**Genomics Assisted Breeding to Enhance Drought Tolerance in Rice Cultivars**

Nabarun Roy1\*, Rahul Kaldate2, Achal Kant3\*, Dharmendra Singh Lagoriya2, Prashant Bisen3 and Biswajit Pramanik4

1School of Smart Agriculture, Adamas University, Kolkata 700126, West Bengal, India

2Department of Agricultural Biotechnology, Assam Agricultural University (AAU), Jorhat 785013, Assam, India

3Narayan Institute of Agricultural Sciences, Gopal Narayan Singh University, Sasaram 821305, Bihar, India

4Department of Genetics and Plant Breeding, Institute of Agriculture, Visva-Bharti University, Sriniketan 731236, West Bengal, India

**\*Corresponding author:**

nabarunroyagartala@gmail.com

786achalgupta90@gmail.com

**Abstract**

Rice is a drought-prone crop due to its small root system, thin cuticular wax, and rapid stomatal closure. Due to the sterility of spikelets, it is highly susceptible to drought stress during the reproductive stage; therefore, identifying QTLs associated with drought tolerance is required in order to develop drought-tolerant rice varieties. Drought tolerance in plants is a highly complex mechanism that is influenced by plant phenology and controlled by several quantitative trait loci (QTLs). Whereas the availability of a complete rice genome sequence, widely distributed SNP markers throughout the genome, and low-cost genotyping platforms aided in the successful dissection of these complex traits, resulting in the identification of QTLs for various yield and physiological traits under drought stress. Some of the major QTLs were fine-mapped, and the genes associated with drought tolerance were studied and validated. Furthermore, the identified QTLs or candidate genes could be used to develop drought-tolerant rice varieties.

**Key words:** **Rice, Genomics, Markers, QTLs, Drought.**

1. **Introduction:**

Around 7.8 billion people are living in this world in the 3rd decade of the 21st century which is expected to hit 9.8 billion in 2050 [1]. An impressive advancement in industry, economy and finance have been reached alongside extraordinary developments in medication hence improving human wellbeing and broadening the life expectancy. Despite this progress, nearly 2 billion people worldwide continue to face moderate to severe food insecurity, with developing countries housing the vast majority of the world's hungry [2]. This outlooks the savior importance of agriculture in the world scenario. Major cereals crops including rice, maize, wheat, millets, and other grains are the world's staple foods, but global agriculture at presently facing a serious threat from climate fluctuations in the form of stress, which is expected to result in lower productivity. Hance, increasing food costs and global food insecurity are the results of decreased production and rising population demand, and if this situation persists, it will inevitably lead to further increases in food prices, as well as social unrest and famine in some cases [3].

Climate fluctuations will have a major disastrous impact on food supply unless steps are taken to improve crop resilience: forecasts for 2030 show a significant decline in major cereals production, including 14% for wheat, 11% for rice and 9% for maize [4]. This situation has compelled plant researchers to develop climate-resilient crops that can withstand broad-spectrum abiotic stresses like drought, heat, cold, flood, submergence, salinity and biotic stresses like diseases and insect pests, thereby contributing to rising productivity. Drought has always been the primary cause of many previous famines, and it has had a devastating impact on agriculture all over the world. Rice (*Oryza sativa* L.) is the second most important staple food crop in the global market, after wheat, and is consumed by nearly half billion of the world's population [4]. The world's rice production is estimated to be 782 million tonnes, with rice acreage totaling 167.13 million hectares. [5]. Rice is a heavy water consumer, requiring approximately 5,000 litres of water to harvest 1 kg of rice, and is less efficient in its water use than wheat or maize. Grain production (particularly rice) has a very high water footprint, followed by meat and dairy products [4].

Rice has two distinct ecosystems. That is, uplands and lowlands with water management options such as rainfed or irrigation. Irrigation, rainfed lowlands, rainfed uplands, and flood-prone rice ecosystems account for 50%, 34%, 9%, and 7% of total rice cultivation area [6]. Under irrigated conditions, current rice varieties yield an average of 4.5t ha-1. As climate change, urbanisation, and competition from high-value agriculture continue to put pressure on rice growing lands around the world, an additional 8-10 million metric tonnes of rice will need to be cultivated over the next decade, with an annual increase of 1.2%-1.5% (0.6 t ha- 1) [7].

Most rice quantitative trait loci (QTLs) were mapped with single sequence repeats (SSRs) markers (see Table 1). Large-effect QTLs were introgressed to improve rice drought tolerance. These marker methods are labor-intensive, technically challenging, and unsuitable for creating a saturated linkage map. Low-density linkage maps make it difficult to include drought-tolerant QTLs into a breeding programme [9]. Whole genome sequencing data in rice made it feasible to construct an endless number of markers. Single nucleotide polymorphisms (SNPs) genotyping has almost fully superseded other genotyping technologies (e.g., microsatellites or AFLPs) in breeding programmes [10, 84, 86]. SNPs are high-frequency, low-mutations rate, and high-throughput. SNPs account for 90% of genetic diversity and are the most abundant molecular marker system. High-throughput SNPs genotyping platforms enable rapid, routine, and cost-effective genotyping solutions for Marker Assisted Selection (MAS) on big effect QTLs or genes of interest. Genome-wide SNPs genotyping enables targeted genomic selection (GS) *viz*., MAS techniques and increases the effectiveness of other breeding efforts [11].

