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Sustainable Rice Yield in Water-Short Drought-Prone Environments: Conventional and Molecular Approaches

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1. Introduction

The growing human population is putting enormous pressure on food security. Agriculture has to respond to this increased food demand by producing more from shrinking land and water resources (Pimentel et al., 1997). The climate change process has caused unpredictable and uneven rainfall patterns, resulting in more competition for water resources for crop cultivation and other socioeconomic uses (Hossain, 1995; Alcamo et al., 1999). Rice is one of the major staple food crops for more than a third of the world's population (David, 1991). It is mostly grown in well-puddled and irrigated conditions, and requires two to three times more water than other food crops such as wheat or maize. In total, rice production in the world uses about 1,600 km³ of water, which accounts for 30% of the fresh water used worldwide (Gleick, 1993). There is an urgent need to increase rice production to meet global demand. It is estimated that the world needs to produce 40% more rice to feed the population by 2025 (FAO, 2002). With the grain yield in irrigated areas reaching stagnation, a large portion of the predicted increase has to come from the water-short drought-prone rainfed lowland and upland rice areas. Rainfed lowland and upland areas occupy about 38% of the total cropped rice area but contribute only 21% to total rice production (Khush, 1997). The lower contribution of the water-short drought-prone rainfed areas to total rice production is due to the lower per unit productivity primarily caused by the frequent occurrence of drought due to a failure of rain or a long spell between two rains. Drought has been identified as the key factor for low productivity in the rainfed ecosystem (Zeigler & Puckridge, 1995). Drought is particularly more frequent in South and Southeast Asia and sub-Saharan Africa, and the ongoing climatic change process is likely to further worsen the scenario in these rice-growing areas. In Asia alone, about 34 million ha of rainfed lowland and 8 million ha of rainfed upland rice experience drought stress of varying intensities at different stages of the crop almost every year (Wopereis et al., 1996; Huke & Huke, 1997). Most of the rice varieties presently cultivated in rainfed areas were developed for irrigated conditions. These varieties are highly popular among farmers because of their high yield potential and good grain quality but are highly susceptible to drought, causing substantial yield losses during years of drought. Breeding rice varieties with increased yield under drought is an important research area to achieve sustainable rice production under water-

short situations. The drought breeding program at the International Rice Research Institute (IRRI) aims to develop high-yielding, drought-tolerant cultivars with good grain quality for rainfed lowland and upland ecosystems by following two-pronged modified conventional and molecular breeding approaches. In this chapter, we discuss in detail the progress achieved in the application of conventional and molecular approaches to develop drought-tolerant rice cultivars suitable for cultivation in water-short rainfed areas.

2. The major drought-prone rice ecosystems

Rice ecosystems are mainly classified into four types: irrigated, rainfed upland, rainfed lowland, and deepwater. Rainfed upland and lowland ecosystems are highly drought prone because of their uneven topography and heavy dependence on rainfall for the water source. Rainfed upland rice constitutes 13% of global rice production area and is generally the lowest yielding ecosystem. The main features of upland area are non-bunded fields, no/poor accumulation of water, low-input production practices, and cultivation of rice by direct seeding. Most of the rice varieties grown in upland areas are traditional landraces/varieties, low-yielding, prone to lodging, but adapted to aerobic soils. Upland rice is highly prone to drought because of poor accumulation of water in the field due to uneven upper toposequence, absence of bunds, and lower water-holding capacity of the soil (Serraj et al., 2009). Grain yield in the upland ecosystem is the lowest because of poor soil fertility, frequent occurrence of drought, high weed infestation, and low input use. Upland rice is mostly grown by small or subsistence farmers in the poorest region of Asia, Central and West Africa, and Latin America. India and China are the two countries with the largest area under upland. Indonesia, Thailand, the Philippines, Vietnam, Laos, and Myanmar (Burma) are the other countries practicing rice cultivation in the upland ecosystem.

Rainfed lowland rice is the second most important rice ecosystem after the irrigated ecosystem and it represents about 25% of total rice production area. The main physical features of the rainfed lowland rice areas are bunded fields, complete reliance on rainfall or drainage from higher lands for a water source, and variable soil water-table depth depending on the position of the field in the toposequence. Most of the rainfed lowland area is located in South and Southeast Asia, with the largest area of approximately 14.4 million hectares in India. Thailand, Bangladesh, Indonesia, and the Philippines are other countries with large rainfed lowland rice cultivation area. More than 90% of the area planted to rainfed lowland rice is in Asia. The yield of rainfed lowland rice is low and varies from 1.5 t ha⁻¹ in Cambodia to 3.0 t ha⁻¹ in Indonesia. In East Africa, around 70% of the cultivated rice area is rainfed lowland. Depending upon the toposequence, rainfall pattern, and amount of total rainfall received, rainfed lowland has been further classified as drought-prone shallow lowland, favorable shallow lowland, drought-prone mid-lowland, favorable mid-lowland, and flood-prone mid-lowland. Favorable rainfed areas account for about 20% of the total rainfed lowland area (Mackill et al., 1996). The frequency and severity of drought decreases from shallow to mid-lowland. Within the rainfed lowland ecosystem, certain regions in eastern India and Bangladesh are prone to both flood and drought at different periods in the same season or in different years depending upon the rainfall pattern. In the rainfed lowland ecosystem, a high association between percentage of rice area under irrigation and rice yield and poverty has been reported in India (Hossain, 1995).

