Bridging the Rice Yield Gaps under Drought: QTLs, Genes, and their Use in Breeding Programs

Nitika Sandhu and Arvind Kumar *

International Rice Research Institute, DAPO BOX 7777, Metro Manila 1301, Philippines; n.sandhu@irri.org
* Correspondence: a.kumar@irri.org; Tel.:+63-2-580-5600 (ext. 2586)

Abstract: Rice is the staple food for more than half of the world's population. Although rice production has doubled in the last 30 years as a result of the development of high-yield, widely adaptable, resource-responsive, semi-dwarf varieties, the threat of a food crisis remains as severe as it was 60 years ago due to the ever-increasing population, water scarcity, labor scarcity, shifting climatic conditions, pest/diseases, loss of productive land to housing, industries, rising sea levels, increasing incidences of drought, flood, urbanization, soil erosion, reduction in soil nutrient status, and environmental issues associated with high-input agriculture. Among these, drought is predicted to be the most severe stress that reduces rice yield. Systematic research on drought over the last 10 years has been conducted across institutes on physiology, breeding, molecular genetics, biotechnology, and cellular and molecular biology. This has provided a better understanding of plant drought mechanisms and has helped scientists to devise better strategies to reduce rice yield losses under drought stress. These include the identification of quantitative trait loci (QTLs) for grain yield under drought as well as many agronomically important traits related to drought tolerance, marker-assisted pyramiding of genetic regions that increase yield under drought, development of efficient techniques for genetic transformation, complete sequencing and annotation of rice genomes, and synteny studies of rice and other cereal genomes. Conventional and marker-assisted breeding rice lines containing useful introgressed genes or loci have been field tested and released as varieties. Still, there is a long way to go towards developing drought-tolerant rice varieties by exploiting existing genetic diversity, identifying superior alleles for drought tolerance, understanding interactions among alleles for drought tolerance and their interaction with genetic backgrounds, and pyramiding the best combination of alleles.

Keywords: drought; marker; pyramiding; QTLs; rice; genomics

1. Introduction

Rice feeds more than half of the global population. Global rice (paddy) production in 2015 trails 0.8 percent behind the 2014 outcome, 738.2 million tons (490.3 million tons, milled rice), obtained from an area of 160.6 million hectares, a decrease of 1.3% [1]. Asia, where 60% of the earth's population lives, is the major producer and consumer of the world's rice. Water, climate, season, rainfall, soil conditions, agriculture inputs, and genetic potential of germplasm are key determinants of crop productivity. Increasing population (Figure 1a), increasing demand for water (Figure 1b), water crisis (Figure 1c), drought (Figure 1d), failure to adapt to climate change, declining farm land, soil moisture, soil characteristics, deterioration in nutrient content, weed competitiveness, increasing intensity, and the frequency of biotic/abiotic stresses will amplify the challenges of achieving future food requirements. This will affect the economic growth and social stability of regions with food shortages. Farmers will earn a profit only if they successfully solve the algebraic puzzle of farming. Wheat, rice, maize, and other grains that are the staple food of the human population and the

sources of feed for livestock account for more than 60% of the total crop evapotranspiration requirement, while soybeans and other oilseed crops account for 17%, and sugarcane 6% [2]. In such circumstances, the available water resources will not be sufficient to produce enough food for the increasing population. With changes in the climate and unpredictable rainfall, there is a possibility that nearly half of the world's population may face water scarcity by 2030 [3]. Water scarcity will worsen in the world's extremely dry regions and areas where water is already in short supply.
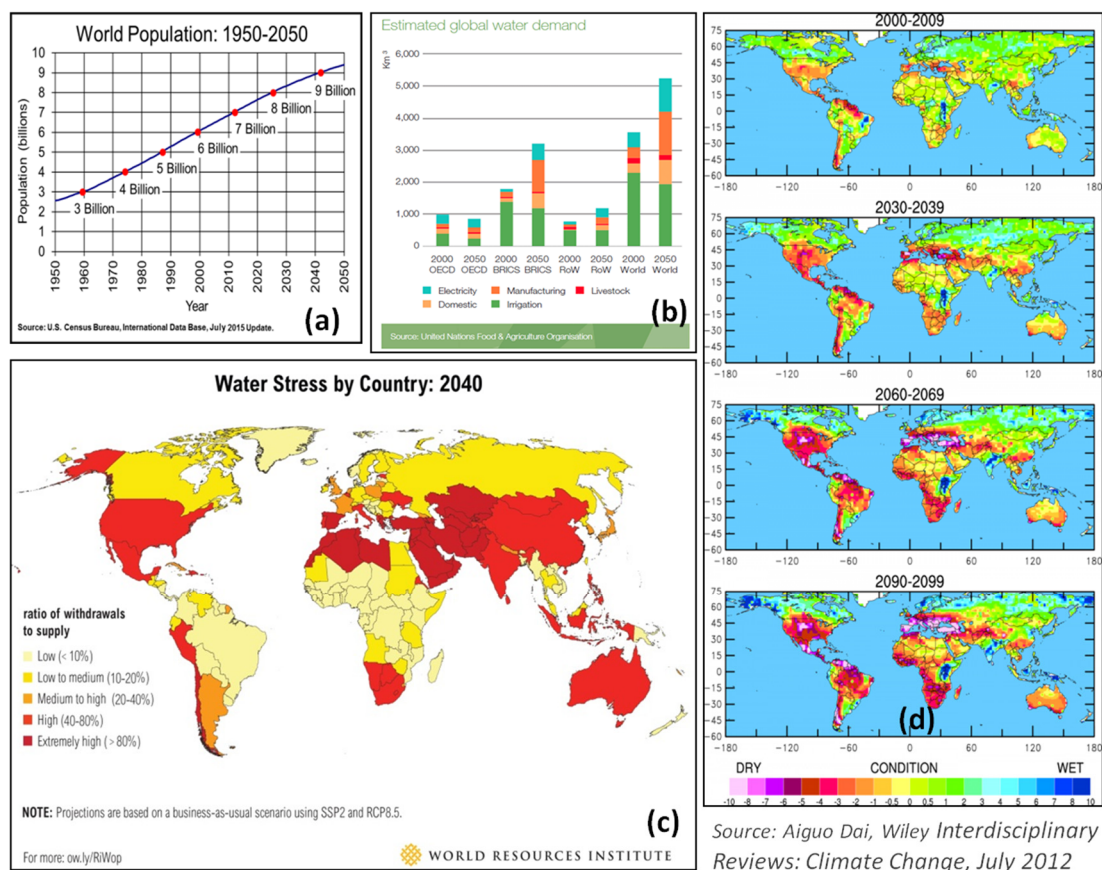

Figure 1. (**a**) Projected population curve (source: U.S. Census Bureau, International database 1950–2050, July 2015 update); (**b**) estimated global water demand (OECD: Organization for Economic Cooperation and Development; BRIC: Brazil, Russia, India and China; RoW: Rest of world; source: United Nation Food & Agriculture Organization); (**c**) severity pattern of water stress by country by 2040 (source: World Resource Institute); (**d**) estimated possibilities for future drought worldwide based on the Palmer Drought Severity Index (source: Aigup Dai, Wiley interdisciplinary Reviews: Climate Change, July 2012).

The contribution of plant breeding to improving commercially important crops, including major ones such as rice, maize, wheat, cotton, and pearl millet, at a global level is remarkable. Before the Green Revolution, traditional rice and wheat varieties were tall, photoperiod-sensitive, low-yielding and drought-tolerant, having a broad maturity duration and good grain quality. In the post-Green Revolution era, these traditional varieties were replaced by a few widely adapted varieties including inbreds and hybrids that are dwarf and photoperiod-insensitive, with early maturity, higher yield, poor grain quality, and low pest resistance. The dwarf rice varieties were bred by targeting irrigated ecosystems wherein ample water was thought to remain available for traditional practices of puddled transplanted system of rice cultivation. These varieties have high yield potential and good resistance to biotic stresses, but are highly susceptible to abiotic stresses such as drought. They are also prone to heavy yield losses even under mild drought stress [4]. In the course of post-Green Revolution breeding over the past 50 years, unknowingly, the drought tolerance contributing alleles of traditional cultivars have not been properly maintained in the

modern cultivars. Recent understanding of molecular and physiological mechanisms for different abiotic stresses has opened up new opportunities to improve yield under adverse climatic conditions for many crops. There is still a need to bridge the large gap between yields in most favorable and stress conditions. Strategies involving bridging the yield gap and increasing yield stability and adaptability under variable environmental conditions are of importance in assuring food security and sustainability in the future. There is a need to move forward from the Green Revolution to a 'gene revolution,' which is more productive and more 'green' in terms of conserving natural resources and the environment [5].