1. **Drought as a constraint in rice production:**

60% of the world's population depends on rice. Growing population, water demand, reduction in arable land, nutrient depletion, weed competition, and biotic/abiotic stress make food production for the poor and rich difficult [12, 85]. As home and industrial demands rise, agricultural water supply declines [13]. Almost half of the world's population may face water scarcity/drought by 2030 due to climate change and erratic rainfall. Every year, droughts strike unexpectedly. The Deccan famine and droughts in the U.S., Vietnam, Australia, Brazil, Kenya, Tanzania, Ethiopia, Somalia, China, India, and Bangladesh were the worst [7, 8]. Between 2003 and 2013, moderate-to-large natural disasters generated US$70 billion in crop and livestock output losses, with drought accounting for 44%. Asia's crop and livestock production losses amount $28 billion (40% of overall losses), followed by Africa's $25 billion. Drought causes rice panicle initiation (PI) stage damage [14]. To ensure food sufficiency, boost rice output in these regions during droughts.

Water stress/drought affects rice's morphology (reduced germination, plant height, biomass, number of tillers, root and leaf traits), physiology (reduced photosynthesis, transpiration, stomatal conductance, water use efficiency, relative water content, chlorophyll content, photosystem II activity, membrane stability, carbon isotope discrimination and abscisic acid content), and biochemistry (accumulation of osmoprotectants like proline Drought renders rice more sensitive to biotic stressors (bacterial blight, blast, tungro, yellow mosaic virus), lowering grain production. Drought affects 23 million hectares of rainfed rice [12, 13]. Over-exploitation of groundwater has hampered rice production in South and Southeast Asia. In northern China, the groundwater table has decreased 100-300 cm per year, and in India, 50-70 cm per year. In 2019, 135 million individuals in 55 countries or territories, or 16% of the global population, were food insecure. 29 million people were under acute food insecurity due to climate shocks like drought, floods, extreme temperature occurrences (heat waves, cold waves), pest, locust, and disease infestations, etc. [15]. With limited water supplies for agriculture worldwide, it's necessary to increase rice's drought tolerance and screen for resistant/tolerant types. To select or produce drought-tolerant rice varieties, it's necessary to understand the mechanisms that influence rice yield under water stress [16].

To filter alleles conferring stress tolerance, genetic resources must be evaluated for abiotic stress tolerance. However, genomics is required for their precise and stable incorporation into the genome. Physical mapping of genes/QTL, followed by cloning and functional characterization, is required for marker-assisted introgression. After identifying good donor parents, they are introgressed into elite varieties using a variety of methods such as marker assisted backcross breeding (MABB) or marker assisted recurrent selection (MARS) [7, 8, 87].

1. **Response of rice towards drought and adaptation:**

Drought resistance has been divided into three major mechanisms to systematically understand the plants' response to drought stress: drought escape, avoidance, and tolerance.

**Drought escape:**

Drought escape is when a plant is able to finish its life cycle before a drought hits. This is possible because of the flexibility of development, especially fast phenological development. It's a way for plants to adapt to their environment so they can avoid the most important times for their growth. Farmers use this plant strategy to make sure that the crop cycle happens when conditions are good. For example, making varieties with shorter growth cycles so that plants can avoid the most stressful times of the year, changing the date of sowing, and/or choosing varieties that don't need as much water. This is an important way to stop drought from getting worse [17].

**Drought avoidance:**

Drought avoidance is a plant's capacity to resist drought even in low soil moisture by maintaining ambient water levels. Increased soil water uptake or reduced water loss can achieve this. Better root design helps plants resist drought by increasing water intake. Plants with improved stomatal control or waxy leaves can minimize transpiration and escape drought [17].

**Drought tolerance:**

Drought tolerance is defined as plant tolerance at 23% or 0.3 g of fresh tissue moisture. A plant is tolerant if it yields more than sensitive plants. Tolerance helps cells survive despite water shortages. Drought tolerance methods include cellular modifications, physiological acclimation, and morphological adaptations. Increased chlorophyll, decreased osmotic potential, and higher harvest index improve drought tolerance. Physiological acclimation increases stomatal density and conductance, decreases transpiration rates, reduces and early blooming and maturation asynchrony, and improves production, accumulation, assimilation, and seed and biomass yield partitioning. Morphological adaptations include thicker and longer roots, waxy or thick leaf coatings, fewer epithelial cells, delayed leaf senescence, and more green leaf area [14, 17].

Drought responses vary by rice genotype. In drought-prone locations, it's wise to genetically modify drought-resistant crops. Rice has many genetically variable features that help it endure drought. Most conventional drought breeding focuses on secondary traits like root architecture and mass, physiological parameters like water use efficiency, relative water content, osmotic adjustment, oxidative stress management, leaf rolling, stomatal conductance, cell membrane stability, epicuticular wax, canopy temperature and stem reserve mobilization [14, 17]. Poor heredity, inconsistent or little association with yield under stress, low contribution to phenotypic variance of yield during drought, difficulty in precision phenotyping, and many metabolic pathways prevented progress in breeding for drought tolerance [4, 7]. Despite the moderate heritability of yield traits, detailed research has been done to identify meta-QTLs for yield under stress as a breeding criterion. These reflect the hotspot locations for drought tolerance in rice crop. The rice genome sequencing project and advances in genotyping have allowed us to map the genetic basis of drought tolerance [18].

