. Critical research issues

##### (1) Drought characterization and matching the phenotype to the environment

Drought occurring at different stages in crop development in different soil types and under various management regimes affects crop growth differently; hence, particular patterns of drought occurrence may require different sets of adaptive traits. For example, some drought resistance traits and mechanisms affecting performance in upland systems may not be relevant under transplanted lowland systems. The timing, severity, and frequency of occurrence of drought stress must be modeled using available information on rainfall, soils, topography, and cropping patterns in the major rainfed rice-growing areas and used to identify combinations of traits and types of germplasm that fit the target environment.

The large genotype-by-environment ( $G \times E$ ) interactions observed in drought-prone environments have stymied progress in exploiting drought traits in the past because the expression of genetic effects was unreliable.  $G \times E$  for drought traits results to a large extent from the variation in the weather patterns among growing environments. The impact of any given drought trait is usually highly sensitive to the rate at which the drought develops, when in the season it develops, and its severity. A drought trait that might offer substantial benefit in one weather scenario might well result in a negative response in another (Sinclair and Muchow, 2001). Simulation models provide a tool to combine mechanistic understanding of a drought trait with a range of weather scenarios (Hijmans and Serraj, 2009). Given a historical record of weather for a location, the probability of a yield increase (or maybe a decrease) resulting from the incorporation of any trait into the crop can be simulated. Combining the probabilities for yield change with understanding of growers' tolerance for risk would help breeders to assess the desirability of incorporating a particular drought trait in cultivars to be grown at a specific location. A good example was recently provided by the integration of short-term physiological responses of leaf growth to drought into whole-plant and crop-level modeling in maize (Chenu et al., 2008).

##### (2) High-throughput and precise phenotyping predicts crop performance

Although these advances have fulfilled some of the requirements toward the development and deployment of drought-resistant rice varieties, important bottlenecks remain. The rapid progress made in rice genomics must be matched with a better understanding of drought

physiological mechanisms and their relationship to the performance of varieties in drought-affected farmers' fields. The identification of donors, mapping, and use in marker-aided breeding of QTLs and genes that affect performance under stress, and screening of improved varieties in NARES breeding programs, all depend on the development of repeatable, low-cost, high-throughput phenotyping procedures that reliably characterize genetic variation for drought resistance and its component traits (Serraj et al., 2009b). Therefore, a special effort is needed for the conceptualization, design, and management of phenotyping programs for drought resistance, to maximize the chances of identifying donors, QTLs, and breeding lines that will be useful in the future improvement of drought resistance in the target environment.

### (3) Identifying donors of genes and QTLs for drought resistance

Even though rice is more sensitive to water deficits than other cereals, large genotypic variation in drought resistance still exists within the cultivated rice gene pool and its wild relatives (Lafitte et al., 2006; Jongdee et al., 2006; Liu et al., 2004). Because of the difficulty of screening for drought resistance in conventional breeding programs, marker-aided breeding (MAB) using QTLs with large effects on drought resistance is among the most promising routes to the development of cultivars with improved yield in drought-prone environments. Progress in breeding and identifying genes for drought resistance will result from the identification of traditional and improved varieties and wild species accessions that have unusually high drought adaptation or traits that can contribute to it. Some potential donors have had their drought resistance confirmed by researchers at IRRI and other institutions (<http://koios.generationcp.org/drought>), but many more are needed to serve as sources of useful alleles for breeding programs. To date, several QTLs with large and consistent effects on grain yield under drought stress have been identified at IRRI. Many more such QTLs are likely to exist. They must be fine-mapped and their effects assessed in a range of backgrounds and environments for deployment in MAB.

## 5. A strategy for improving drought resistance

The overall goal of IRRI's strategy for improving drought resistance is to develop new rice genotypes that can potentially double yield under drought stress in rainfed environments. In addition to the recent path to success in conventional breeding for drought resistance based on direct selection for yield (Kumar et al., 2008) and the promising progress being made in QTL mapping (Bernier et al., 2007), the strategy for improving drought resistance in rice aims to harness recent scientific breakthroughs in breeding and biotechnology and the wide genetic diversity in rice to develop and deliver

improved drought-resistant rice varieties through the following approaches.