2. Drought: The Key Concern in Food Security

Drought has been the main catalyst of many large famines of the past and has a major destructive effect on rice production in rainfed areas across Asia and sub-Saharan Africa. The most vulnerable, drought-prone areas are shown in Table 1. The most devastating drought events around the world were the Deccan Famine and those in the Horn of Africa, the United States, Vietnam, Australia, China, Brazil, the Sahel, Malawi, East Africa, Ethiopia, India, and Bangladesh. From 2003 to 2013, at least one medium- to large-scale natural disaster caused $70 billion in crop and livestock production losses; drought alone accounted for 44%. Asia is the most affected region, with total crop and livestock production losses amounting to $28 billion (40% of total losses), followed by Africa with $25 billion (Table 2) [6]. The 1987 drought in India, the 2004 drought in Thailand, and the 1978–2003 drought in China were estimated to have affected 60% [7], 2 million ha [8], and 14 million ha of cropped area, respectively. Drought events between 1980 and 2014 in sub-Saharan Africa affected 203, 86, 74, 61, and 48 million people in eastern Africa, southern Africa, western Africa, Ethiopia, and Kenya, respectively [6].

Drought induces critical losses in crop yield. Yield integrates many of the physiological and biochemical responses at cellular and molecular levels, influenced by a number of predictable and unpredictable factors that are genetically difficult to understand and manipulate. Therefore, long-term and systematic attention should be given to the complex issues surrounding drought in order to develop a better understanding and devise sustainable solutions.

Table 1. Most vulnerable drought-prone areas across the world.

Region	Areas Most Vulnerable to Drought	Drought Events
Asia/Pacific	India, Nepal, Bangladesh, China, Laos, Cambodia, Pakistan, Afghanistan, Sri Lanka, Bhutan, Indonesia, Thailand, Myanmar, Vietnam, Malaysia	1876, 1878, 1896, 1902, 1907, 1928, 1930, 1936, 1941, 1942, 1944, 1958, 1961, 1964, 1972, 1973, 1974, 1983, 1987, 1993, 1996, 2000, 2002, 2010
Middle East	Yemen, the United Arab Emirates, Saudi Arabia, Iraq, Iran, Syria	1940, 1998, 2000, 2007, 2010
Europe	France, Italy, Germany, northern Spain, Czech Republic	1955, 1957, 1962, 1968, 1971, 1974, 2005, 2009, 2012
United States	Arizona, Kansas, Arkansas, Georgia, Florida, Mississippi, Alabama, South, North Carolina, Texas, Oklahoma, California	1934, 1936, 1939, 1940, 1983, 2002, 2010, 2011
Africa	Ethiopia, Kenya, Eritrea, Somalia, Uganda, Djibouti, Mauritania, Angola, Zambia, Zimbabwe, Mozambique, Malawi, Lesotho, Swaziland	1888, 1972, 1973, 1983, 1985, 1991, 1992, 1999, 2002, 2002, 2003, 2010, 2011, 2012
Latin America	Peru, Chile, Argentina, Brazil, Mexico	1630, 1640, 1650, 1782, 1884, 1992, 1999, 2011, 2015
Australia	New south wales, Queensland, Victoria, Tasmania, Sydney, Northam, York area of Western Australia	1813, 1826, 1829, 1835, 1838, 1850, 1888, 1897, 1902, 1982, 1983, 2000

Source: Modified from Spring 2015 global attributes survey.

Table 2. Effect of drought on crops and livestock across the world.

Region	Crop Losses (Billion USD)	Livestock Losses (Billion USD)	Total (Billion USD)
Africa	21	4	25
Asia	27	1	28
Latin America and Caribbean	9	2	11
Near East	4	0	4
Central Asia	1	0	4
% share of total Global losses	42.4	35.8	78.2

Source: FAO based on data from FAOSTAT, 2003–2013.

3. Effect of Drought on Different Crops

Approximately 34% of rice is grown in rainfed lowland, 9% in rainfed upland, and 7% in flood-prone areas, while irrigated ecosystem covers 50% of total world rice area. Drought has been reported to produce devastating effects in rice at panicle initiation and flowering [4,9]; in maize at the tasseling and silking stages [10,11]; in sorghum and pearl millet at the booting and flowering stages [12]; in finger millet at the flowering stage; in sunflowers at head formation and the early grain-filling stage [13,14]; in groundnuts at the peg penetration and pod development stages; in soybean at the flowering and pod filling stages [15,16]; in black and green gram at the flowering and early pod development stages [17]; in cotton at the square formation and ball development stages [18,19]; and during the reproductive stage in rice [20,21]. Like in other crops, in rice drought has the most devastating effect at the reproductive stage. In rice, the damage to the crop is also significant at the seedling as well as vegetative stages. At the seedling stage, delay in monsoon rains, insufficient rain to puddle land, and preparation for transplanting force farmers to leave their land uncultivated. Severe drought at the vegetative stage reduces biomass production, causes the death of the plant and in severe cases, forces farmers to allow the grazing of the crops by cattle. Drought has a complex effect on plants [22–42], and plants respond with many defensive adaptations (Figure 2). The major determinants of grain yield under drought are the variety [43], type of soil [44], length and timing of drought [45], severity of drought [46,47], season (early season, mid-season, or terminal stage, Table 3 [48–68]), the age, period, and development stage of the plant [69], plant responses after stress elimination, and the interaction between the biotic/abiotic factors [70] and the region. Apart from this, drought stress also makes the rice crop more susceptible to biotic stresses (rice blast, brown spot, and bacterial blight), leading to a further decline in rice production. In many rice-growing areas in rainfed ecosystems, drought and submergence can occur in the same season at different growth stages of the plant or in different seasons, thus creating more complexity. Drought tolerance is a means for the rice plant to survive and produce a stable and satisfactory yield. There is urgent need for a strategy to get the highest yield out of every single drop of water on existing cropland to satisfy food needs in the future.

Table 3. Yield losses in different crops as a result of drought.

Crop	Stress	Yield Reduction	Reference
Rice	Lowland moderate reproductive stage	45%–60%	[48–50]
Rice	Lowland severe reproductive stage	65%–91%	[48–51]
Rice	Upland mild reproductive stage	18%–39%	[48,52]
Rice	Upland moderate reproductive stage	70%–75%	[48,52]
Rice	Upland severe reproductive stage	80%–97%	[48,49,53]
Wheat	Moderate reproductive stage	10%–50%	[54–57]
Pearl Millet	Prior and beginning of flowering	65%	[58]
Pearl Millet	Early stress	62%	[59]
Pearl Millet	Late stress	28%	[59]
Maize	Mild-moderate-severe reproductive stage	1%–76%	[60–63]