**4. Donors, recipients, mapping population and genetic mapping:**

Identifying donors is the first stage in every breeding operation. Choosing a donor from a big germplasm collection is crucial. Using a donor with specialized qualities for a specific environment can boost variation and trait development. Most conventional donors have undesirable features and aren't suited for breeding. These landraces exhibit unfavourable features such little ground cover, towering plant height, low yield potential, and poor grain and eating quality [7, 13]. Modern rice varieties have excellent yield, enhanced plant type (early vigour, medium height, lodging resistance), tolerance to biotic stress, and good grain type (medium to long and slender). They're drought-sensitive, thus they're beneficiaries. To breed for a particular characteristic and obtain new gene combinations, old landraces with desirable qualities and current enhanced varieties with high yield potential must be used [7, 8]. Genetic mapping can be done by crossing donor and recipient plants.

Aday Sel, Dagaddeshi, Kali Aus, Aus276, N22, Apo, Dular, and IR77298-14-1-2 were utilized in traditional breeding and QTL mapping at the International Rice Research Institute (IRRI). Mapping populations incorporating these traditional donors yielded drought-tolerant lines without negative links for conventional breeding operations. In marker-assisted breeding projects, lines with identified drought grain yield QTLs were employed to develop mega cultivars [7, 8].

Genetic mapping or linkage mapping is based on surveying recombination frequencies for specific genes (or markers) in the mapping population, which consists of offspring descended from two or more parents of a species or similar species. First, create a mapping population for linkage or genetic maps. Biparental mapping uses extremely homozygous, inbred parents to develop the population. F2 progeny, immortal F2 populations, backcross populations (BC), recombinant inbred lines (RIL), double haploids (DH), near isogenic lines (NIL), nested association mapping (NAM), exotic libraries and advanced backcross populations, chromosome segment substitution lines (CSSL), backcross inbred lines (BIL), advanced crossing lines (AIL), backcross populations with recurrent selection, linked mapping populations, fo. Each population type has advantages and limits, thus choosing one is key to accurate genetic mapping. Next section details some of this work.

Association mapping uses accessions from germplasm collections of cultivars, landraces, or breeding material to discover QTLs by assessing the connections of markers with the characteristic that can be explained by "linkage disequilibrium" between markers and polymorphisms in a set of diverse genotypes. Multiple generations of recombination link markers to trait-related genes. Association mapping is used to detect rice QTLs [20]. Six marker-trait associations (MTAs) for GY under drought stress were found on chromosomes 2, 3, 5, 6, and 10 [21].

**5. QTL identification on grain yield and other secondary traits as selection criteria in mapping populations and candidate gene identification:**

Using DNA markers to generate genetic linkage maps and discover agronomically significant genes has enabled the development of improved plant varieties through marker-assisted selection. Molecular mapping is used to examine physiologically complicated processes with quantitative properties. Rice QTLs have been found for height, flowering time, panicle number, and yield components. QTL discovery, independent of the crop, identifies the relationship between a genetically determined phenotypic and genetic markers. Well-characterized QTLs are called QTLomes. QTL analysis helps plant breeders and molecular geneticists manage complicated trait components [17, 22].

In the past, cereal crop productivity, i.e., the green revolution, was increased by selecting above-ground plant parts, but in an era of climate change, the focus has changed to exploiting below-ground components, i.e. roots, which play a crucial role in overcoming abiotic challenges. To accomplish the next green revolution, breeding efforts must address rice's drought-resistant root design. Traditional breeding methods rely on extensive phenotypic screening, but this is a tedious and time-consuming procedure that slows the development of climate-resilient cultivars. Molecular techniques can speed up climate-resilient breeding [18, 22].

In 1995, 18 QTLs for drought tolerance in rice crop were discovered using RILs from CO39 and Moroberekan and RFLP markers [23]. In the same year, 37 QTLs for 12 quantitative characteristics, including grain yield (GY), were mapped from a BIL population using RFLP markers [24]. In 2002, it was determined that leaf water potential and osmotic adjustment could improve rice's drought tolerance [25]. 47 QTLs in rice for water stress, phenology, and production traits [26]. All of these efforts to improve drought resistance relied on secondary features such as root architecture, leaf water potential, osmotic adjustment of crown surface temperature, and relative water content. Later, these secondary variables rarely had higher heritability (H) than GY under drought stress and were rarely linked with GY [27,28].

Seven QTLs were found on chromosomes 3, 4, 6, and 10 for GY from a subset of DH lines resulting from a hybrid between CT9993-510-1-M and IR62266-42-6-2 [29]. GY was associated with biological yield (BY), harvest index (HI), days to flowering after start of irrigation gradient (DFAIG), total spikelet number (TSN), percent spikelet sterility (PSS) and plant height in well-watered conditions (PH). Only BY and HI were related with GY during drought condition. Under full irrigation and extreme drought stress, the same population showed a strong QTL for GY, *qDTY1.1* [30]. *qDTY1.1* came from CT9993-510-1-M, accounting for 15% of yield PVE. The region was linked to grains per panicle (control), panicle number (control and stress), plant height (control and stress), root dry weight, leaf curl, and leaf dryness (stress). Here is the dwarfing gene sd1. This locus didn't affect plant height.

Good response to direct selection for GY in highland rice during reproductive stage drought stress (RS) shows the relevance of donor selection in producing drought-tolerant rice [31]. Most rice drought QTLs are in less attractive genotypes. Previously, IRRI researchers has shown moderate to higher heritability of GY under RS condition, supporting effective direct selection. Therefore, Direct selection for GY under RS has found promising breeding lines under rainfed lowland and highland habitats.