### (1) Marker-assisted selection (MAS)

As conventional breeding attempts to select simultaneously for more and more target traits, there tends to be an overall loss of breeding gain and an increase in the number of breeding cycles required to generate a finished product. In contrast, MAS offers the potential to assemble target traits in the same genotype more precisely, with fewer unintentional losses in fewer selection cycles (Xu and Crouch, 2008). In this way, target traits can be selected indirectly using molecular markers that are closely linked to underlying genes or that have been developed from the actual gene sequence (Xu and Crouch, 2008). Drought has been a trait difficult to manage through the conventional phenotypic selection and is one of the most ideal traits for improvement through MAS (Collins et al., 2008; Serraj et al., 2005). When breeding systems are adapted to make best use of large-scale genotyping for both multiple target traits and the genetic background. The recent, identification of major QTLs governing grain yield under drought (Bernier et al., 2007; Kumar et al., 2007; Venuprasad et al., 2009) has made possible the use of MAS for improving drought resistance.

Progress in mapping QTLs for secondary traits associated with drought resistance has been extensively reviewed (Bernier et al., 2008; Kamoshita et al., 2008), but MAS for such QTLs has not been successfully used to improve yield under drought stress in rice. Two recent reports indicated that QTLs with large effects on yield under drought stress may not be rare. Bernier et al. (2007) reported a QTL on chromosome 12 in a Vandana/Way Rarem population explaining about 51% of the genetic variance for yield under severe upland drought stress over two years. Kumar et al. (2007) reported a major QTL for grain yield under lowland drought stress in a CT9993/IR62266 population on chromosome 1 explaining 32% of the genetic variance for the trait over two years.

With the prevalence of a few mega-varieties being cultivated on millions of hectares in major drought-prone areas in eastern India and northeastern Thailand, the two major drought-prone areas in the world, identifying major QTLs for grain yield in the background of improved mega-varieties and introgressing the identified QTLs in the same background to improve the drought resistance of current mega-varieties have been suggested as an alternative approach. Recently, Venuprasad et al. (2009), using this approach and bulk segregant analysis, identified two major QTLs located on chromosomes 2 and 3 for grain yield under lowland drought and one QTL on chromosome 6 for yield potential and tolerance of aerobic soil conditions. These QTLs have been identified in the background of drought-susceptible variety Swarna, grown on millions of hectares in India, Nepal, and Bangladesh, and they are

being introgressed using MAB to improve the drought resistance of Swarna.

Progress has been made with the introgression in rice of the major genes for improving tolerance of bacterial leaf blight, brown spot, brown planthopper, and several other traits. However, there are only a few reports of the introgression of major QTLs in rice. Recently, *SUB1*, a major QTL for submergence tolerance (Xu et al., 2006), has been introgressed into Swarna, Sambha Mahsuri, IR64, and BR11 mega-varieties (Septiningsih et al., 2009). In the case of drought, QTLs related to grain yield under drought stress have been reported on numerous occasions in rice (Babu et al., 2003; Lafitte et al., 2004; Lanceras et al., 2004; Bernier et al., 2007; Kumar et al., 2007), but there have been no reports of the successful use of such QTLs in MAS (Bernier et al., 2008). The lack of repeatability of QTL effects across different populations (QTL x genetic background interactions) and across environments (QTL x environment interactions) are the two factors limiting the use of QTLs for MAS by plant breeders (Price et al., 2002; Courtois et al., 2003; Lafitte et al., 2004; Bernier et al., 2008).

Although the physiological basis of the recently identified major QTLs for yield under drought is still unknown, they have great potential for improving the drought resistance of mega improved varieties such as cultivar Swarna (Venuprasad et al., 2009), through introgression of the identified region after fine mapping. Similarly, grain yield and drought resistance of upland cultivars can be improved using major QTLs for grain yield under upland drought stress (Bernier et al., 2007) by marker-assisted recurrent selection (MARS).