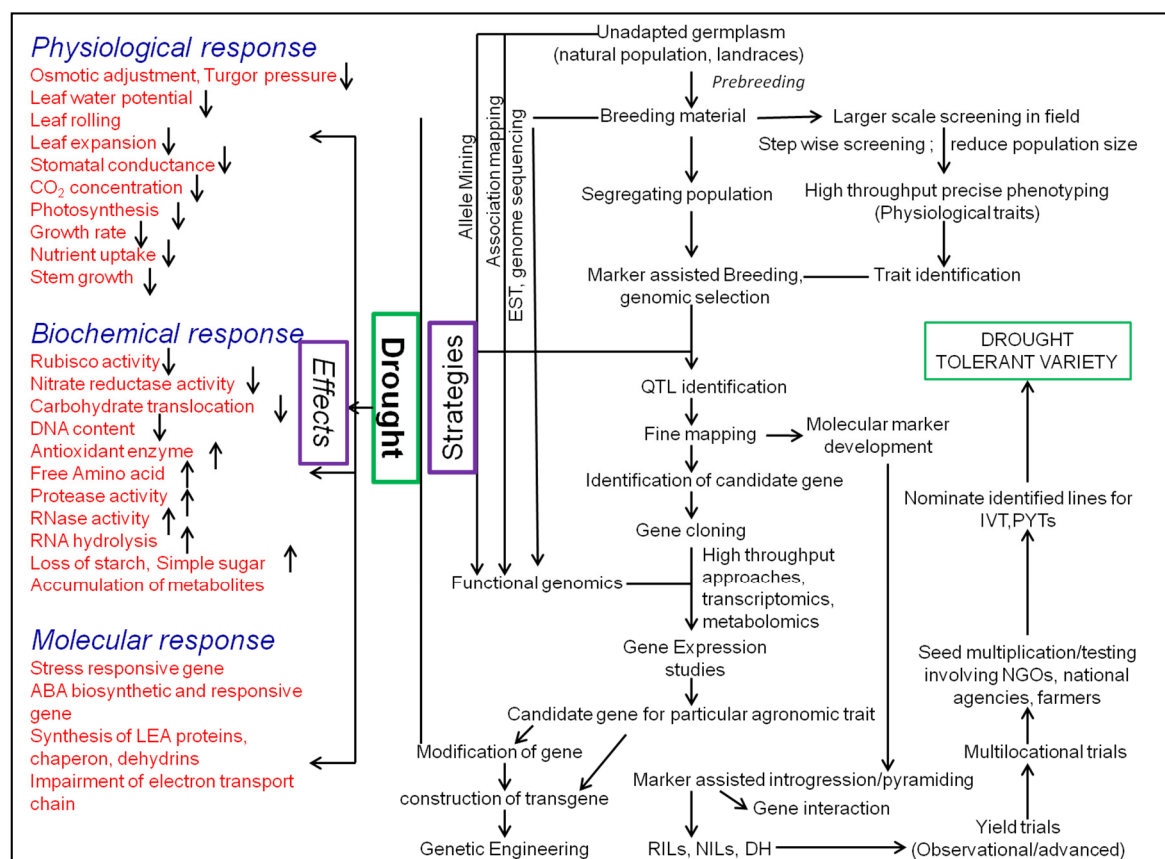| Barley | Severe reproductive stage | 73%–87% | [64] |
Chickpea	Late terminal drought	49%–54%	[65]
Chickpea	Reproductive stage	45%–69%	[66]
Pigeon Pea	Reproductive stage	40%–55%	[67]
Canola	Reproductive stage	15%–35%	[68]

Figure 2. Effect of drought and approaches in developing drought-tolerant rice varieties. RILs: Recombinant inbred lines, NILs: Near-isogenic lines, DH: Double haploid, NGO: Non-Governmental Organization; IYT: Intermediate Yield Trial, PYTs: Preliminary yield trial, ↑ (increase/enhance), ↓ (decrease/reduce).

Water availability (drought and flood), soil problems (salinity, nutrient deficiencies, and toxicities), extreme temperatures (heat and cold) and biotic stresses (brown planthopper, gall midge, blast, tungro, bacterial blight) are the main constraints in South Asia, Southeast Asia, and Africa, where rice often suffers from extensive shock to sustain full yield potential. Surveys conducted by the Africa Rice Center in 12 sub-Saharan African countries reported a yield decline of 33% [71] when drought and flooding occurred together. Another study by the Africa Rice Center reported yield losses of 40% and 25% in Senegal and Uganda, respectively, due to salinity and iron toxicity [72]. Therefore, it is advantageous to select cultivars with multiple stress tolerance (drought, salinity, submergence, stagnant flooding, biotic stress, and high temperature) to allow the crop to survive if multiple stresses come at the same time.

4. Strategies to Manage Drought

Comprehensive information, early warning systems and cultivation of high-yielding, high-quality, drought- plus biotic stress-tolerant varieties in drought-prone areas could provide a solution to the problem of drought. Identification and introduction of suitable traits that narrow the gap between expected and actual yield; understanding realistic physio-morpho-molecular mechanisms of drought tolerance; and designing a standard screening method for a large

population [73] could contribute to the development of drought-tolerant rice varieties. Adopting proper strategies such as larger scale standardized screening for grain yield under drought and understanding the components of yield based on morpho-physiological traits could contribute to breeders' efforts to develop better drought-tolerant varieties. Conventional and marker-assisted breeding strategies based on the use of drought-tolerant donors, pre-breeding to use the lines derived from crosses involving donors, and the development of suitable mapping populations to identify QTLs/genes affecting yield could result in yield improvement and stability under drought stress. Breaking undesirable linkages between drought tolerance and tall plant height, drought tolerance and earliness, and drought tolerance and low yield potential [74] could help to develop semi-dwarf drought-tolerant varieties without any yield penalty. Molecular, cellular, physiological, biochemical, and developmental responses to abiotic stress involve several genes and gene functions controlling drought tolerance. Several efforts have been made to better understand the expression of drought-tolerance-related traits and the complex network of drought-related genes. Exogenous application of hormones and osmoprotectants to seed or growing plants, engineering for drought resistance, and high-throughput novel technologies could be useful tools in identifying genes to improve yield under drought (Figure 2).

4.1. Screening Strategies

Although it is difficult to understand how plants build up, combine, and exhibit the changing processes over the entire growth and development cycle, efforts have been made to standardize screening protocols, understand the mechanisms related to drought tolerance, and develop varieties that are tolerant of drought. The assessment of the type, intensity, degree of drought, and appropriate selection/screening for drought tolerance is a very crucial step. Each method has some advantage and limitations. Identification of drought-tolerant and -susceptible cultivars based on a few physiological measures (such as canopy temperature, water potential, and osmotic adjustment) [75] and specific environmental factors (such as weather and soil water availability) may not be adequate for breeders to use such donors in the breeding program. Screening of donor lines for grain yield under drought, performance of such lines under both stress and non-stress conditions [76–79], and use of robust statistical methods to clearly differentiate drought-tolerant and drought-susceptible lines [80–83] could be considered an appropriate methodology for drought screening [84]. Simultaneous screening for resistance to multiple biotic and abiotic stresses could be more beneficial to improve yield under multiple stress-prone environments.

4.1.1. Secondary Traits

Secondary traits are distinct components of prime plant traits such as grain yield. Secondary traits are important indicators of different physiological, molecular, and developmental changes involved in drought resistance, tolerance, and adaptation mechanisms. The effectiveness of selection for secondary traits such as root thickness, penetration ability and depth, greater hydraulic conductance, xylem thickness and osmotic adjustment, leaf area [85,86], leaf water potential [87], fresh and dry root weight, root volume, relative water content [26], root length [25], photosynthesis [88], early flowering, and harvest index [89] in rice to improve yield under drought is yet to be successfully demonstrated. This also goes for the anthesis-silking interval in maize [90], greenness in sorghum [91], and water-use efficiency in wheat [92]. Improvement in yield potential and yield stability across variable environments has also been reported by considering stay-green [93,94], an essential trait in several crops (maize, rice, sorghum) that gives plants resistance to drought, premature senescence [95], and lodging.

Selection for effective mobilization of the reserves from source to sink [96], osmoregulation [97], cuticular resistance, surface roughness [98], and membrane composition [99] suggested the importance of these traits in reducing drought-dependent yield loss. Stomatal conductance, maximal rates of photosynthesis [100], and developmental plasticity [101] were reported to be positively correlated, whereas leaf temperatures were negatively correlated with yield increase under stress in semi-dwarf spring wheat cultivars [100]. Another example of a successful breeding program for

drought stress using carbon isotope discrimination as a substitute for water-use efficiency in increasing yield in wheat was reported by Rebetzke et al. [102] and Cattivelli et al. [103]. The limitations associated with these techniques involved the screening of only a limited number of plants because of high cost and screening under controlled conditions that may not reflect field conditions.