In 2007, an F3 population from a Vandana and Way Rarem hybrid had *qDTY12.1*. It explained 51% of GY's genetic variance under RS, had positive impacts on HI, BY, and PH, and shortened blooming days. This QTL increased grain yield in severe or moderate highland drought, but not in upland non-stress or transplanted lowland drought [32]. *qDTY12.1* boosts drought grain yield by 7%. This was the first QTL found in rice with a large and recurrent influence on GY under severe drought stress in the field vs numerous recipient genetic backgrounds, such as Sabitri, for high GY under RS [33].

In 2009, two QTLs, *qDTY2.1* and *qDTY3.1*, were found in an Apo-Swarna RIL population. In lowland drought, QTLs affected GY (R2=13-31%) [34]. *qDTY3.1* was mapped again using a BC1F3:4 population obtained from an IR55419-04 / TDK1 cross, accounting for 7.9% of PVE [35].

Using RILs from a hybrid between shallow-rooting IR64 and deep-rooting Kinandang Patong, a significant QTL *Dro1* was found on chromosome 9. This QTL explained 66% of plant height. Higher photosynthetic rates and grain filling increased yield in *DRO1*-introduced lines. Backcrossing DRO1 into shallow-rooted rice cultivars improves drought resistance [36].

In 3 F3:4 mapping populations produced from crossings of N22 with Swarna, IR64, and MTU1010, four QTLs were mapped [37]. QTL *qDTY1.1* had a large and consistent influence in all three RS and NS populations. Three QTLs were population/environment-specific. *qDTY1.1* was also identified in Dhagaddeshi, Apo, Swarna, and IR64 RIL populations [38, 39]. *qDTY1.1* was substantially related with PH in dry and wet seasons due to the *sd1* locus. The large-effect QTL *qDTY3.2* was identified in Backcross inbred lines (BIL) produced from separate crossings of IR77298-5-6-18/ Sabitri and Swarna/ WAB 450-I-B-P-157-2-1 [40, 41]. Stress boosts *qDTY3.2*'s impact.

Large-effect QTL *qDTY6.1* for GY under severe and mild drought stress in 3 populations: Apo /IR72 BIL, Vandana /IR72 RIL and Apo/Swarna RIL [42]. qDTY6.1 and qDTY6.2 were mapped for GY during drought in rice using a BIL population derived from IR55419-04 / TDK1, which demonstrated consistent effect across seasons under lowland drought-stress conditions [43].

Four QTLs, *qDTY2.2*, *qDTY4.1*, *qDTY9.1* and *qDTY10.1*, for GY under drought were identified using BILs from an Aday Sel/IR64 hybrid [44]. Non-stress situations did not correlate these four qDTY QTLs with GY. They also found several differentially expressed genes (DEGs)/candidate genes inside the 4 QTL zones, some for biotic and abiotic stress defence.

Two major-effect GY QTLs, *qDTY2.2* and *qDTY2.3*, were discovered under drought stress in 2 BIL populations, Kali Aus/MTU1010 and Kali Aus/IR64 [45]. *qDTY2.2* and *qDTY2.3* explained 6% and 9% of PVE. *qDTY2.2* and *qDTY2.3* were likewise mapped in Kali Aus/MTU1010 and Kali Aus/IR64 [46]. *qDTY1.2* and *qDTY1.3* from the same populations were likewise substantial and consistent effect QTLs.

In rice, three important impact QTLs were identified: *qDTY11.1*, *qDTY1.1*, and *qDTY3.3* under irrigated transplant conditions and terminal stage drought (TSD), respectively. The positive additive effects of these QTLs, with the exception of *qDTY3.3*, show that the alleles at these loci boost grain yield under various conditions and are derived from the tolerant parent Dagaddeshi [47]. In a BIL population derived from the cross of Moroberekan and Swarna/MTU7029, two QTLs, *qDTY3.2* and *qDTY11.1*, for GY under drought were identified. These QTLs account for a PVE of 16.0% and 25.0% under lowland severe stress (LSS) and upland mild stress (UMS), respectively [35]. When compared to *qDTY3.3*, *qDTY11.1* had a much larger percentage of retrotransposon proteins, and *qDTY3.2* had a significantly higher percentage of genes involved in the production and function of enzymes. It was known that 8% of the genes in *qDTY3.2* and 6% of the genes in *qDTY11.1* were directly linked to the stress response or those that might be essential for maintaining plant function under stress. These comprised the genes for zinc finger proteins, heat shock proteins, no apical meristem proteins, membrane, and cell cycle-related proteins. While *qDTY11.1* demonstrated the presence of numerous nucleotide-binding site leucine-rich repeats (NBS-LRR) genes, which are well-known to be important candidates for blast resistance, *qDTY3.2* also demonstrated the presence of flowering-related genes, such as AP2 domain-containing proteins and MADS box family genes. Swarna also supplied two more QTLs (*qDTY9.2* and *qDTY10.2*) for GY under NS. The biggest and most reliable QTL for the trait plant height was found to be *qDTH1.1*.

From a population of IR20 and Nootripathu, three GY QTLs—RM8085, I12S, and RM6836—were identified on chromosomes 1, 4, and 6 and were discovered to be persistent under drought over seasons [48]. A PVE of 20.9% and 19.6% for GY under drought stress was explained by QTL RM8085 and I12S. This experiment was continued, and it was discovered that two more reliable impact QTLs, RM11873 and RM11943, connected to GY during drought, were present in the same biparental population and were present across trials [60]. The GY QTL discovered at peak marker RM11943 was identical to that of GY under QTL *qDTY1.1* [49].