3. Conventional breeding approaches

Drought is the primary limiting factor for rice production in rainfed ecosystems and drought at the reproductive stage particularly causes a severe reduction in grain yield (Cruz & O'Toole, 1984). Due to the inherently high variable nature of rainfed environments, breeding for drought-prone rainfed ecosystems requires strong research commitments for a longer period to see changes in farmers' fields. There are not many examples of concerted and product-oriented long-term breeding efforts that led to a significant yield increase at the farmers' level in rainfed water-short drought-prone environments. Even now, most of the varieties grown in rainfed environments are either high-yielding but drought-susceptible varieties or traditional local varieties/landraces that are drought tolerant but low yielding and poor in grain quality. The varietal characteristics that need to be considered during the development of genotypes for rainfed environments are farmers' preferred grain quality traits, high yielding ability with good drought tolerance, and resistance to/tolerance of prevalent biotic stresses (Atlin, 2003; Kumar et al., 2008).

3.1 Precise phenotyping under drought stress

Standardized phenotyping under well-managed water stress conditions is a prerequisite for the success of a drought breeding program. Drought screening (DS), which clearly distinguishes high-yielding but drought-susceptible lines from drought-tolerant lines, is necessary for effective selection for higher grain yield under drought. A breeding program has to develop a suitable screening methodology depending upon the crop growth stage (seedling/vegetative/reproductive) at which drought occurrence is more frequent and severe in the region. Most breeding programs carry out large-scale screening of breeding/mapping populations in natural field conditions and make an adjustment in date of sowing and planting to synchronize the crop growth stage with the period most likely to have the least rainfall. In recent years, some advanced programs have developed a rainout shelter facility for uninterrupted drought screening. In some cases, a line-source sprinkler irrigation system that allows the development of different severity of stress, along the line away from the source, is also followed (Cruz & O'Toole, 1984; Fukai et al., 1996; Lanceras et al., 2004). The crop growth stage when drought should be imposed in the field depends upon the water-holding capacity of the soil. In general, in upland, drought appears in severe form in 7-10 days after stopping irrigation whereas in lowland it takes 18-21 days for severe drought occurrence. The severity of drought to be applied in a drought screen should be very close to the drought situation prevalent in the region. In a region with moderate drought stress every year, screening under severe drought stress that leads to a significant yield reduction will not be appropriate.

In lowland, in screening experiments, a yield reduction of 30% for regions with mild drought occurrence, a yield reduction of 31-65% for regions with moderate drought occurrence, and a yield reduction of 65-85% for regions with severe drought occurrence have been reported to be appropriate (Kumar et al., 2007). In upland, due to prevalent conditions, drought mostly occurs in severe form and screening under severe drought conditions is recommended. However, for places with favorable rainfall, screening under conditions that bring a yield reduction of 40% or less for regions with mild drought occurrence, a yield reduction of 41-75% for regions with moderate drought occurrence, and a yield reduction of 76-90% for regions with severe drought occurrence will be appropriate.

In drought screens, adequate precautions need to be taken to irrigate the experiments at an appropriate time before drought is too severe to cause a loss of all genetic variability and affect an efficient selection strategy.

Severe drought screening at the reproductive stage is targeted in drought screens at IRRI. In upland screens, to initiate stress, experiments are drained at 35-45 days after seeding depending upon the duration of varieties. Stress plots are irrigated only when the soil water tension fall below -50 kPa at 30-cm soil depth. At this soil water potential, most lines wilt and exhibit leaf drying. This type of cyclic stress is considered to be efficient in screening for drought tolerance in populations consisting of genotypes with a broad range of growth duration (Lafitte, 2003) and ensures that all lines receive adequate stress during reproductive development. In lowland, to initiate stress, the field is drained 25-30 days after transplanting and experiments are irrigated only when the soil water tension falls below -60 kPa at 30-cm depth or alternatively when drought-susceptible checks along with around 70% of the lines show severe leaf rolling at 10 a.m. At IRRI, every season, several mapping and breeding populations are screened under severe reproductive-stage drought stress and the desired yield reductions as compared to yield in irrigated control situation are achieved (Table 1).

S. no.	Population	Sesaon/year	% yield reduction
1	N22/Swarna	2010DS	78
2	N22/IR64	2010DS	82
3	IR77298-5-6-18/IR64	2009DS	80
4	IR77298-14-1-2-10/IR64	2010DS	63
5	Dhagad desi/Swarna	2010DS	65
6	Dhagad desi/IR64	2010DS	66

Table 1. Yield reduction in different populations under managed drought stress

3.2 Use of traditional and improved donors

The selection of parents is an important critical step in breeding for drought tolerance. A large variation exists for drought tolerance in the available rice germplasm (Mackill et al., 1996). Traditionally grown landraces and wild species accessions have high adaptability to drought, and the hidden genetic potential available in these accessions provides a better opportunity to improve the drought tolerance of popular rice varieties. However, most of the drought-tolerant donors used in the breeding programs so far are either from the cultivated rice gene pool or traditional landraces. Even though wild species can offer better genes for drought tolerance, no population with wild species has been developed for drought studies. Wild species such as *Oryza rufipogon*, *O. australiensis*, *O. glaberrima*, and several accessions of rice germplasm consisting of traditional varieties, landraces, and breeding lines were screened at IRRI under drought over the seasons/years to identify new donors. Efforts are also being made to develop wild species-derived populations for selection and qunatitative trait loci (QTL) mapping. Several important drought-tolerant donors such as Apo, Aday Sel, N22, Dular, and Dhagad Desi were identified (Table 2) and used effectively in developing populations to select high-yielding lines under drought following a pedigree breeding approach.