A number of putative secondary traits such as root density, root thickness, root distribution pattern [104,105], rooting depth [106,107], root branching, root-to-shoot ratio, root penetration [108–112], root length, root hydraulic conductance, transpiration demand [113], and water and nutrient uptake [111,114,115] have been suggested to confer drought tolerance [116]. Traits such as transpiration rate, biomass accumulation, stomatal conductance, leaf area [117–119], osmoregulation [93], relative water content, and leaf water potential [120] reported a positive association with grain yield under drought stress. Various reports suggested the role of genetic regions associated with secondary traits (Table 4, [121–136]) in enhancing grain yield under drought stress.

Table 4. Genetic regions reported to be associated with secondary traits enhancing drought tolerance.

Crop	Chr	Trait Improved	Reference
Rice	1	Root-shoot growth, deep root growth	[109,121]
	9	Root length, root thickness, straw yield	[122,123]
	12	Biomass, panicle number, lateral root, panicle branching	[124,125]
Wheat	2B, 4A, 5A, 7B	Carbon isotope ratio, osmotic potential, chlorophyll content, flag leaf, rolling index	[126]
	2A, 2B, 3A, 3B, 5A, 5B, 6B, 7A,	Osmotic adjustment	[126,127]
Barley	6HL	Relative water content, leaf osmotic potential, osmotic adjustment, carbon isotope discrimination	[128–130]
	2H, 3H, 6H, 7H	Carbon isotope discrimination	[131]
	2H, 4H, 6H, 7H	Chlorophyll, fluorescence	[132]
	1H, 2H, 3H, 5H, 6H,7H	Relative water content	[133,134]
	2H, 3H, 4H, 5H	Osmotic potential	[134]
Sorghum	1, 2, 3, 4	Leaf area, delayed leaf senescence, stay green	[91]
Cotton	06, 02, 25	Biomass production; panicle number, specific, leaf weight and chlorophyll, osmotic potential, stomatal density, stomatal conductance	[135,136]

4.1.2. Grain Yield as a Selection Criterion under Drought

Even though screening for physiological traits is more accurate than the screening of complex quantitative agronomic traits, drought is still a complex process involving multiple steps starting from moisture-nutrient uptake by roots to grain formation by the panicle. Each physiological trait in turn fulfills one or two of the multiple sequential components needed to produce higher yield. Moreover, the appropriate combinations of these components to achieve increased yield under drought are not well understood. Grain yield, being a complex quantitative trait, was not considered earlier as a suitable selection criterion in breeding [93,105,137]. On the contrary, exploitation of genetic variation using direct selection for the trait for grain yield under drought and combining high yield potential with this trait has now been suggested as an appropriate alternative [138–142]. Several studies on comparative phenotypic screening of breeding material for grain yield under reproductive-stage drought stress and under a controlled environment [138–143] showed moderate

heritability of grain yield under drought stress. Several experiments to standardize the procedure of phenotypic screening involving direct selection for grain yield as selection criteria (Figure 3) reported grain yield advantage under reproductive-stage drought stress with comparable yield under irrigated situations in uplands [53] and lowlands [50,144], and in multiple locations [145]. This type of cyclical stress will allow development, phenotyping, and selection for drought resistance in populations consisting of genotypes with broad growth duration.
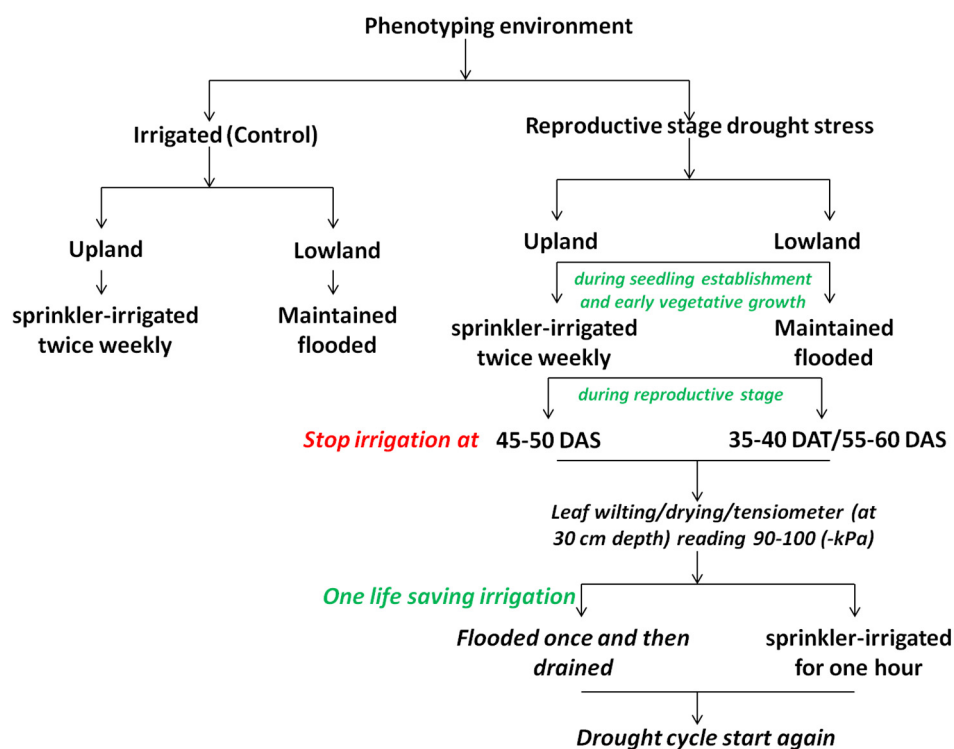

Figure 3. Standardized protocol for drought phenotyping screening at IRRI. DAS: days after seeding, DAT: days after transplanting.

4.1.3. High-Throughput Screening

The new tools of phenomics, such as carbon isotope discrimination (CID) [146], infrared thermography, canopy spectral reflectance [104,147], pulse amplitude-modulated fluorometry for chlorophyll fluorescence [148], normalized difference vegetation index (NDVI) [149] and photosynthetic reflective index (PRI) [150], positron emission tomography (PET), magnetic resonance imaging (MRI), and nuclear magnetic resonance [151,152] are now available to better understand the contribution of different morpho-physiological traits to grain yield. Planes, airborne instruments, and moving equipment with multispectral sensors can estimate the plant cover and nutrient needs of crops. The information collected from phenomics tools such as a high-density soil map to track porosity and mineral content, detectors to predict nutrient content and changes in response to inputs, contour mapping to observe water movements, and soil moisture detectors at multiple depths, when combined with GPS data, can give useful information about land productivity and will be useful for the following season's planting pattern. Well-developed analytical tools/packages are essential for analyzing and interpreting the large amount of data produced by these modern techniques in the future.

4.2. Breeding Strategies

Research work is needed in breeding rice varieties with high grain yield potential, good yield under drought, yield stability, resistance to existing biotic stresses, good grain and cooking quality,

and good relative performance in multiple locations and environmental (managed under drought-stress and non-stress environments) conditions.