From a mapping population obtained from a hybrid of Dular and IR64-21, three significant consistent-effect QTLs for GY (*qDTY1.1*, *qDTY1.3*, and *qDTY8.1*) were discovered under NS and RS conditions [50]. Grain yield and features of the roots and agronomy that are connected to grain yield have been linked to the genetic locus *qDTY1.1*. Other 2 QTLs, *qDTY1.3* and *qDTY8.1*, were novel and had additive effects of 9.0–43.7 percent and heritability values of 3.1–7.6. *qDTY8.1* has been reported to contain QTLs for root-to-shoot ratio, maximum root length, relative germination vigour, and filled grain weight per plant, as well as genes for drought tolerance such as dehydration-responsive element-binding transcription factor and heat shock factor.

From a hybrid of Banglami and Ranjit, two QTLs for GY were identified with PVE ranging from 0.04% to 84% under both RS and NS circumstances [51]. The parent plant 'Banglami,' which is drought resistant, contributed to the identification of the QTL for GY (*qGYP7.1*) under RS. However, the high yielding, drought-prone parent 'Ranjit' contributed another QTL for GY (*qGYP9.1*) under NS. Three QTLs were discovered for GY under RS and NS after mapping the same biparental population in a later generation. Among these, a QTL (*qGY1.1*) derived from Banglami under RS, whereas, two QTLs (*qGY1.2*, *qGY11.1*) derived from Ranjit under NS conditions [52]. From the same biparental cross, 2 advanced breeding lines (B-15 and B-23) were also established for high GY under drought stress [51]. Under drought stress, there was significant heritability found among the lines for a variety of physiological and yield traits.

Using an F2 population from a cross between Cocodrie and Vandana, six QTLs for GY under drought were mapped [53]. Alleles from Vandana were responsible for QTLs *qGYD1.2*, *qGYD1.3*, *qGYD5.1*, and *qGYD8.1*. Alleles from Cocodrie were responsible for QTLs *qGYD1.1* and *qQYD9.1*. An F2:F3 population made up of plants from Cocodrie and Nagina 22 was used to find 4 GY QTLs: *qGY1.1*, *qGY7.1*, *qGY8.1*, and *qGY11.1*. These QTLs explained why PVE ranged from 7.9% to 13.3% [54]. For all of the QTLs, the drought-resistant parent N22 contributed the alleles that increased the average grain yield.

1. **Fine mapping of drought responsive GY QTLs in rice:**

Identifying genomic areas with a large and consistent effect on GY during stress allows for Marker Assisted Selection (MAS) of large-effect QTLs to develop high-yielding but drought-susceptible types. For MAS to work, the target QTLs must be unlinked. Many rice QTLs associated with grain output under stress were connected to QTLs influencing plant height and flowering days. Co-localization of these qualities is not desirable to breed variations for different habitats; consequently, an appropriate MAB approach to break the linkage with these traits must be created. Fine-mapping these areas is the greatest way to promote precise introgression and discover potential genes [16, 19].

*qDTY2.1*, *qDTY2.2*, *qDTY9.1* and *qDTY12.1* were fine-mapped for GY during drought [55]. *qDTY9.1* and *qDTY12.1* were resolved into several QTL regions. *qDTY2.1* and *qDTY2.2* were shrunk to 1.6 and 6.7 cM, respectively. The *qDTY9.1* area of 32.1 cM was shrunk into two segments of 9.4 (*qDTY9.1A*) and 2.4 cM (*qDTY9.1B*). The *qDTY12.1* region of 10.6 cM was shrunk into two segments of 3.1 (*qDTY12.1A*) and 0.4 cM (*qDTY12.1B*). Multiple intra-QTL genes (OsNAM 12.1 transcription factor-'no apical meristem' and co-localized target genes) were discovered in *qDTY12.1* NILs, which boosted root and panicle branching, transpiration efficiency, and yield during drought. Studies reveal drought-tolerance QTLs are complex loci where numerous genes may function independently or in collaboration to boost GY under drought. The 3.0 Mb QTL *qDTY6.1* was fine-mapped to 94.04 kb [56]. The consistent effect grain yield QTL *qDTY1.1* was fine mapped and found to harbour the green revolution gene '*sd1*'-semi dwarf region and other QTLs for plant height and flowering under water deficit condition [57].

Fine mapping of 2 GY QTLs under drought was also done [58]. The 6.7 cM *qDTY2.2* area was shrunk to 2.1 cM, and *qDTY8.1* was resolved into two sub QTLs between RM23132 and RM1578 (75.75 cM-77.66 cM), RM515 and RM1578 (75.11 cM-77.66 cM). *qDTY2.2* boosted tillers and *qDTY8.1* enhanced panicle length and productive tillers, boosting drought yield. Fine mapping of RM8085-RM3825 on chromosome 1 for GY under drought to 42.8 Kb from 1.6 Mb was done [48, 49].

1. **QTLian breeding in rice for drought tolerance:**

Now, QTLs are being put into leading cultivars to help breed rice that can handle drought better. This method focuses mainly on using marker-assisted breeding to improve mega-varieties, either by transferring a single QTL or by pyramiding several QTLs under a single stress condition, such as drought, flooding, or high salt levels, to combine high yield potential with good yield under multiple stress conditions [13, 18, 22].