## (2) Application of association studies

An association approach is being applied in rice to determine correlations between molecular variation within drought-responsive candidate genes and phenotypic responses to drought stress. A mini-core collection of representative accessions was selected from the International Rice Genebank. These accessions were contained in a larger set that has been genotyped with 48 SSR markers and its population structure was determined using Instruct (Gao et al., 2007) with good correspondence to varietal groups and structure previously identified (Glaszmann, 1987; Garris et al., 2003). Candidate genes related to drought stress were identified by converging evidence from expression analyses including transcriptomics and proteomics, functional annotation including evidence from other species, and co-localization with QTLs and allele frequency shifts under selection. Eight candidate genes with strong evidence of their involvement in drought stress were selected and natural molecular variation within the mini-core collection was determined using agarose-based EcoTILLING (Raghavan et al., 2007) in samples contrasted independently against

Nipponbare (japonica type) and IR64 (indica type). Representative samples were sequenced to validate and identify corresponding SNPs. Haplotypes obtained based on scores of the two contrasts were largely supported by sequence data. The mini-core collection was stratified into varietal groups by the structure analysis with each group partitioned into haplotypes.

Accessions were phenotyped under field conditions over three consecutive dry seasons. The large variation in days to flowering (99 days) made it unfeasible to apply drought stress at flowering for all accessions; therefore, stress was imposed at the vegetative stage and secondary traits associated with performance under drought stress (plant water status, biomass accumulation, and flowering delay) were measured. Large phenotypic variation for drought resistance was observed within each subpopulation. The magnitude of significant differences between haplotypes within varietal groups was highest for the AP2 domain transcription factors, consistent with their potential effect on multiple drought traits. Only rare haplotypes were observed for TPP (trehalose-6-phosphate phosphatase) and the primary haplotype was shared across varietal groups, suggesting that this locus is under intense selection (IRRI, unpublished).

A major drawback of targeted genotyping is the need to identify candidate genes before screening whereas drought stress affects thousands of genes. Whole genome scans can detect new regions associated with interesting phenotypes by testing the association of SNP variation with contribution to the trait. The OryzaSNP project ([www.oryzasnp.org](http://www.oryzasnp.org)) has discovered 160,000 SNPs across the rice genome in 20 diverse rice varieties (McNally et al., 2009). IRRI is working with Cornell University and other partners to develop a high-density genotyping platform for querying 600,000 SNPs from the OryzaSNP and other projects. This platform will be used to genotype at least 2,000 diverse accessions that will also be phenotyped for a range of traits, including drought resistance, allowing whole-genome associations to be performed. Success of this approach will depend on developing methods and designs for accurate drought phenotyping that will not be compromised by extreme differences in phenology.

## (3) Gene discovery and transformation

The development of transgenic rice with improved drought resistance can be achieved through two complementary approaches: (i) mobilizing genes for resistance within rice germplasm using high-throughput QTL analysis and allele mining leading to map-based cloning of rice alleles affecting growth and yield under drought stress, and (ii) exploiting in rice sequences demonstrated to enhance drought resistance in other species.

Rice germplasm has extensive unexploited variation for drought resistance. IRRI research has shown that variation

for the trait can be strongly influenced by alleles of a relatively small set of QTLs with large effects. We have developed efficient “selective genotyping” strategies that allow many potential donors to be searched quickly and inexpensively for these valuable genes (Navabi et al., 2009). This allows the search for useful alleles to be quickly narrowed down to small chromosome segments suitable for bioinformatics analysis. This approach, begun at IRRI in 2003, has already led to the identification of three genomic regions with large effects on yield under severe upland drought stress, one of which has been localized to a chromosome interval of less than 10 cM.

Genes and their control sequences previously determined to improve drought resistance in other species are also of potential value in rice, and will be evaluated using high-throughput transformation and phenotyping systems (Hervé and Serraj, 2009). Sequences licensed from both the public and commercial sectors and already proven to enhance performance under drought stress will be evaluated using this approach to assess the effect of these sequences on a range of drought-related traits, and move the most promising ones into widely grown, high-quality rice mega-varieties.