4.2.1. Donor Identification

The preliminary and important step of any breeding program involves the identification of suitable donors. Selection of a specific donor from a large germplasm collection is a crucial step. The use of a specific donor with special characteristics for a specific environment may lead to the success of any varietal and trait development program. Most of the traditional donors have several undesirable traits and therefore are not suitable for direct use in any breeding program. These landraces have undesirable traits such as little ground cover, tall plant height, low yield potential, and poor grain and eating quality, but they have a desirable drought tolerance trait. On the other hand, modern rice varieties have desirable traits such as high yield, improved plant type (early vigor, medium height, and lodging resistance), tolerance of biotic stress, and good grain type (medium to long slender). However, they are drought-susceptible. Breeding for any desired trait to get new gene combinations requires exploitation of genetic variation (intra-specific, inter-specific, or inter-generic) that exist in traditional landraces carrying desirable characteristics and modern improved varieties with high yield potential [153]. The genotype at par performance in the target environment [154] and the trait with high heritability [155] can account for further high-throughput screening. The identified drought-tolerant donors such as PSBRc68, PSBRc80, PSBRc82, Aday Sel, Dagaddeshi, Kali Aus, Aus276, Kalia, N22, Apo, Dular, and IR77298-14-1-2 have been used in conventional breeding and QTL mapping studies at IRRI. Among these, improved donors such as PSBRc68, PSBRc80, PSBRc82, and IR77298-14-1-2 have been directly used in conventional breeding programs, whereas improved drought-tolerant lines free from undesirable linkages were derived from the mapping populations that involve traditional donors such as Aday Sel, Dagaddeshi, Kali Aus, Aus 276, Kalia, N22, Apo, and Dular and used in conventional breeding programs. In marker-assisted breeding programs, lines possessing the identified QTLs for grain yield under drought, which come from mapping populations that involve traditional donors, were used to improve mega-varieties.

A model drought-resistant rice variety for drought-prone environments can be considered as having better yields than any other presently available cultivar, not only under drought stress but also under irrigated conditions across different seasons and environments, being less sensitive to variable conditions [83,156–158], and possessing good grain quality and resistance to biotic stresses.

4.2.2. Conventional Breeding

Over the last 10 years, conventional breeding at distinguished worldwide research centers has made significant progress in developing biotic and abiotic stress-tolerant lines/cultivars of some important food crops such as chickpea [159], soybean [160], wheat [161–163], barley [164,165], rice [89], and common bean [166] using different protocols and designs. The drought breeding program at IRRI has led to the development of several high-yielding, drought-tolerant lines with a release of varieties across South and Southeast Asia and Africa since 2009 (Table 5). However, it is time-consuming, costly, and labor-intensive, and there is a high probability of transferring undesirable genes. A modified conventional breeding approach (Figure 4) involving an integrative sequential phenotyping, genotyping, and selection strategy to screen a large number of plants will improve the assessment of plant response to drought stress. This efficient, precise, cost-effective breeding approach may expedite the development of drought-tolerant rice varieties with a high frequency of favorable genes.

Table 5. High-yielding drought-tolerant varieties released from IRRI's drought breeding program.

Name	Designation	Country	Ecosystem [a]	Release Year	Days to Maturity	Plant Height (cm)
Katihan 1	IR 79913-B-176-B-4	Philippines	UP	2011	105	90
Sahod Ulan 3	IR 81412-B-B-82-1	Philippines	RL	2011	120	107

Sahod Ulan 5	IR 81023-B-116-1-2	Philippines	RL	2011	115	130
Sahod Ulan 6	IR 72667-16-1-B-B-3	Philippines	RL	2011	115	100
Sahod Ulan 8	IR 74963-262-5-1-3-3	Philippines	RL	2011	125	100
Inpago LIPI Go 1	IR 79971-B-191-B-B	Indonesia	UP	2011	110	115
Inpago LIPI Go 2	IR 79971-B-227-B-B	Indonesia	UP	2011	113	114
CR dhan 40	IR 55423-01	India	UP	2012	110	100
Sahod Ulan 12	IR 81047-B-106-2-4	Philippines	RL	2013	105	119
M'ZIVA	R77080-B-B-34-3	Mozambique	RL	2013	120	130
CR dhan 201	IR 83380-B-B-124-1	India	Aerobic	2014	118	100
CR dhan 202	IR 84899-B-154	India	Aerobic	2014	115	100
CR dhan 204	IR 83927-B-B-279	India	Aerobic	2014	110	100
Sukha dhan 5	IR 83388-B-B-108-3	Nepal	RL	2014	125	105
Sukha dhan 6	IR 83383-B-B-129-4	Nepal	RL	2014	125	105
BRRI dhan 66	IR 82635-B-B-75-2	Bangladesh	RL	2014	113	116
Katihan 3	IR 86857-101-2-1-3	Philippines	UP	2014	107	87
DRR dhan 43	IR 83876-B-RP	India	RL	2014	115	105
DRR dhan 44	IR 93376-B-B-130	India	RL	2014	115	105
Katihan 2	IR 82635-B-B-47-2	Philippines	UP	2014	107	84
BRRI dhan 71	IR 82589-B-B-84-3	Bangladesh	RL	2015	115	112
Swarna Shreya	IR 84899-B-179-16-1-1-1-1	India	RL	2015	112	121
Sahod Ulan 15	IR 83383-B-B-129-4	Philippines	RL	2015	115	110
Sahod Ulan 20	IR 86781-3-3-1-1	Philippines	RL	2015	115	112
MPTSA	IR 82077-B-B-71-1	Malawai	RL	2015	120	110
ATETE	IR 80411-B-49-1	Malawai	IR, RL	2015	118	112
CAR 14	IR80463-B-39-3	Cambodia	IR, RL	2015	115	110
Identified	IR 84878-B-60-4-1	Philippines	RL	2016	113	97

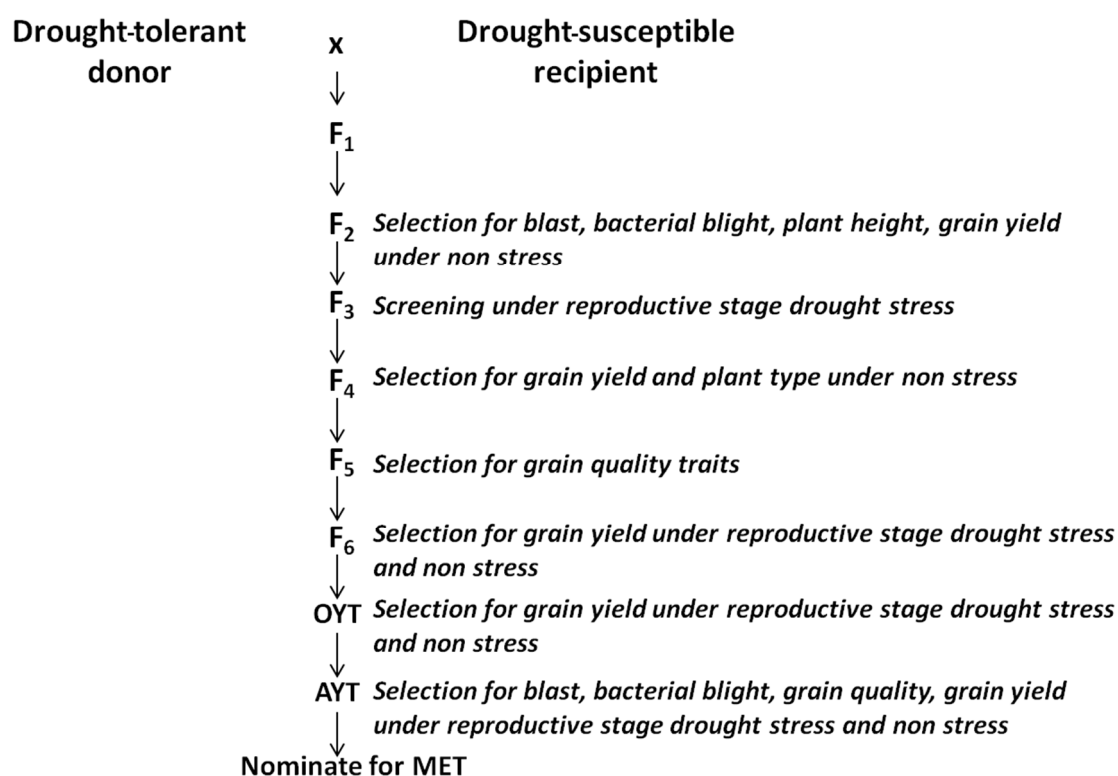[a] UP: upland, RL: rainfed lowland, IR—irrigated ecology. Source: Modified from Kumar et al. [89].