In the background of Vandana [59], *qDTY12.1* was introduced successfully. When there wasn't enough water, the Vandana-introgressed lines with *qDTY12.1* had a yield advantage of 0.5 t/ha over Vandana. When there was enough water, they had the same yield as Vandana. The QTLs *qDTY2.2*, *qDTY4.1*, *qDTY9.1*, and *qDTY10.1* were put into BC lines with an IR64 background. These QTLs came in four, three, and two different ways. Introgressed lines with three and two QTLs had a yield advantage of 1.2–2.0 t/ha during drought, had the same yield as IR64 during normal irrigation, and had the same quality traits as IR64. The major-effect QTLs found for grain yield during drought have a genetic gain of 10% to 30% and a yield advantage of 150 to 500 kg/ha over the recipient parents. When different combinations of QTLs like *qDTY9.1*, *qDTY2.2*, *qDTY10.1*, and *qDTY4.1* were done [44], it was found that several backcross-derived lines in the background of IR64 had a yield advantage of 500 to 1800 kg/ha over the background cultivar, IR64, under different levels of stress.

Seven consistent QTLs *qDTY1.1*, *qDTY2.1*, *qDTY2.2*, *qDTY3.1*, *qDTY3.2*, *qDTY9.1* and *qDTY12.1* for GY under drought were used to make submergence-tolerant versions of three high-yielding mega rice varieties: Swarna-Sub1, Samba Mahsuri-Sub1, and IR-64-Sub1. The developed lines did better than the original varieties in both submergence and Introgression of two GY QTLs, *qDTY3.2* and *qDTY12.1*, along with *Sub1* in the Sabitri background and three GY QTLs, *qDTY3.1*, *qDTY6.1*, and *qDTY6.2*, along with Sub1 in the TDK1 background, were done in two different works, and NILs were made that had higher yields than Sabitri/TDK1 and were more resistant to drought and flooding than Sabitri/TDK1.

Through marker-assisted selection (MAS) and marker-assisted recurrent selection (MARS), different GY QTL combinations were used to increase the grain yield of the popular lowland-adapted rice variety Samba Mahsuri (MARS). Under RS and irrigated control, the average grain yield of pyramided lines (PLs) with *qDTY2.2*+*qDTY4.1* in MAS is significantly higher than that of lines with only one QTL. MARS PLs with 4 qDTYs (*qDTY1.1*+*qDTY2.1*+*qDTY3.1*+*qDTY11.1*) and 2 QTLs (*qDTY1.1*+*qDTY11.1*) had higher yields than PLs with other qDTY combinations. Under RS, the chosen PLs had a yield advantage of 0.3–2.0 t/ha [63].

Marker-assisted breeding (MAB) of the QTLs: *qDTY1.1*, *qDTY2.1*, and *qDTY3.1* with *Sub1* in the background of the drought-prone Swarna [7] has led to the release of three climate-resilient rice varieties that can handle both drought and flooding.

The grain yields of the NILs with one or more QTL were higher than those of Swarna. The background recovery of the selected NILs ranged from 93 to 98%, and they were released as improved varieties: CR dhan 801 (*qDTY1.1* + *qDTY2.1* + *qDTY3.1* + *Sub1*), Bahuguni dhan-1 (*qDTY1.1* + *qDTY3.1* + *Sub1*), and Bahuguni dhan-2 (*qDTY3.1* + *Sub1*).

1. **Genomics based approaches to enhance drought tolerance in rice:**

Genotyping by sequencing (GBS) and different array-based technologies (SNP array) are two of the most common high throughput SNP identification systems based on genomics. GBS can be used to make a lot of markers, which can be used to make a genetic map that is full of markers so that QTLs can be found with high confidence. As a type of Reduced Representation Sequencing (RRS), GBS makes it possible to reduce the complexity of the genome before sequencing, which lowers the cost per sample and the amount of work needed to analyse the data [64]. In GBS, a large number of SNPs are made for genotyping and genetic analysis. These are used in genome-wide association studies (GWAS), molecular diversity analysis, genomic selection (GS), marker and gene discovery, genome profiling, and high-resolution QTL mapping in different crop species in recent years [65]. Reducing complexity can be done by either digesting DNA with a single restriction enzyme (1 enzyme GBS) or with two different restriction enzymes (2 enzyme GBS). In GBS, digested fragments are joined to barcoded adapters and common adapters with an overhang that matches the restriction site. This is done with a single sticky-end ligation. Several systems from Illumina, Roche 454, and Ion Torrent are examples of next-generation sequencing technologies. These technologies allow for the cost-effective and time-efficient sequencing of large amounts of DNA. Bioinformatics tools are used a lot in GBS analysis pipelines to look at the data from next-generation sequencing platforms [65, 84].

GBS can give many orders of magnitude more useful information than older, more complicated and expensive genotyping methods, such as those based on RFLP and SSR. Commercial SNP arrays still have more markers and are easier to analyze, but they can be very expensive compared to GBS. When combined with phenotypic data, GBS approaches are a powerful way to quickly find and map the QTLs and genes that control a number of agronomic traits. These QTLs and genes can then be introduced into crop germplasm to make it more resistant to abiotic stresses. Even whole genome resequencing (WGR), which gives a higher resolution of the genome than a previously sequenced genome, is a type of GBS. Both RRS and WGR benefit from genomic information that was already known [65].