Traditioal donors have largely been low yielding and they carry undesirable linkage drag. Improved donors through pre-breeding between traditional donors and improved cultivars

have been developed. At IRRI, traditional donors are used in developing mapping populations for the identification of major QTLs for grain yield under drought and better segregants combining appropriate plant type, high yield, and drought tolerance identified from such mapping populations are used in breeding programs. These improved pre-breeding lines are crossed with high-yielding drought-susceptible popular varieties and appropriate segregants are selected. With popular high-yielding varieties, such poor-combining donors can also be used in a backcross breeding program and appropriate segregants can be selected from BC₁F₂ or BC₂F₂ generation onwards. Some of the traditional and improved donors that showed consistent performance in drought screening at IRRI are listed in Table 2.

S. no.	Designation	Plant height (cm), non-stress	Days to 50% flowering, non-stress	Grain yield (kg ha ⁻¹), drought
1	IR86931-B-414	95	76	2827
2	IR77298-14-1-2	102	82	2725
3	Aus Bak Tulsi	128	76	2472
4	IR86918-B-382	95	77	2405
5	Aus 299	125	76	2353
6	IR77298-5-6-18	96	85	1171
7	IR77298-14-1-2-10	85	85	1183
8	Kali Aus	103	76	2126
9	IR55419-04	117	69	2128
10	IR80461-B-7-1	120	80	1574
11	IR74371-70-1-1	95	77	1971
13	IR74371-54-4-1	104	78	2131
14	IR81896-B-B-74	120	84	1984
15	IR80461-B-7-1	106	78	1684
16	IR84878-B-60-4-1	78	85	2418
17	IR83380-B-B124-1	76	87	1482
18	IR83373-B-B-24-4	84	82	2271
19	IR71525-19-1-1	127	85	1036
20	Apo	110	84	1125
21	N22	120	75	2992
22	Dhagad Desi	93	84	1482
23	Dular	136	76	1539
24	Swarna (check)	85	115	178
25	IR64 (check)	81	115	342
26	MTU1010 (check)	97	85	542

Table 2. Traditional and improved donors for drought tolerance

3.3 Development of populations

While developing a breeding or mapping population, one of the parents should be a drought-resistant donor and the other parent should be a well-adapted local cultivar. The

selected parents should have good combining ability and complement each other to overcome their specific drawbacks in terms of pest and disease resistance or grain quality. Different breeding populations such as recombinant inbred lines (RILs), backcross inbred lines (BILs), doubled haploids (DH), chromosomal segment substitution lines (CSSLs), and multiparent advanced generation inter-cross (MAGIC)-derived lines are used for breeding drought tolerance in rice. It is always desirable to have a large breeding population as it provides a better chance for breaking linkage drag and to obtain segregants with the right combinations of traits to meet local conditions and farmers' preferences. The population size runs up to 2500 to 5000 F₂ plants in breeding populations and 400 to 500 plants in mapping populations. Backcross-derived populations are more preferred for both breeding and mapping, as they help in the recovery of all the good traits of recipient parents and up to a certain extent break undesirable linkages. MAGIC populations are also being used in drought breeding but the development of populations is laborious. However, this offers the advantages of testing multiple drought-tolerant alleles in a single population and broadened genetic base of the recipient parent. Populations developed by marker-aided recurrent selection (MARS) and genome-wide selection are also being used in drought breeding.

3.4 Grain yield as a selection parameter under drought

In the past, secondary yield component traits and physiological traits such as harvest index, spikelet fertility, root length, root dry weight, root volume, osmotic adjustment, stomatal conductance, and relative water content were used as selection criteria for improving grain yield under drought in rice (Jongdee et al., 2002; Pantuwan et al., 2002). Through selection for secondary traits, desired improvement in grain yield under drought could not be achieved. Several experiments conducted at IRRI and elsewhere have clearly demonstrated that grain yield has moderate to high broad-sense heritability under drought. Further, the heritability of grain yield was comparable with the heritability of secondary yield traits or physiological traits under drought stress (Kumar et al., 2007). An increase in heritability of grain yield with an increase in severity of stress has also been reported (Kumar et al., 2007). Recently, grain yield has been suggested as a selection parameter in drought breeding programs under both upland and lowland situations (Bernier et al., 2008; Kumar et al., 2007; Kumar et al., 2008). By using this approach, improved breeding lines are developed at IRRI and in partner countries such as the Philippines, India, Nepal, and Bangladesh (Verulkar et al., 2010; Mandal et al., 2010). In Brazil and Thailand also, direct selection for yield has been successfully applied in breeding for drought tolerance in upland and rainfed lowland conditions (Ouk et al., 2006).

4. Combining high yield potential with good yield under drought

Farmers in the water-short rainfed drought-prone environment need rice varieties that provide high yield in seasons with good rainfall and good yield in seasons with moderate to severe drought. Moreover, these varieties need to have resistance against prevalent insects and diseases and farmers' preferred quality traits. This requires that segregating populations be exposed to selection under normal irrigated situations, drought screens, diseases, insects, and grain quality traits. Drought conditions favor rice infestation by blast

(caused by *Pyricularia oryzae*) and brown spot (*Helminthosporium oryzae*) (Shrivastava & Verulkar, 2009). One of the parents used in developing segregating generations should possess tolerance of blast and brown spot and selection for blast and brown spot is practiced in segregating and advanced generations. A description of the detailed selection protocol followed is provided in Appendix 1.