Figure 4. Modified conventional breeding approach. OYT: Observational yield trials, AYT: advanced yield trials, MET: multi environmental trials.

4.2.3. Marker-Assisted Breeding: Identification, Introgression, and Pyramiding of QTLs

Marker-assisted breeding adopted at IRRI involves: the development of mapping populations involving traditional drought-tolerant donors and modern high-yielding varieties; precise phenotyping in multi-environment, controlled, and drought-stress conditions; repeated years;

identification of polymorphic markers; genotyping with polymorphic markers; linkage map construction; and QTL mapping using genotypic and phenotypic data.

Large-scale systematic study with several mapping populations for identification of major quantitative trait loci (QTLs) using yield as a selection criterion [89] led to the identification of several QTLs for grain yield under drought, followed by introgression of identified QTLs to develop drought-tolerant rice cultivars.

The success of screening strategies with careful assessment of size and structure of population has led to the development and release of several drought-tolerant lines with high yield under irrigated conditions [89]. Identification of genetic regions linked to drought tolerance using genotyping strategies such as selective genotyping (SG), whole-genome genotyping (WGG), bulk segregant analysis (BSA) [50,51,167,168], genome-wide association studies (GWAS, an improved version of marker-assisted selection) [169–172], and successful introgression in different genetic backgrounds using marker-assisted backcrossing [42,46,52,144,167,168,173,174], marker-assisted recurrent selection [175,176], and marker-assisted QTL pyramiding [89] has been reported. Mapping populations segregating for drought-tolerance-related traits led to the identification of 12 quantitative trait loci (QTLs) (Table 6) showing a large effect against high-yielding, drought-susceptible popular varieties: Swarna, IR64, MTU1010, TDK1, Sabitri, and Vandana [49–53,167,168,177–180] (Table 6). Gathering all data on the donors/recipients, factors, traits, genes, mechanisms, and technologies that sustain yield under drought and accumulating them into elite genotypes without negative effects on yield potential could be the best solution for rainfed environments.

Table 6. QTLs identified for grain yield under drought in different backgrounds.

QTLs	Donors	Backgrounds	Ecosystems	Reference
$qDTY_{1.1}$	N22, Dhagaddeshi, Apo, CT9993-10-1-M, Kali Aus, Basmati 334	Swarna, IR64, MTU1010	Lowland, Upland	[50–52,179]
$qDTY_{2.1}$	Apo, Aus 276	Swarna, MTU1010	Lowland	[52,144]
$qDTY_{2.2}$	Aday sel, Kali Aus	MTU1010, IR64, Samba Mahsuri	Lowland, Upland	[178,180]
$qDTY_{2.3}$	Kali Aus	IR64	Upland, Lowland	[52,180]
$qDTY_{3.1}$	Apo, IR55419-04	Swarna, TDK 1	Lowland	[49,144]
$qDTY_{3.2}$	N22, IR77298-5-6-18, Aday sel	Swarna, Sabitri	Lowland, Upland	[50,158]
$qDTY_{4.1}$	Aday Sel	IR64, Samba Mahsuri	Lowland	[178]
$qDTY_{6.1}$	Apo, Vandana, IR55419-04	IR72, TDK 1	Upland, Lowland	[49,177]
$qDTY_{6.2}$	IR55419-04	TDK 1	Lowland	[49]
$qDTY_{9.1}$	Aday sel	IR64	Lowland	[178]
$qDTY_{10.1}$	N22, Aday sel, Basmati 334	IR64, MTU1010, Swarna	Lowland	[50,178]
$qDTY_{12.1}$	Way Rarem, IR74371-46-1-1	Vandana, Sabitri	Upland, Lowland	[53,167]

The drought marker-assisted breeding program at IRRI has led to the development and release of high-yielding drought-tolerant lines (Table 7).

The major and consistent drought grain yield (GY) QTLs were reported to be collocated with QTLs for plant height and/or days to flowering [50,53,144,177]. The developed drought-tolerant lines possessed earliness, root plasticity traits, greater root length density, better water-use efficiency mechanism, better regulation of shoot growth [106,121,181], and a yield advantage of 0.8–1.0 t·ha⁻¹ under severe drought. These short-duration varieties of 105–110 days without any yield decline possessed better adaptability to less water and variable environmental growing conditions. QTLs related to traits enhancing drought tolerance have been reported in cotton [136], pearl millet [182], maize [156], Sorghum [91], and barley [183]. Fine-mapping of QTLs to facilitate exact introgression devoid of undesirable linkages; identification of useful candidate genes; effectiveness in various

genetic backgrounds and variable environment; and effective use, pyramiding, and interaction studies may now open new windows to the development of drought-tolerant rice cultivars. Fine-mapping of $qDTY_{12.1}$ resulted in the partitioning of the $qDTY_{12.1}$ into sub-QTLs and multiple intra-QTL genes ($OsNAM_{12.1}$ transcription factor and co-localized target genes). This strengthened the view of more than a single gene underneath the functionality of one QTL and reiterate grain yield under drought, a complex trait [124]. Insertion mutants in the co-localized target genes in the $qDTY_{12.1}$ region lead to an increase in the lateral roots compared to the wild type [124]. Fine-mapping of $qDTY_{1.1}$ shows that $qDTY_{1.1}$ harbors the green revolution gene 'sd1' [121].

Table 7. High-yielding drought-tolerant varieties released from IRRI's drought marker-assisted breeding program.

Name	Designation	Country	Ecosystem	Release Year	Days to Maturity	Plant Height (cm)
Sukha dhan 4	IR 87707-446-B-B-B	Nepal	RL	2014	125	102
DRR 44	IR 87707-445-B-B-B	India	RL	2014	115	110
Yaenelo 4	IR 87707-446-B-B-B	Myanmar	RL	2015	115	117
Yaenelo 5	IR 87705-44-4-B-B	Myanmar	RL	2016	115	117
Yaenelo 6	IR 87707-182-B-B-B	Myanmar	RL	2016	115	117
Yaenelo 7	IR 87705-83-12-B-B	Myanmar	RL	2016	115	117

Source: Modified from Kumar et al. [89].

Genetic linkages; complex gene network; QTL × QTL, QTL × background, QTL × environment interactions [175,184]; and pleiotropy are the most important aspects in breeding when studying the complexity of genetic regions related to drought biotic and abiotic stress traits. The linkage of $qDTY_{1.1}$ and sd1 supports the fact that during the green revolution era the drought-tolerant alleles were not maintained properly during the development of dwarf varieties for the irrigated ecosystem. The debate continued on the pleiotropic effect of dominant allele of sd1 on drought vs. linkage of dominant allele of sd1 with drought tolerance. The possibility of a pleiotrophic effect indicated the separation of the drought-susceptible allele and dwarfness is impossible. Vikram et al. [121] have successfully demonstrated the linkage of $qDTY_{1.1}$ with the sd1 gene, nullifying the debate on the linkages or pleiotropic effects of the sd1 gene. The development of new drought-tolerant dwarf lines is a successful example of breakage of linkages between $qDTY_{1.1}$ and sd1 loci. Many studies reported the collocation of major and consistent drought grain yield (GY) QTLs such as $qDTY_{1.1}$, $qDTY_{2.3}$, $qDTY_{3.1}$, $qDTY_{3.2}$ and $qDTY_{12.1}$, with QTLs for days to flowering and plant height [50,52,53,144]. The linkages of the drought QTLs were successfully broken and drought-tolerant lines in Swarna, IR64, and Vandana background were developed [74].