Since GBS was first made, it has been constantly improved, which has led to at least 15 approaches based on RRS. Restriction site-associated DNA sequencing (RADseq), Original Elshire GBS, Two-enzyme GBS, Double-digest RAD sequencing (ddRAD), 2bRAD, Sequence-based genotyping (SBG), ezRAD, Restriction fragment sequencing (RESTseq), restriction enzyme site comparative analysis (RESCAN), Specific length amplified fragment sequencing (SLAF-Seq), Multiplexed shotgun genotyping (MSG), Complexity reduction of polymorph All of these techniques do the same thing, which is to make the genome simpler and look for QTLs and genes. The only difference is in how the sequencing is done. For example, RADseq and ddRAD involve sequencing fragments with moderate coverage between 5x and 15x, but original Elshire GBS and two-enzyme GBS studies tend to have low coverage of 1x [65].

RNA sequencing (RNA-seq) and exome sequencing are two important ways to do reduced-representation studies that are not as common. Both of these methods make sequencing more selective, making it easier to focus on areas that code for proteins. Even though coding sequences might only make up 1%–2% of the genome, they are likely to have a lot of functional variants and few repetitive regions. A big benefit of RNA-seq is that you don't need to know anything about the genome beforehand. But exome sequencing methods depend on the existence of high-quality reference genomes that have been annotated correctly. Even though exome sequencing doesn't let you look at how much a gene is expressed, it does let you look at alleles and genes that wouldn't be found with RNA-seq. RNA-seq and exome sequencing are better than GBS because most transcripts and exons can be annotated using existing databases [64, 65]. This gives SNPs a functional context. WGR is different from RRS in that there are no steps for simplifying things before sequencing. SkimGBS is a WGR method that uses genomic reads with low coverage, usually less than 1x, to call SNPs and genotypes. This makes genotyping large populations cheaper. This low coverage is enough for genomic analyses in recombinant populations with high-quality parental genome sequences and a reference genome sequence [65]. No restriction enzymes are needed for RNA-seq, exome sequencing, or WGR. So, GBS and its different versions avoid the high cost of deep whole genome sequencing and have become the most popular way for breeders to use SNP markers to map QTLs.

For the first time, a 384-plex GBS protocol was used to add high density SNP markers to a RIL population made from IR64 and Azucena [66]. Using the final dataset of 30,984 SNP markers that had been imputed and fixed, they mapped two QTLs for aluminium tolerance on chromosome 1 and re-identified three of the four QTLs for aluminium tolerance that had already been mapped [67]. On chromosome 1, two important QTL for leaf width were also found. GBS was used to do Genome-Wide Association Studies (GWAS) for 19 agronomic traits, such as yield and yield components, in a group of elite irrigated tropical rice breeding lines. The population was genotyped with 71,710 SNPs, and 52 QTLs were found for 11 agronomic traits, including large effect QTLs for flowering time and grain length/grain width/grain-length-breadth ratio on chromosomes 3 and 7, respectively [68].

GBS was used to map a total of 32 QTLs for seven root traits on all chromosomes except for chromosome 12. This explained a PVE that ranged from 2.23 to 37.08 percent. There were also positive links found between GY and root traits [69]. GBS was used to type a rice F2 population that came from a cross between Oryza sativa sp. japonica cv. Nipponbare and O. longistaminata, an African wild rice species. This produced 8154 informative SNP markers, which were used to make a 1536-cM genetic map. For the trait "number of tillers," QTLs were found on chromosomes 1, 3, 4, and 8 [70]. In a similar way, 96 plex GBS was used on genotype 1316 S6:8 indica MAGIC (MI) lines, and the eight founder parents and QTLs for agronomic traits (yield, flowering time, and plant height) were mapped [71]. By genotyping a BIL population in the background of O. sativa ssp. indica cv. PR114, QTLs for thousand grain weight, grain width, and grain length were also mapped [72].

Fourteen additive QTLs related to root and shoot traits like root length, shoot length, fresh root mass, fresh shoot mass, number of tillers, dry root mass, dry shoot mass, and root-shoot ratio under drought stress at the vegetative stage and twenty-one QTLs for yield and their agronomic traits like days to flowering (DTF), plant height (PH), leaf rolling score (LRS), plant dry matter content (DM), spikelet fertility (SF), grain yield (GY), yield index. Through the GBS genotyping procedure, the large effect QTLs (*qGY1.4*, *qDTF3.1*, *qPH1.3*, and *qLRS1.3*) found in these studies can be added to elite breeding lines to make rice varieties that can handle drought [9, 73].

The GBS approach was used to find out the genetic makeup of two mapping populations (Swarna x Dular and IR11N121 x Aus196) that were different for GY. The high-quality SNP markers that were found were used to make high density linkage maps so that consistent grain yield QTLs could be found under drought stress. Six qDTY QTLs were found in the Swarna x Dular population (*qDTY1.1*, *qDTY1.3*, *qDTY3.3*, *qDTY4.3*, *qDTY4.4*, and *qDTY6.3*), and six were found in the IR11N121 x Aus196 mapping population (*qDTY1.1*, *qDTY1.4*, *qDTY2.4*, *qDTY3.4*, *qDTY4.5*, *qDTY4.6*). In this study, three new qDTYs (*qDTY2.4*, *qDTY3.3*, and *qDTY6.3*) were found to be consistently expressed under a range of drought conditions from moderate to severe, with *qDTY2.4* explaining the most variation at 14.92%.