Rainfed upland and lowland drought-prone environments are highly variable. Large genotype $\times$ environment interactions lead to differential performance of breeding lines in different environments. This requires that advanced breeding lines be tested at several locations and for several seasons to identify lines suitable to different regions. Further, breeding lines need to be tested for several seasons to generate reliable data on their performance under different severity of drought and normal irrigated situations. From such multilocation-multiseason evaluation, identified lines providing high yield under normal irrigated situations, good yield under drought, acceptable grain quality traits, and resistance to insects and diseases should be tested in on-farm participatory varietal selection (PVS) experiments to identify breeding lines preferred by farmers. Farmers' preferred breeding lines should be promoted for release as varieties through the national system.

Drought-tolerant breeding lines developed at IRRI are tested in multilocation trials under a drought breeding network that runs across India, Bangladesh, and Nepal in South Asia; Laos and Cambodia in Southeast Asia; and Tanzania and Mozambique in East Africa. High-yielding, drought-tolerant, farmers' preferred lines are promoted to national systems for release as varieties. The developed breeding lines are shared with other national systems in other countries and are also tested under the International Network for Genetic Evaluation of Rice (INGER) in different countries.

5. Molecular breeding approaches

Crop genetic improvement for environmental stresses such as drought is challenging due to its complex genetic nature and poor understanding of the physiological and molecular mechanisms associated with drought (Blum, 1988; Sinclair, 2011). It is a challenging task for any breeder to manipulate grain yield under drought with precision by traditional breeding approaches. The availability of complete rice genomic sequence information, rice linkage maps, and molecular marker technology has made it possible to dissect complex traits into individual quantitative trait loci (QTLs) (Temnykh et al., 2001; McCouch et al., 2002; Tuberosa, 2004; Tuberosa & Salvi, 2004, 2006). Linkage mapping, association mapping, nested association mapping, marker-aided recurrent selection (MARS), and genome-wide selection (GWS) are different approaches presently followed for the mapping and introgression of QTLs for drought tolerance (Tsonev et al., 2009). Major-effect QTLs can be exploited in marker-assisted selection more precisely to breed for drought tolerance. The drought molecular breeding program at IRRI aims at identifying and introgressing major-effect QTLs for grain yield under drought in rice mega-varieties.

5.1 Mapping of major-effect QTLs for grain yield under drought

Molecular breeding approaches are a fast-track approach to improve grain yield under drought of popular high-yielding varieties. The complex nature of drought, multigenic

inheritance of grain yield, and the complexity to maintain quality and other desirable traits of well-established varieties necessitate the use of markers to track QTLs/genes controlling these traits. Molecular approaches were suggested to be appropriate for effective drought-tolerance improvement in rice (Price et al., 2002b, 200b; Tuberosa 2004; Tuberosa & Salvi, 2004, 2006). Earlier, several efforts made to improve grain yield under drought in rice through the introgression of the identified QTLs for yield-related secondary traits did not yield the desired results. The identification and introgression of major-effect QTLs for grain yield under reproductive-stage drought stress in drought-susceptible rice varieties could be a suitable marker-assisted breeding (MAB) strategy. For marker-assisted introgression to be successful, the identification of QTLs with a high and stable effect in an improved genetic background is one of the essential requirements. Understanding all the sources of genetic variations such as QTL main effects, QTL × QTL, and QTL × environment interactions is very important before embarking on marker-assisted selection (MAS) of drought QTLs (Xing et al., 2002). To date, several QTLs with large and consistent effects on grain yield under drought stress have been identified at IRRI. Bernier et al. (2007) reported *qDTY_{12.1}*, a QTL on chromosome 12 in the Vandana/Way Rarem population, explaining about 51% of the genetic variance for yield under severe upland drought stress over two years. A consistent major-effect QTL for grain yield, *qDTY_{1.1}*, was identified to show an effect in several populations. Vikram et al. (2009) detected *qDTY_{1.1}* in three RIL populations derived from the donor N22 crossed to drought-susceptible varieties Swarna, IR64, and MTU1010 consistently over two years Ghimire et al. (2011) also detected *qDTY_{1.1}* in two RIL populations derived from donor Dhagad deshi crossed to Swarna and IR64 consistently over two seasons. Two major-effect QTLs, *qDTY_{3.1}* and *qDTY_{2.1}*, were identified in an Apo/2*Swarna population explaining 30% and 15% of the phenotypic variance, respectively (Venuprasad et al., 2009). Four major-effect QTLs, *qDTY_{2.2}*, *qDTY_{4.1}*, *qDTY_{9.1}*, and *qDTY_{10.1}*, were identified in Adaysel/IR64-derived populations (Swamy et al., 2011b, unpublished). It is important to mention that most of the major-effect QTLs were consistent across water regimes and are suitable for improving varieties for different severities of water stress (Zou et al., 2005; Kamoshita et al., 2008). The major-effect QTLs and their additive effect on grain yield are provided in Table 3. Epistatic QTLs were also detected for grain yield under drought; they can be simultaneously introgressed together with the major-effect QTLs to

Genetic background	QTL	Ecosystem	Additive effect (%) over trial mean
Vandana	<i>qDTY_{12.1}</i>	Upland	47
IR64	<i>qDTY_{1.1}</i>	Lowland	32
IR64	<i>qDTY_{9.1}</i>	Lowland	27
IR64	<i>qDTY_{10.1}</i>	Lowland	22
IR64	<i>qDTY_{2.2}</i>	Lowland	13
IR64	<i>qDTY_{4.1}</i>	Lowland	14
Swarna	<i>qDTY_{1.1}</i>	Lowland	25
Swarna	<i>qDTY_{2.1}</i>	Lowland	19
Swarna	<i>qDTY_{3.1}</i>	Lowland	25
Swarna	<i>qDTY_{8.1}</i>	Lowland	16
MTU1010	<i>qDTY_{1.1}</i>	Lowland	17