Additionally, the increasing appreciation of variation occurring through molecular evolutionary processes such as exon-shuffling and differential gene splicing, which cannot be effectively captured by transcriptome analysis, will be captured through proteome analysis. This will form an important part of gene discovery programs that will simultaneously address protein post-translational modifications (PTM), including protein oligomerization.

Differential PTM of some genes under different environmental conditions have been shown to be responsible for altered activity response (North et al., 2005). Preliminary studies on proteomic response to drought and salt stress in rice at IRRI revealed that, apart from an increase in abundance of some stress-responsive proteins, certain other proteins exhibited altered electrophoretic mobility, indicating altered status of PTM (Salekdeh et al., 2002). Manifestation of PTM-mediated responses through protein oligomerization is now being recognized as an important component of biotic and abiotic stress responses. A number of proteins exhibit differential oligomerization, which is commonly dependent on cell redox status, which in turn is highly affected under stress conditions. For example, NPR1, a master regulator of salicylic acid-mediated plant defense genes in biotic stress (Tada et al., 2008), and SAP12, an abiotic stress-inducible plant gene (Stroher et al., 2009), are both affected in quaternary structures under variable redox environments. An important family of proteins whose hetero-dimerization under variable redox regimes may dictate cellular responses to stress conditions is the bZIP family of plant proteins (Amoutzias et al., 2006).

Similarly, heat-stress transcription factors (HsF) undergo variable homo- or hetero-oligomerization in response to heat stress (Baniwal et al., 2007). Other proteins responsive to stress through differential oligomerization will be captured through advanced proteomic techniques.

The availability of saturated transposon insertion-mediated knockout rice libraries with IRRI collaborators in France, Korea, and Taiwan may provide another route to gene discovery for drought resistance under appropriately standardized phenotyping screens. Finally, *in silico* neural network-mediated analysis of the promoter sequences of various known drought-responsive genes used as bait will help discover additional and novel genes tightly co-regulated under drought stress.

Novel genes identified as useful in enhanced drought resistance will need to be transformed, most likely as a suite of genes. The general approach on transgenic rice for improving drought resistance has been recently reviewed (Hervé and Serraj, 2009). IRRI has also undertaken research on multigene and targeted gene delivery methods, which could be used to deliver transgenes at chosen positions in the genome to minimize position effects associated with transgene expression (Kohli et al., 2006). The drought resistance genes located by these approaches at IRRI are and will be international public goods that are freely available to IRRI's clients and stakeholders.

#### (4) Physiology and high-throughput phenotyping

In order to identify sources of drought resistance, it is necessary to develop screening methods that are simple, reproducible, and predictive of performance in the target environment. Therefore, managing drought-screening nurseries requires a careful analysis of likely sources of non-genetic variation among plots, replications, and repeated experiments, and establishing procedures for minimizing these factors. Detailed information about the spatial variability of different soil characteristics within a field is essential for improving the precision of phenotyping. New precision-agriculture sensors and technologies can be used for soil mapping based on physical and chemical properties using electrical and electromagnetic sensors (Adamchuk et al., 2004). IRRI is now using these technologies (e.g., EM-38) for mapping the mechanical, physical, and chemical soil properties of the drought-phenotyping fields at the IRRI station and at multi-location screening sites in South Asia.

The physiological mechanisms of “drought tolerance” remain elusive and little progress has been made in crop improvement using plant survival strategies under severe stress (Serraj and Sinclair, 2002). Dehydration avoidance is more relevant as a strategy for combating agricultural drought and maintaining crop performance, before survival drought develops. In rice, the conclusion emerging from long-term multi-location drought studies

was that rainfed lowland rice is mostly a drought avoider, with the genotypes that produce higher grain yield under drought being those that are able to maintain better plant water status around flowering and grain setting (Fukai et al., 2009).

IRRI is using several field and laboratory screening methods for phenotyping rice germplasm for drought resistance with a focus on dehydration avoidance (Serraj et al., 2009b; Bernier et al., 2009; Farooq et al., 2010; Parent et al., 2010), including drip and line-source sprinkler irrigation systems (Centritto et al., 2009), drained paddies, and the development of remote-sensing techniques for monitoring plant water status in the field (Jones et al., 2009). Further in-depth research is needed to identify the physiological bases for differences in genotype performance in these screens, as well as the relationship to performance in farmers' fields under naturally occurring drought-stress scenarios.