Pyramiding QTLs for a quantitative trait such as grain yield may be an effective approach to combine superior alleles and achieve the desirable phenotypic level of variation [185]. QTL pyramiding may be an appropriate approach to improve the efficiency of marker-assisted selection for desirable loci in rice breeding programs and to understand the interactions among genetic loci. Under severe reproductive-stage drought stress, grain yield advantage of 0.8–1.0 t·ha^{-1} was reported in QTL introgression programs involving popular high-yielding varieties IR64 and Swarna [144,178]. The QTL pyramiding program ongoing at IRRI in the background of popular rice varieties Swarna, IR64, Vandana, Sabitri, TDK1, Anjali, Samba Mahsuri, MRQ74, MR219, and some Korean lines (Jinmibyeo, Gayabyeo, Hanarumbyeo, and Sangnambatbyeo) uses the different marker-assisted breeding approaches shown in Table 8. It is evident from Table 8 that, even for the same QTL, researchers may have to find and use different sets of peak and flanking markers depending on the polymorphism of the donor and recipient and the identification of such polymorphic markers within the QTL region. Fine mapping, physiological and molecular characterization of the QTL interval to capture all the desirable genes with positive interactions contributing to drought tolerance is an important step before initiating a QTL introgression program.

Table 8. QTL pyramiding program ongoing at IRRI in the background of popular rice varieties through marker-assisted breeding.

Breeding Approach [a]	QTLs	Marker	Target Variety	Target Ecosystem
MAS	$qDTY_{3.1}$, $qDTY_{12.1}$	$qDTY_{3.1}$: RM416, RM16030, RM520 $qDTY_{12.1}$: RM28048, RM28130, RM28099, CG29430, indel8	Anjali	Rainfed upland
	$qDTY_{12.1}$	$qDTY_{12.1}$: RM28048, RM28130, RM28099, CG29430, indel8	Kalinga	Rainfed upland
	$qDTY_{2.2}$, $qDTY_{4.1}$	$qDTY_{2.2}$: RM236, RM279, RM555 $qDTY_{4.1}$: RM518, RM335, RM16368	IR64	Rainfed lowland
	$qDTY_{1.1}$, $qDTY_{1.2}$, $qDTY_{2.2}$, $DTY_{2.3}$, $qDTY_{3.2}$, $qDTY_{4.1}$, $qDTY_{12.1}$	$qDTY_{1.1}$:RM11943, RM12023, RM12233 $qDTY_{1.2}$:RM212, RM3825, RM315 $qDTY_{2.2}$: RM236, RM279, RM555 $qDTY_{12.1}$: RM28048, RM28130, RM28099, CG29430, indel8 $qDTY_{2.3}$: RM3212, RM573, RM1367 $qDTY_{3.2}$:RM523, RM22, RM545 $qDTY_{4.1}$: RM518, RM335, RM16368	IR64	Rainfed lowland
	$qDTY_{1.1}$, $qDTY_{2.1}$, $qDTY_{3.1}$	$qDTY_{1.1}$:RM11943, RM12023, RM12091, RM12233 $qDTY_{2.1}$: RM5791, RM521, RM3549, RM324, RM6374 $qDTY_{3.1}$: RM416, RM16030, RM520	Swarna	Rainfed lowland
	$qDTY_{12.1}$	$qDTY_{12.1}$: RM28048, RM28130, RM28099, CG29430, indel8	Vandana	Rainfed upland
MAB	$qDTY_{2.2}$, $qDTY_{4.1}$	$qDTY_{2.2}$: RM236, RM279, RM555 $qDTY_{4.1}$: RM518, RM335, RM16368	Samba Mahsuri	Rainfed lowland
	$qDTY_{3.1}$, $qDTY_{6.1}$, $qDTY_{6.2}$	$qDTY_{3.1}$: RM55, RM168, RM186, RM293, RM468 $qDTY_{6.1}$:RM204, RM217, RM508, RM586, RM587 $qDTY_{6.2}$: RM3, RM541	TDK1	Rainfed lowland
	$qDTY_{3.2}$, $qDTY_{12.1}$	$qDTY_{3.2}$: RM231, RM517 $qDTY_{12.1}$: RM28048, RM511, RM28199, RM28166	Sabitri	Rainfed lowland
	$qDTY_{2.2}$, $qDTY_{3.1}$, $qDTY_{12.1}$	$qDTY_{2.2}$: RM236, RM279, RM12460 $qDTY_{3.1}$: RM416, RM16030, RM520 $qDTY_{12.1}$: RM28048, RM511, RM28099, RM28166, CG29430, indel8, RM28130	MR219	Rainfed lowland
	$qDTY_{2.2}$, $qDTY_{3.1}$, $qDTY_{12.1}$	$qDTY_{2.2}$: RM154, OSR17, RM12460 $qDTY_{3.1}$: RM416, RM15935, RM520 $qDTY_{12.1}$: RM28048, RM511, RM28099, RM28166, CG29430, indel8, RM28130	MRQ74	Rainfed lowland
	$qDTY_{1.1}$, $qDTY_{2.2}$	$qDTY_{1.1}$:RM431, RM11943, RM12023, RM12091, RM12233 $qDTY_{2.2}$: RM236, RM279	Jinmibyeo	Rainfed lowland
	$qDTY_{1.1}$, $qDTY_{2.2}$	$qDTY_{1.1}$: RM12023, RM12146 $qDTY_{2.2}$: RM236, RM279	Gayabyeo	Rainfed lowland

	QTLs	Markers	Recipient	Ecosystem
	$qDTY_{1.1}$, $qDTY_{2.2}$	$qDTY_{1.1}$: RM11943, RM12233 $qDTY_{2.2}$: RM236, RM279	Hanarumbyeo	Rainfed lowland
	$qDTY_{1.1}$, $qDTY_{2.2}$	$qDTY_{1.1}$: RM11943, RM12233 $qDTY_{2.2}$: RM109, RM279	Sangnambatbyeo	Rainfed lowland
MARS	$qDTY_{1.1}$, $qDTY_{2.1}$, $qDTY_{3.1}$, $qDTY_{11.1}$	$qDTY_{1.1}$: RM212, RM486 $qDTY_{2.1}$: RM525, RM221 $qDTY_{3.1}$: RM16, RM520 $qDTY_{11.1}$: RM287	Samba Mahsuri	Rainfed lowland

[a] MAS: marker-assisted selection, MAB: marker-assisted backcrossing, MARS: marker-assisted recurrent selection

4.3. Interactions between QTLs (Q × Q), QTLs and Genetic Background (Q × G), and QTLs and the Environment (Q × E)

Undesirable genetic linkages, QTL × genetic background (Q × G), and QTL × environmental interaction (Q × E) play an important role in restricting the use of QTLs in marker-assisted breeding [109,186,187]. The combined effect of alleles at more than one locus on a trait of interest, which departs from simply adding up the effects of the alleles at each locus, represents the case of genetic interaction. Many examples of such interactions are known [188], but the relative contribution of interactions to trait variation is questionable. The large sample size population, effective screening strategy, screening under variable conditions and environment, accurate genotyping, and analytical approach increase the power to detect the QTLs, Q × Q, and Q × E interactions. These interactions could be one of the possible reasons for the variable effect of QTLs in different genetic backgrounds and environments. Identification and pyramiding of positively interacting large-effect QTLs may provide a wider adaptability of QTLs across genetic backgrounds and environments. The effect of the QTLs varies with donors and recipients [50,51]. To achieve success in QTL pyramiding, there is a need to identify QTLs with large and consistent effect under variable environmental conditions; different intensities of stress; multiple genetic backgrounds; and positive interaction between QTLs different genetic backgrounds, QTLs × environment, and QTLs × genotype × environment for appropriate yield increase under drought [50,125]. The selection of donor and recipient varieties in a breeding program requires the consideration of factors such as flowering synchronization, cross compatibility, maturity duration, resistance/susceptibility to biotic and abiotic stresses, and adaptability to environment, and grain quality traits. Stability of grain yield QTLs under drought, different backgrounds, and environments have been reported by Bernier et al. [125] ($qDTY_{12.1}$; 21 experiments conducted at IRRI and in eastern India), Mishra et al. [167] ($qDTY_{12.1}$; at IRRI and Nepal) and Yadaw et al. [168] ($qDTY_{3.2}$ at IRRI, Nepal). Seven *DTY* QTLs—$qDTY_{1.1}$ [50,51,177], $qDTY_{2.2}$ [52,178], $qDTY_{3.1}$ [50,144], $qDTY_{3.2}$ [51,168], $qDTY_{4.1}$ [178], $qDTY_{6.1}$ [50,177], and $qDTY_{12.1}$ [54,167]—have shown consistent effect across two or more genetic backgrounds and ecosystems. Four of the identified *qDTY* QTLs—$qDTY_{1.1}$, $qDTY_{2.2}$, $qDTY_{6.1}$ and $qDTY_{12.1}$ [49,52,173] are also known to be associated with increased yield under dry direct-seeded/aerobic situation. Dixit et al. [189] reported positive interaction of $qDTY_{2.3}$ and $qDTY_{3.2}$ with $qDTY_{12.1}$ and Shamsudin et al. [190] reported the positive interaction of $qDTY_{2.2}$ and $qDTY_{3.1}$ with $qDTY_{12.1}$, significantly increasing the yield of $qDTY_{12.1}$ positive lines. Identification of major QTLs for grain yield under drought with a larger and more consistent effect across genetic backgrounds and ecosystems has opened new opportunities of developing new rice varieties with better adaptations to predicted future scenarios.