Table 3. Major-effect QTLs for grain yield under drought identified at IRRI

improve the yield of the recipient parent (Xing et al., 2002; Lanceras et al., 2004; Zou et al., 2005; Dixit et al., 2011). Many more such QTLs are likely to exist and need to be extracted from novel drought-tolerant donors. Wild progenitor species are an appropriate source for exploiting naturally occurring variation to harness QTL alleles for drought tolerance in rice. The AB-QTL analysis approach has been successful in exploiting favorable alleles for various traits of agronomic importance (Xiao et al., 1998; Zhang et al., 2006; Mc Couch et al., 2007).

5.2 Selective genotyping and bulk segregant analysis

The genotyping of large populations to identify QTLs involves high costs, and is laborious. To reduce the cost and time associated with whole genotyping, alternative approaches such as selective genotyping and bulk segregant analysis (BSA) were proposed (Darvasi & Soller, 1992; Bernier et al., 2007; Venuprasad et al., 2009; Vikram et al., 2009). In selective genotyping, only tail lines selected based on phenotype are genotyped and used for QTL detection. Major-effect QTL *qDTY_{12.1}*, which was initially identified in a population of 436 lines, was detected by selective genotyping of only 169 lines (Navabi et al., 2009). Vikram et al. (2009) detected two major-effect QTLs, *qDTY_{1.1}* and *qDTY_{8.1}*, explaining up to 11.9% and 15.6% of the phenotypic variance by genotyping only 36.5% of the lines from the populations. BSA is a cost-effective and efficient genotyping method to detect major-effect QTLs (Michelmore et al., 1991). It has been used successfully in identifying QTLs for grain yield under drought in rice by Shashidhar et al. (2005). Venuprasad et al. (2009) used BSA to identify two large-effect QTLs, *qDTY_{2.1}* and *qDTY_{3.1}*. Vikram et al. (2009) detected two major-effect QTLs, *qDTY_{1.1}* and *qDTY_{8.1}*. Ghimire et al. (2011) detected a major-effect QTL, *qDTY_{1.1}*, for grain yield under drought in more than one population. These cost-saving genotyping methods are more efficient and accurate in identifying major QTLs for grain yield under drought. With the availability of genome-wide polymorphic SNP markers, Single nucleotide polymorphism (SNP) genotypic arrays, and cheaper SNP assays, marker-assisted breeding can become a common breeding practice (McNally et al., 2009; Fukuoka et al., 2010).

5.3 Fine mapping of major-effect grain-yield QTLs

Fine mapping is necessary to further narrow down the confidence interval of major-effect QTLs for precise linkage-drag-free introgression of the QTLs in marker-assisted selection. Fine mapping is carried out either in the same QTL mapping population or in a large advanced backcross population segregating only for the QTL region and genotyping the population with additional markers in the QTL region. There are several reports of fine mapping of QTLs for different traits under drought. A QTL for leaf rolling and leaf drying on chromosome 1 was fine-mapped to 3.8 cM region (Salunkhe et al., 2011). Ding et al. (2011) fine-mapped a major-effect QTL (*qFSR4*) for root volume per tiller to a 38-kb region using NILs. Nguyen et al. (2004) fine-mapped a QTL (*oa3.1*) for osmotic adjustment under drought and identified the candidate genes. A major-effect QTL for drought recovery score (DRS) was fine-mapped on chromosome 9 (Lang & Buu, 2008). Efforts were also made at IRRI to fine-map four large-effect grain-yield QTLs under drought such as *qDTY_{2.1}*, *qDTY_{2.2}*, *qDTY_{9.1}*, and *qDTY_{12.1}* in backcross-derived advanced populations (Bernier et al., 2007;

Venuprasad et al., 2009, Dixit et al., 2011). Uga et al. (2011) fine-mapped a major-effect QTL (*Dro1*) on chromosome 9 to a 608.4-kb region.

5.4 Validation of major-effect QTLs

The effect of major-effect grain-yield QTLs identified at IRRI is validated across different backgrounds and environments. All these QTLs showed a consistent effect across different environments. The first major-effect QTL identified at IRRI, *qDTY_{12.1}*, was evaluated in 21 field trials in the Philippines and eastern India. The effect of this QTL was consistent across the environments (Bernier et al., 2009). It was also interesting to note that the effect of *qDTY_{12.1}* increased with an increase in severity of stress (Bernier et al., 2009). The major-effect QTLs *qDTY_{3.1}*, *qDTY_{2.2}*, *qDTY_{4.1}*, *qDTY_{9.1}*, and *qDTY_{10.1}* were evaluated at IRRI during 2010DS and 2011DS and the effects were consistent. The markers linked to the major-effect QTLs were validated on a panel of drought-tolerant lines to confirm their presence in a larger set of lines. It is notable that major-effect QTL *qDTY_{12.1}* was present in 85% of the lines. *qDTY_{3.2}*, *qDTY_{2.1}*, *qDTY_{3.1}*, *qDTY_{1.1}*, *qDTY_{8.1}*, and *qDTY_{1.2}* were present in more than 50% of the lines. The study also indicated the presence of at least one major-effect grain-yield QTL in every drought panel line.