#### **(5) Development and delivery of productive, high-quality "platform" varieties**

Farmers require much more than drought resistance from a variety. Only varieties that combine drought resistance with high yield potential in favorable seasons, high quality, and resistance to diseases and pests will be adopted by farmers. Highly stress-tolerant lines that are deficient in many other aspects will be rejected by farmers and these lines are not usable as donors in national breeding programs. IRRI will develop elite breeding lines that can be delivered to breeders and farmers. These varieties will have drought resistance alleles identified through genetic analysis and functional genomics research. Some hybrids have been shown to be more resistant to water and nutrient deficiency than pure lines (IRRI, unpublished) and stress-resistant hybrids are therefore a promising "delivery platform" for drought resistance genes.

The products from drought resistance improvement must be proven in the target environment and adopted by farmers in order to have impact. However, the breeding process itself has limits in achieving that goal. Germplasm selection is usually conducted on-station under standardized conditions, including much higher input use and crop management intensity, often not representative of the conditions in farmers' fields. Critical factors for the adoption of new varieties may be varietal traits difficult to capture in the selection process, such as weed competitiveness, performance on poor soils and under widespread crop management constraints, and a range of post-harvest characteristics such as straw quantity, harvestability, storability, and cooking/eating quality. Therefore, the most promising drought-resistant breeding lines are evaluated with farmers in farmers' fields through participatory varietal selection, using the "mother and baby trial" methodology (Snapp, 2002). In addition, promising

breeding lines need to be tested in conventional agronomic trials under the most common crop management constraints occurring in the target environments, for example, late transplanting, beushening, and low nutrient availability.

#### **(6) Agronomic management for drought-prone lowland rice**

An improved germplasm is without a doubt a critical step to significantly reducing risk and increasing productivity in drought-prone rice-based lowlands, but optimal use of new germplasm will require a combination with adequate, improved management techniques. Management strategies for alleviating drought stress are either to escape drought (by increased water input or by avoiding dry periods) or to moderate drought by reducing nontranspirational outflows so that more water is left for transpiration. Bouman (2007) and Debaeke and Aboudrare (2004) systematically described generic options to implement these strategies.

Irrigation is, of course, the most obvious way to avoid drought, and this approach was practiced in many previously purely rainfed lowland systems. Examples are the establishment of large numbers of tube wells in eastern India and Bangladesh (Singh et al., 2003) or the establishment of village or farm ponds for rainwater harvesting in northeast Thailand, some regions of eastern India, the Philippines, and Indonesia (Patamatamkul, 2001; Bhuiyan, 1994; Pal and Bhuiyan, 1995). Such measures can still help to reduce drought damage in many regions but government coordination is needed to ensure a sustainable use of available water resources and to help with the investment and infrastructure needed. Given the large area of rainfed lowland rice, irrigation will not be the most feasible option in the near future.

Drought escape can be achieved by adjusting the cropping season to the time when water availability by rainfall is best, which is usually accomplished by reducing the length of the cropping season with the help of shorter-duration varieties. This option still has considerable potential in some rainfed lowlands but breeders need to balance the benefits from shorter duration with the various other demands on varietal characteristics by farmers and the environment.

The most important management components to avoid drought damage are target crop establishment and crop nutrition. Transplanting rice seedlings remains the preferred crop establishment practice in many drought-prone rainfed lowlands despite higher unproductive water losses from deep percolation and evaporation before crop establishment (Haefele and Bouman, 2009), and the danger of yield losses if delayed rainfalls cause the transplanting of old seedlings. Improved seedbed management, including lower seed density and some fertilizer application (IRRI, unpublished), together with

germplasm having some tolerance of late transplanting, could help to reduce yield losses in transplanted systems.