Besides the contribution of a single genetic region, linkage, pleiotropy [191], and epistasis were reported to be key factors of quantitative traits [192] in wheat, soybean, and rice [109,193–197]. However, few studies have been conducted on the existing positive and negative interactions among different rice yield-related traits/QTLs under drought stress. Unfavorable linkages between desirable and undesirable traits such as high yield under drought, tall plant height, and very early flowering were successfully broken through breeding to develop high-yielding, medium-duration,

drought-tolerant rice varieties [121,178]. *qDTY*3.2 was reported to interact with *qDTY*1.1 and *qDTY*12.1 for reduction in flowering duration [74]. Strong interactions between QTL-affecting quantitative traits have also been observed in maize, soybean, and other cereal crops [198–201].

A multi-disciplinary approach involving understanding physiological and molecular mechanisms associated with QTLs/genes across variable environments, identification and validation of genomic coordinates for correlated traits, differential expression of genes involved in metabolic processes, signal transductions, and response of identified genes can be used to explain drought tolerance in detail and to select/identify genotypes with stable and improved yield under multiple stresses.

4.4. Transgenic Approaches

Transgenic approaches involve the incorporation of specifically cloned genes by limiting the transfer of unwanted genes from the donor organism. Transgenic approach is being practiced throughout the world to improve resistance to biotic stresses and tolerance of abiotic stresses in a number of crops. Rapid progress in recombinant-DNA technology and development of accurate and efficient gene-transfer protocols have resulted in efficient engineering of genes encoding compatible organic solutes [202], and biosynthesis of glycine betaine in tobacco and maize [203,204]; trehalose-6-phosphate synthase or phosphatase (TPSP) in rice [205], and tobacco [206,207]; choline dehydrogenase in maize [204]; and pyrroline-5-carboxylate synthetase (P5CS) in wheat [208], tobacco [209], soybeans [210], and petunias [211].

Although the transgenic approach is expected to be faster and more precise, there are still constraints associated with it, including gene silencing, undesirable genetic alterations resulting from the transformation process, ethical issues, public acceptability, and the assurance time in biosafety regulations and release. Sometimes the transgenic lines that had shown remarkable performance under controlled laboratory or glasshouse conditions would not be able to survive under natural field conditions where they encounter a myriad of environmental factors. The growth and development stages of plants play a significant role in defining tolerance as the tolerance seen in transgenic lines at one particular stage may not be the same at other growth stages.

4.5. Novel Strategies

Besides conventional and marker-assisted selection, heterosis breeding, recurrent selection, bi-parental mating, disruptive mating, candidate gene identification, gene cloning, plant tissue culture, and foreign gene transfer, novel opportunities of exploiting the full potential of genomics-assisted breeding are on the way and will require an integrated knowledge of high-throughput phenotyping and molecular, physiological, and developmental processes that influence drought tolerance. Genomic selection allows breeders to consider the effect of a huge number of markers to calculate the Genomic Estimated Breeding Value (GEBV), and select a few desired individual plants for phenotypic selection in the field. On the other hand, traditional breeding involves many cycles of selections based on plant phenotypic evaluation or taking the result of a few trait-linked markers into account for quality, disease, and pest resistance. Breeders no longer need to select for individual traits; instead, they can select the combination of traits based on breeding value. This allows for easy selection; breeding cycles are shortened and several breeding programs can run at the same time by planting even a few good progenies within a limited budget.

The supplementation of old with modern breeding techniques and innovative technologies based on the science of genomics may greatly help in increasing crop productivity under drought. With the rapid progress in structural and functional genomics, proteomics will certainly be beneficial to polish existing approaches to achieve significant progress in future crop improvement. The development of genome-wide analytical tools may constitute a turning point towards the easier transfer of beneficial traits to locally adapted varieties. Genome-wide association studies (GWAS) have been widely used as a popular method to identify genetic regions related to drought tolerance traits in plants [169–172]. GWAS provides a better platform in screening a large number of accessions for genetic variation underlying diverse complex traits. Recent studies reported the combined

approach of GWAS and candidate-gene sequencing as a more powerful approach than separate individual approaches [212].

The available rice genome sequence information will make it feasible to produce comprehensive datasets on all existing information on genes; gene function; biochemical and molecular pathways; protein profiles; metabolites and gene expression; comparison of the genome, genes, and intergenic regions between cereal species; and allele mining in the large collection of rice germplasm and wild species. A compilation of all this information will be a boon for the scientific community as it tries to develop new varieties with high yield and stabilize this trait along with resistance to pests and disease; tolerance to drought, salinity, flood, and cold; and improved nutritional quality. The involvement of similar transcription factors, various common stress-inducible genes, and similar physiological and molecular responses in both dicotyledonous and monocotyledonous plants under abiotic stress was reported in *Arabidopsis*, wheat, and rice [213–216]. The syntenic relationships between different cereal crops and grasses allow developmental biologists, biochemists, and physiologists to inspect the gene complements in related species to see which pathways are common and which are unique, and how these pathways may have been modified. The vast reservoir of available genetic resources (introgression lines, mapping populations, wild species, mutants, NILs (near-isogenic lines), RILs (recombinant inbred lines), improved breeding populations, and double haploids) and the huge amount of genomic, transcriptomic, proteomic, and metabolomic information in rice would be valuable materials in the structural and functional genomics of designing novel rice varieties for a particular ecosystem. High-throughput approaches such as DNA sequencing, SNP chips, microarray, serial analysis of gene expression (SAGE), site directed mutagenesis (T-DNA insertion, transposon tagging and homologous recombination), RNA-mediated interference, yeast two-hybrid screening, and metabolite quantification will help in identifying the conditions under which various genes are expressed and the phenotype that results when they are knocked out or when their expression is altered. This will assist with the identification of alleles conferring a superior phenotype. Bioinformatics will be useful to inter-link the phenotypic data gathered from different locations under different conditions for diverse germplasm with sequence information, which will ultimately provide information on candidate gene, gene function, and phenotypic and genotypic expression of specific genotypes, thereby helping with breeders' development of elite cultivars [217]. Crop models involving the interaction of breeding, genomics, physiology, and system and functional biology will enable us to fill the gap between genotype and complex phenotype [218].

5. Conclusions

Agriculture has undergone dramatic shifts starting from the introduction of new semi-dwarf rice varieties in 1966. This shift has been less evident in rainfed areas due to the susceptibility of modern semi-dwarf varieties to most of the abiotic stresses prevalent in rainfed ecosystems. Under ongoing climate change, which is predicted to increase the frequency of moderate to severe drought, there is an immediate need to improve existing technologies and compile all the information we have for developing better rice varieties for drought-prone areas. This challenge can only be met with long-term systematic research on drought to generate a better understanding of rice plants that can survive with less water like other cereals.

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