5.5 Meta analysis and comparative genomics of grain-yield QTLs

The identification of the most accurate and precise major-effect QTLs across genetic backgrounds and environments through Meta analysis is a prerequisite for the successful use of QTLs in MAS across different genetic backgrounds. Khowaja et al. (2009) carried out Meta analysis of QTLs for various phenotypic traits identified under drought stress. Courtois et al. (2009) identified the meta-QTLs for root traits under drought. The number of QTLs was considerably reduced to a few consistent meta-QTLs and confidence intervals of QTL regions also decreased. MQTL regions with small genetic and physical intervals are important regions for MAS, fine mapping, candidate gene identification, and functional analysis. Meta analysis of 53 grain-yield QTLs identified from 15 reports resulted in 14 meta-QTLs (Swamy et al., 2011a). There were seven meta-QTLs of around 1.3 Mb and they corresponded to a reasonably small genetic distance of 6 cM and they are suitable for use in marker-assisted selection. These QTLs can be introgressed in popular rice mega-varieties to develop drought-tolerant and high-yielding lines. Meta-QTL regions were compared for synteny in other cereal crops. The major-effect MQTL_{1.4} was also found in maize on chromosome 3 near marker *msu2*, in wheat on chromosome 4B near marker *Rht-b1*, and in barley on chromosome 6H near marker *Bmac0316*, while major-effect MQTL_{3.2} was also found in maize on chromosome 1 near marker *Umc107a* (Swamy et al., 2011a).

5.6 Marker-assisted backcross to improve drought tolerance

Even though many QTLs have been identified for various drought-related traits in rice, there are few efforts to introgress them to develop improved breeding lines (Price et al., 2002b; Courtois et al., 2003). The lack of success may be due to the use of small-effect QTLs for secondary traits/physiological traits in introgression or the unavailability of tightly linked markers (Shen et al., 2001). Now, with the detection of several major-effect, consistent

QTLs for grain yield under drought, the introgression of yield QTLs may produce desired results. The identified major-effect QTLs for grain yield under drought $qDTY_{12.1}$, $qDTY_{3.1}$, $qDTY_{2.2}$, $qDTY_{9.1}$, $qDTY_{10.1}$, $qDTY_{4.1}$, and $qDTY_{1.1}$ increased grain yield under stress conditions and did not have any adverse effect on grain yield under non-stress conditions. The introgression of these QTLs by marker-assisted backcross breeding provides an opportunity to improve the drought tolerance of well-adapted high-yielding but drought-susceptible popular rice mega-varieties of South and Southeast Asia, and Africa. The main objectives of MAS are to introgress and pyramid these QTLs and enhance yield by 1.0-1.2 t ha⁻¹ under drought. $qDTY_{12.1}$ has been successfully introgressed in the background of Vandana. The Vandana-introgressed lines with $qDTY_{12.1}$ showed a yield advantage of 0.5 t ha⁻¹ over drought-tolerant cultivar Vandana under drought and yielded similar to Vandana under normal irrigated situations. $qDTY_{2.2}$, $qDTY_{4.1}$, $qDTY_{9.1}$, and $qDTY_{10.1}$ have been introgressed in an IR64 background.

The major-effect QTLs $qDTY_{1.1}$, $qDTY_{2.1}$, $qDTY_{2.2}$, $qDTY_{3.1}$, $qDTY_{4.1}$, $qDTY_{9.1}$, $qDTY_{10.1}$, and $qDTY_{12.1}$ are being introgressed in several popular rice mega-varieties. In general, the major-effect QTLs identified for grain yield under drought have a genetic gain of 10% to 30%, with a yield advantage of 150 to 500 kg ha⁻¹ over recipient parents. However, considering significant economical benefit to farmers, the development of drought-tolerant rice varieties with a yield advantage of at least 1.0 t ha⁻¹ could be the desired target for rice breeders. Marker-aided QTL pyramiding of major-effect QTLs through backcross breeding can be considered as an option for achieving this target. We have successfully pyramided four QTLs ($qDTY_{2.2}$, $qDTY_{4.1}$, $qDTY_{9.1}$, and $qDTY_{10.1}$) and introgressed lines with four, three, and two QTLs in an IR64 background developed. Introgressed lines with three and two QTLs in an IR64 background showed a yield advantage of 1.2-2.0 t ha⁻¹ under drought, yielded similar to IR64 under normal irrigated situations, and possessed quality traits similar to those of IR64. Efforts are also under way to combine drought and submergence tolerance in Swarna-Sub1 and IR64-Sub1 backgrounds. The improved drought-tolerant NILs of IR64 and Vandana are ready for field testing by farmers (Kumar, 2011). The protocol procedure for pyramiding three QTLs is described in Appendix 2.

6. Marker-aided recurrent selection for grain yield under drought

Marker-aided recurrent selection helps in the introgression of all the significant QTLs detected for a set of traits in a population to develop an improved cultivar. The MARS scheme involves several cycles of selection and crossing based on the genotype. The gains achieved by this approach are suggested to be more than with phenotype-based breeding and other marker-assisted breeding approaches (Charmet et al., 1999; Ribaut & Ragot, 2007). MARS is highly useful in breeding combinations of traits, including grain yield under drought, yield potential under non-stress conditions, disease-insect resistance/tolerance, and grain quality characteristics. This approach has been successfully used in maize (Johnson, 2004; Crosbie et al., 2006). We have initiated programs to apply MARS for improving drought tolerance in rice at IRRI. Two populations, IR55419-04/Sambha Mahsuri and CT9993-5-10-1-M/Sambha Mahsuri, are currently being used to apply MARS.