Direct seeding (dry seed in dry or moist soil) makes much better use of early rains and reduces the risk of damage from late-season drought (Haefele and Bouman, 2009). It also often leads to deeper, finer, and more extensive root development and, as a result, better performance under drought conditions (Fukai et al., 1998). Direct seeding requires less labor than transplanting or biasi and is the main driver for technology adoption in several Asian countries (Pandey and Velasco, 2002). Disadvantages of direct seeding include possibly higher deep percolation rates in unpuddled soils during the growing season, and an increased risk of suboptimal crop establishment due to drought spells immediately after seeding. Also, good weed management is much more important in direct-seeded rice because the rice plants have no size advantage over the germinating weeds and there is no flood layer suppressing weeds as is the case in transplanted rice fields (Johnson et al., 2008). Thus, the successful use of direct seeding depends strongly on the parallel introduction of suitable weed management technologies, including herbicides. On heavy-textured soils, dry direct seeding in dry soils is not possible without mechanized soil preparation, and suitable drill-seeding equipment can further facilitate direct seeding.

The other important management component for moderate drought is nutrient management. Drought is directly linked to crop nutrition through different processes. The uptake of several nutrients (e.g., N, Ca, Mg, Na) is usually dominated by mass flow with the transpiration stream; thus, lower transpiration means lower nutrient uptake. But, lower soil moisture also reduces nutrient diffusion to the roots (especially important for P and K) because the diffusion coefficient decreases. Further on, the change from an anaerobic soil to an aerobic soil generally reduces the availability of N, P, Fe, Si, Mn, and Mo, but increases the availability of S, Zn, and Cu (Ponamperuma, 1978). And, because reduced transpiration and nutrient uptake cause lower (root) growth, access to water and nutrients gets further restricted. Apart from these processes, crop nutrition in the rainfed lowland environment is disadvantaged because of the widespread occurrence of poor to very poor soils, and the generally low application rates of inorganic fertilizer. Consequently, nutrients were repeatedly recognized as a major limiting factor in many rainfed lowlands (Van Bremen and Pons, 1978; Wade et al., 1999).

Improved crop nutrition can therefore moderate the negative effects of drought on crop growth and production by alleviating the nutrient limitation caused by drought and natural soil fertility. Better root growth can contribute to a better use of available water and nutrient resources. And, above ground, better growth and faster development

of a closed canopy lead to reduced evaporation and increased transpiration, which in turn are linearly related to biomass accumulation (Bouman, 2007; Haefele et al., 2009). Fertilizer treatment and related plant biomass should not affect drought risk as long as the soil surface is wet, that is, in short drought spells, because total evapo-transpiration will be similar for fertilized and unfertilized treatments. However, in longer drought spells or terminal drought, when the soil surface becomes dry and evaporation very low, a larger canopy will cause higher total evapo-transpiration. This could lead to a faster decline in remaining plant available water and higher drought damage, a phenomenon called “haying-off” and described for upland crops relying mostly on water stored in the soil (Cantero-Martinez et al., 1995). Crop growth simulation models could offer an option to better evaluate such water-by-nutrient interactions in a variety of typical rice environments (Boling et al., 2007).

Several studies indicated that fertilizer use in drought-prone lowlands seems to be as effective as in irrigated systems, provided that the drought is not extreme and that adjusted nutrient management options are used (Linguist and Sengxua, 2003; Haefele et al., 2008). Necessary adjustments are generally lower fertilizer rates because of lower achievable yields (limited by water and not radiation) and more flexible application schedules because water limitation might occur at the ideal application time (Linguist and Sengxua, 2003; Haefele et al., 2009). Farmers will also need more site-specific advice to manage the spatial variability of available water and nutrient resources within the toposequence. In addition, several studies indicate that P has a more important role in drought-prone rice environments because its availability and uptake are more affected by water stress than N and K (O'Toole and Baldia, 1982; Suriya-arunroj et al., 2000).

#### **(7) Training of the next generation of rice scientists**

Capacity building of NARES has been one of the major reasons behind the historical successes achieved in crop improvement and agricultural research in Asia. For drought research, a tremendous amount of work has been accomplished over the past decade in training rice scientists in biotechnology and its application in plant breeding, with support from donors such as the Rockefeller Foundation and the Generation Challenge Program. However, these efforts need to be sustained and extended to new areas in Asia and sub-Saharan Africa. The program on improving drought resistance should closely involve NARES in capacity building, to increase the number of local rice scientists (breeders, agronomists, molecular biologists) with applied experience in drought breeding and foster the development of a community of practice in the use of upstream tools and best drought-resistant germplasm. On-the-job training for new rice scientists joining NARES through regional, international,

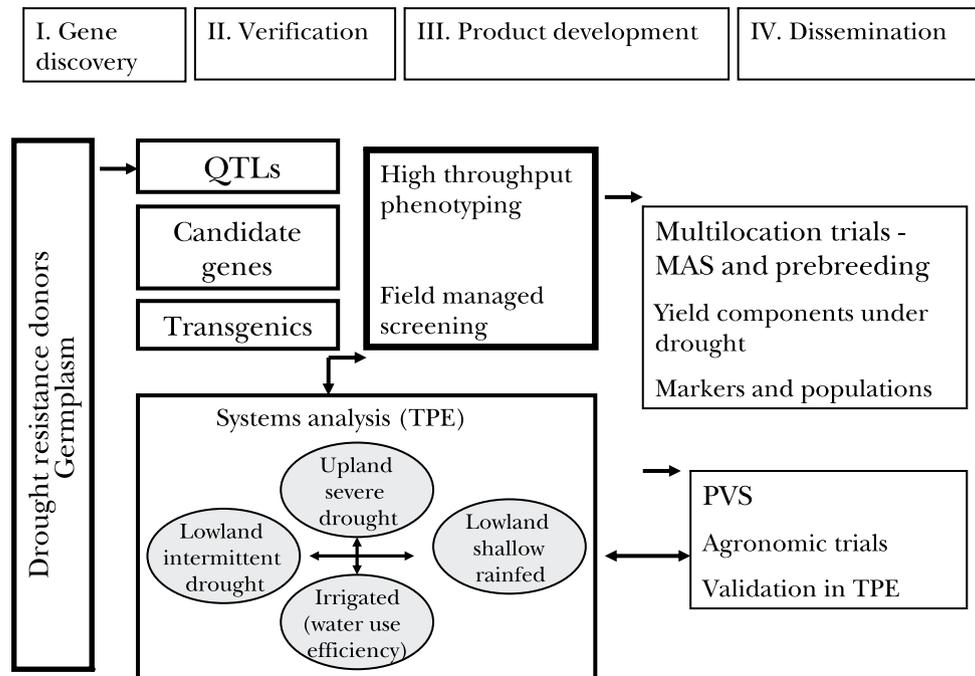


Fig. 1. Framework and pipeline of an integrated strategy for genetic enhancement of drought resistance in rice. The strategy involves the identification of drought resistance donors, major QTLs, candidate genes and transgenics, testing in high throughput phenotyping platforms and field managed stress screening, and validation in the target population of environments (TPE) with systems analysis. The advanced breeding lines and products are further tested in large-scale multilocation trials in collaboration with NARES partners, and in farmers' fields using participatory varietal selection (PVS) and agronomic management trials.

and South-South cooperation should be provided. Building on the past successes and achievements of the RF-funded Indian drought breeding network, NARES should be invited to contribute their breeding lines to the collaborative trial networks across South and Southeast Asia and sub-Saharan Africa.

#### (8) Products, outputs, and research partnership

Building on the recent successes and achievements, the pipeline for improving drought resistance aims at integrating the various approaches and methodologies involved in crop improvement (Fig. 1), to deliver drought-resistant varieties and technologies (Serraj and Atlin, 2009). These efforts include varietal development, genomics and functional genomics, resource management, and research on social sciences and complementary practices. IRRI researchers have developed effective screening methods for identifying drought-resistant varieties, which are being applied to develop drought-resistant cultivars in close collaboration with NARES (Verulkar et al., 2010). Low-cost, high-throughput QTL mapping approaches are also being used to detect and fine-map genes with large effects on drought resistance, with the result that several major QTLs have been recently identified in resistant x susceptible crosses (Bernier et al., 2007; Venuprasad et al., 2009).