7. Development of QTL-NILs for physiological and molecular studies

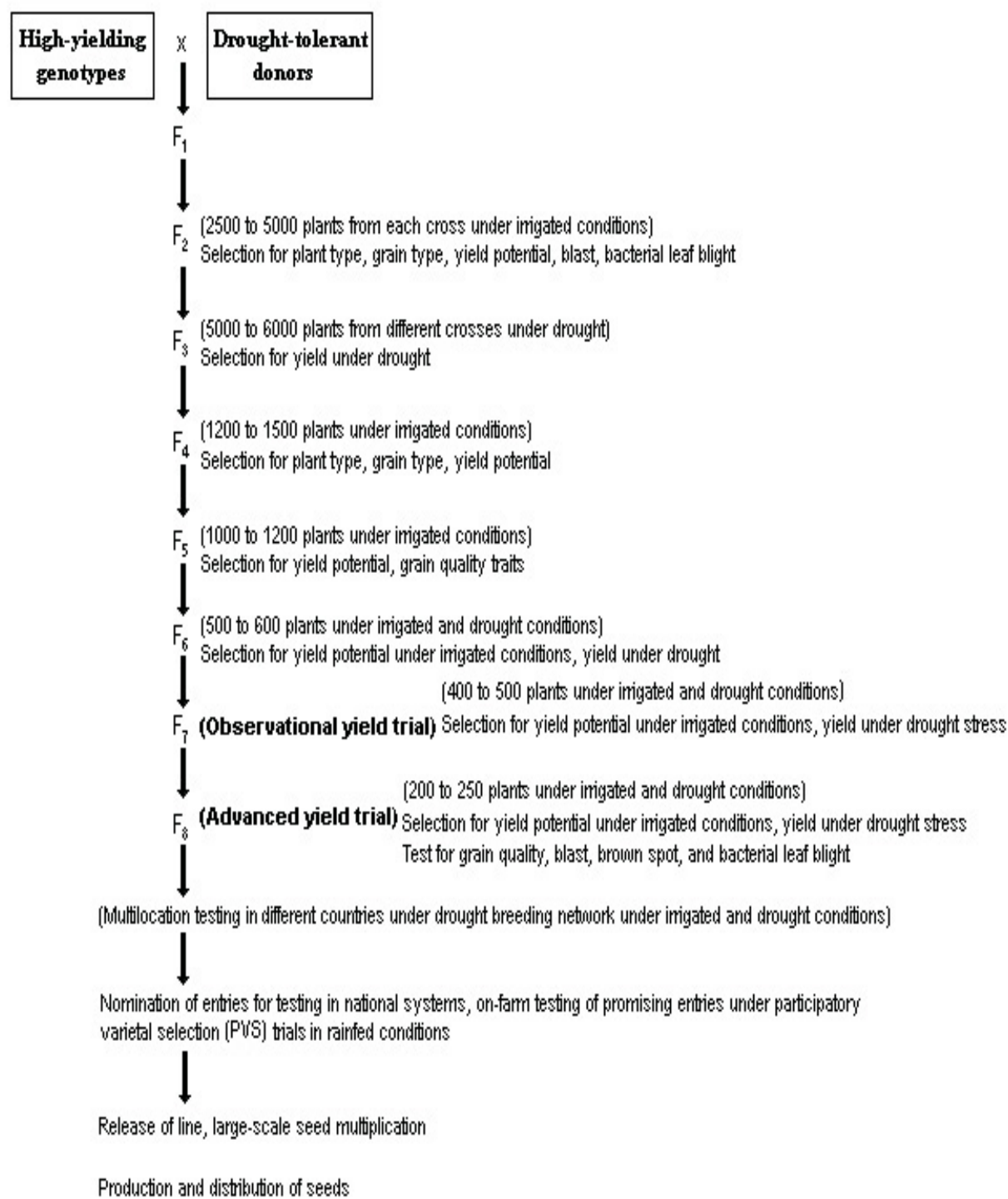
Understanding the physiological and molecular mechanisms associated with drought tolerance of major-effect QTLs is one of the major components of drought breeding. For this purpose, near-isogenic lines for QTLs (QTL-NILs) are being developed through marker-assisted introgression and background recovery of the recipient genome. The NILs differing only at QTLs and similar in the background genotype are used to understand the physiological and molecular mechanisms of increased yield under drought provided by QTLs.

8. Success stories of drought breeding at IRRI

The drought breeding program at IRRI standardized phenotyping under managed drought stress in field conditions. Direct selection for grain yield under drought has been applied as a criterion for developing improved cultivars through conventional as well as molecular approaches. Grain yield under drought has also been used in mapping and introgressing QTLs. Several major-effect, consistent QTLs have been identified in the background of popular rice mega-varieties. Following conventional breeding approaches, many varieties have been developed and released for cultivation in partner countries. During 2009 and 2010, three breeding lines, IR74371-70-1-1 as Sahbhagi dhan in India, IR74371-54-1-1 as Sahod ulan in the Philippines, and IR80411-B-49-1 as Tarharra 1 in Nepal, were released as drought-tolerant varieties. In 2011, three varieties, IR74371-3-1-1, IR74371-46-1-1, and IR74371-70-1-1, were released in Nepal as Sookha dhan 1, Sookha dhan 2, and Sookha dhan 3, respectively. IR74371-70-1-1 has been released as BRR1 dhan56 in Bangladesh. IR77080-B-34-3 and IR81047-B-3-4 are breeding lines identified as promising in Mozambique. Through molecular approaches, major-effect QTLs have been introgressed and pyramided in the background of Vandana and IR64. Many improved lines developed through conventional and molecular approaches are being evaluated through participatory varietal selection in different countries.