The rice gene bank at IRRI, with its 110,000 accessions from 85 countries, is a prime potential source of useful genetic variation for drought resistance. IRRI also has a large collection of wild *Oryza* species and populations of introgression lines, and mutants in the background of IR64, one of the world's most widely grown rice cultivars. IRRI has also developed a large set of near-isogenic stocks for genetic and functional genomics analysis. Identification, mapping, and deployment in MAB of genes conferring improved drought resistance depend on the development of stocks that are identical in most of their genes but that differ substantially in performance under drought stress. These NIL stocks eliminate much of the background variability in gene expression patterns that exists between more distantly related materials, and allow the traits and genes associated with stress resistance to be clearly identified.

Linking researchers in innovative partnerships with extension services and the commercial seed and input supply sectors will be crucial for the multi-location evaluation of drought-resistant varieties under the real conditions faced by farmers. Breeding programs in drought-prone regions are organized into networks of centers that collaborate in multi-environment and managed-stress testing to identify drought-resistant

genotypes. Research and extension institutions from the NARES in Asia and Africa play a central role in doing the field research and disseminating its outputs to farmers and end-users. The drought breeding network initially coordinated in India has been recently expanded to NARES institutions in Bangladesh, Nepal, Thailand, and East Africa. Lines and hybrids proven to combine resistance and yield potential in on-station trials are evaluated on-farm in participatory varietal selection programs managed by the partner centers, using the mother-baby trial model. Once varieties are released by national systems, they are delivered via targeted dissemination to farmers who are facing water shortage, in collaboration with governmental and non-governmental extension and community development partners, including private-sector seed companies. Collaboration with private-sector companies will mainly aim at the exploitation in rice of genetic sequences and products with demonstrated drought resistance characteristics. The regional research networks, such as the Consortium for Unfavorable Rice Environments (CURE) and the drought breeding networks are actively involved in the planning and implementation of the program on improving drought resistance in rice.

## 6. Conclusions and future prospects

The recent advances in our understanding of the physiology and genetics of drought resistance, and the integration of highly efficient breeding and genetic analysis techniques with the power of functional genomics, contribute to the improvement of drought resistance in rice. The strategy described in this paper aims at developing a pipeline for elite breeding lines and hybrids that can be integrated with efficient management practices and delivered to rice farmers. The important steps involved in this multidisciplinary strategy are to

- Define precisely the target drought-prone environment(s) and delineate the predominant type(s) of drought stress and the rice varieties preferred by farmers.
- Characterize the phenological, morphological, and physiological traits that contribute substantially toward adaptation to drought stress(es) in the target environment(s), with a major focus on dehydration avoidance and water productivity processes.
- Use simulation modeling and systems analysis to evaluate crop response to the major drought patterns, and assess the value of candidate physiological traits and their relationship with crop productivity in the target environment.
- Develop and refine the phenotyping methodologies for characterizing genetic stocks that could serve as donors, characterizing the effects of genes and QTLs, and selecting cultivars with resistance to specific stresses.
- Identify, map, and tag marker-aided breeding QTLs within the rice germplasm that are critical for drought resistance, and incorporate them into locally adapted varieties.
- Harness functional genomics, transgenics, and reverse genetics tools to understand the genetic control of the relevant traits, and evaluate the effect in rice of sequences known to affect drought resistance in other species by transforming high-yielding but drought-susceptible varieties.
- Develop near-isogenic versions of important but drought-susceptible varieties containing QTLs/genes that affect specific traits of interest to assess their value in improving drought adaptation of locally adapted varieties.
  - Test the advanced marker-assisted selection products both in well-managed screening facility (rainout shelters) and in farmer participatory multi-location trials.
- Develop flexible and site-specific crop management options with a focus on crop establishment, weed management, and nutrient management, which help farmers to address the large spatial and temporal variability of rainfed rice environments.
- Evaluate promising germplasm for typical management constraints occurring in drought-prone lowlands (e.g., late transplanting, direct seeding, high weed pressure, low nutrient availability).

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