9. Conclusions and future perspectives

Grain yield under drought is a very complex trait. Long-term and consistent efforts are required to make a significant improvement in the drought tolerance of rice varieties. A prior knowledge of the target area with respect to drought pattern, farmers' preferences, and prevailing pests and diseases is essential. The selection of parents and breeding strategies plays an important role in a successful breeding program. The conventional breeding approach with grain yield as a selection parameter has been successful in developing improved drought-tolerant varieties. Through molecular breeding approaches, major QTLs for grain yield under drought have been identified and introgressed in popular rice varieties. Meta analysis and QTL validation of major-effect grain-yield QTLs indicate their consistent effect across environments and variable but significant effect against different genetic backgrounds. The drought breeding program at IRRI has been successful in developing and releasing drought-tolerant varieties in partner countries that showed a yield advantage of 0.8-1.2 t ha⁻¹ under drought over presently cultivated varieties. The challenges ahead are the effective use of the drought QTLs and their combinations in breeding for drought tolerance, fine mapping of QTLs to facilitate precise introgression without undesirable linkages, and understanding the physiological and molecular mechanisms associated with major-effect grain-yield QTLs under drought.



Appendix 1. Conventional breeding approach for developing drought-tolerant rice varieties

Generation	No. of plants	Genotyping	Cross
Selection of parents	-	Foreground selection QTL_{1.1} – M1, M2, M3 (DA1) QTL_{1.2} – M4, M5, M6, M7, M8, M9 (DA2)	Make crosses between plants with QTL_{1.1} and QTL_{1.2}
F ₁ (two QTLs)	50	Confirm F ₁ QTL_{1.1} –M1, M2, M3 (DA1) QTL_{1.2} – M4, M5, M6, M7, M8, M9 (DA2) Select plants with QTL	Make crosses between plants having QTL_{1.1} and QTL_{1.2} with plants having QTL_{1.3}
F ₁ (three QTLs)	100	Confirm F ₁ QTL_{1.1} – M1, M2, M3 (DA1) QTL_{1.2} – M4, M5, M6, M7, M8, M9 (DA2) QTL_{1.3} – M10, M11, M12, M13, M14 (DA3) Select plants with all the QTLs	Cross F ₁ plants with three QTLs to recipient parent (RP)
BC ₁ F ₁	1000	Confirm BC ₁ F ₁ QTL_{1.1} – M1, M2, M3 (DA1) QTL_{1.2} – M4, M5, M6, M7, M8, M9 (DA2) QTL_{1.3} – M10, M11, M12, M13, M14 (DA3) Select plants with all three QTLs Background selection using 100 SSR markers uniformly distributed on all the chromosomes in selected plants	Cross BC ₁ F ₁ with three QTLs to RP
BC ₂ F ₁	2000	Confirm BC ₂ F ₁ QTL_{1.1} – M1, M2, M3 (DA1) QTL_{1.2} – M4, M5, M6, M7, M8, M9 (DA2) QTL_{1.3} – M10, M11, M12, M13, M14 (DA3) Select plants with all three QTLs Background selection for segregating SSR markers in selected plants	Self the selected plants

BC ₂ F ₂	4000	Confirm F ₂ QTL_{1,1} – M1, M2, M3 (DA1) QTL_{1,2} – M4, M5, M6, M7, M8, M9 (DA2) QTL_{1,3} – M10, M11, M12, M13, M14 (DA3) Select plants with all three QTLs in homozygous condition Background selection for segregating SSR markers in selected plants Check for QTL flanking markers (RA) Select plants with QTLs in homozygous condition, flanks with recipient allele, and having more recipient genome background	Select the plants with all three QTLs, RP flanking, and more recipient background Advance the lines
BC ₂ F ₃	60	Screen QTL+ and QTL- lines under drought	

Note* M = marker, DA = Donor allele, RA = Recipient allele

Appendix 2. Protocol for pyramiding of three major-effect grain yield QTLs under drought

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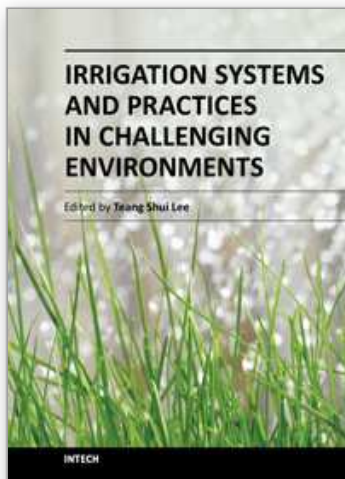
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The book *Irrigation Systems and Practices in Challenging Environments* is divided into two interesting sections, with the first section titled *Agricultural Water Productivity in Stressed Environments*, which consists of nine chapters technically crafted by experts in their own right in their fields of expertise. Topics range from effects of irrigation on the physiology of plants, deficit irrigation practices and the genetic manipulation, to creating drought tolerant variety and a host of interesting topics to cater for the those interested in the plant water soil atmosphere relationships and agronomic practices relevant in many challenging environments, more so with the onslaught of global warming, climate change and the accompanying agro-meteorological impacts. The second section, with eight chapters, deals with systems of irrigation practices around the world, covering different climate zones apart from showing casing practices for sustainable irrigation practices and more efficient ways of conveying irrigation waters - the life blood of agriculture, undoubtedly the most important sector in the world.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

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