SNP array is an automatic genotyping assay with a high throughput and a low cost. It has been used a lot in genetic studies of plants, like genome-wide association studies (GWAS), building linkage maps, genomic selection, analyzing population structure, and mapping genes. Array-based genotyping platforms are used to do high-, medium-, and low-density genome scans, high-quality allele calling, easy handling, and simplified analysis [10, 75]. When compared to data generated by NGS-based methods, SNP array data is easier to analyze. This is especially true when you consider how much time and money NGS library preparation and bioinformatics data analysis require for accurate SNP calling. Illumina and Affymetrix are two platforms that have been used for SNP arrays. Between Affymetrix and Illumina, assays and genotype calling use different chemicals and computer programmes. SNP arrays, the hybridization principle (complementary base pairing), and the captured signal intensity principle (calculation of amount of target DNA and the affinity between target DNA and probes) are all the same.

SNP array, on the other hand, has its own problems, such as the need for prior genomic information, the fact that it can only genotype known SNP locations, and the need for manual dosage scoring (in some case). It can also take a lot of time to design and continue to improve. Ascertainment bias is a common problem with genotyping arrays. This is because polymorphisms in the population of interest are not picked at random or because SNP discovery panels only use a small number of samples [10, 75]. Several low-, medium-, and high-resolution SNP arrays have been made for rice and used successfully by researchers around the world for molecular diversity analysis, QTL mapping, GWAS, marker assisted backcrossing (MABC), and pedigree verification among breeding lines. The 384-plex BeadXpress array technology [76] found 54,465 SNPs between two Indica varieties, Minghui 63 (MH63) and Zhenshan 97 (ZS97), and 20,705 SNPs between the MH63 and Nipponbare genomes. In another study, 395 different accessions of O. sativa were genotyped with the GoldenGate 1536 SNPs to look at population structure, genome-wide polymorphism, and the history of introgression in domesticated Asian rice [77]. A whole-genome SNP array called RICE6K, which is based on Infinium and shows 500 rice landraces, was made [78]. This array can be used for germplasm fingerprinting, genotyping of bulked segregating pools, testing the authenticity of seeds, and choosing genetic background. This RICE6K SNP array was used successfully to determine the genetic makeup of the RIL population, which was made by crossing Zhenshan 97 and Xizang 2 [79]. The Illumina Infinium-based 6 K SNP chip for rice, called C6AIR, has SNPs from re-sequencing data and BeadXpress 384-SNP sets. This has been used successfully to genotype more than 40,000 rice samples at the International Rice Research Institute (IRRI) to get fast and high-quality genotypic data for many genetics and breeding projects [80].

The high density arrays were made for rice to be very informative across different germplasms and different rice subpopulations. They were optimized to study phylogenetic relationships and associations between phenotype and genotype. The 700 K High Density Rice Array (HDRA700K) was made to help map associations across the whole rice genome [81]. A SNP array called RiceSNP50K was made using the Illumina Infinium platform. It has 51,478 evenly spaced markers that come from the re-sequencing data of 801 rice varieties [76]. This next-generation tool for genotyping will be very important for molecular breeding and functional genomics research. In another study, a high density Affymetrix 50 K chip was made. It has 50,051 SNPs from 18,980 different genes spread across all rice chromosomes. It also has 3,710 genes that are the same in both wheat and rice, 14,959 single-copy genes that are the same in both, 194 cloned rice genes that are important for agriculture, and 117 rice genes that have more than one copy. This chip was used to test the recovery of the background in mega rice varieties that were made more resistant to flooding through MABC [81].

Different high-throughput SNP arrays were made and used to help with genome-wide association studies (GWAS) in the rice diversity panel. GeneChipRice44 K was used to get the genotypes of 413 different types of rice. This was done to find out the genetic architecture of different physiological, developmental, and developmental traits that affect yield, quality, and sustainability [77]. In another study, 242 tropical rice accessions were genotyped with the 700 K High Density Rice Array (HDRA700K) and phenotypes with the imaging platform PANorama [82]. This showed the shape of the panicle in domesticated rice, a genetic model for complex panicle traits, and subtle links between panicle size and yield performance. Recently, an amplicon-based SNP assay called 1k-RiCA was made for more accurate and faster genotyping of breeding lines and populations of Oryza sativa [83]. This test worked well for studying diversity and making genomic predictions for breeding programmes based on indica.

**Conclusion:**

Recent improvements in next-generation sequencing (NGS) and single nucleotide polymorphism genotyping (SNP genotyping) have the potential to speed up crop improvement if they are used in the right way. High-throughput SNP genotyping has many advantages over older marker systems. For example, there are a lot of markers, large populations can be processed quickly, there are different genotyping systems to meet different needs, and because SNP markers are bi-allelic, it is easy to call alleles and store them in a database. So, genomics has become the thing to do, and labor-intensive gel-based genotyping methods done in a wet lab have been replaced by automation. With these highly sophisticated genotyping platforms, scientists can take a close look at a complex trait like drought and find the genes that make it possible for plants to tolerate drought. As a staple crop, rice is under a lot of stress from both natural and human causes. Genomic science makes it possible to look for QTLs and candidate genes in local landraces and cultivars. This helps in QTLian breeding to create rice varieties that can handle stress better.

Competing Interests:

The authors declare no conflict of interest.

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**Table 1.** Major effectQTLs identified for Grain Yield (GY) under drought in different backgrounds

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **QTL** | **Chromosome****no.** | **Marker interval** | **Donor** | **Background** |
| *qDTY 1.1* | 1 | RM11943- RM431 | Dhagaddeshi, N22, | Swarna, IR64, MTU1010 |
| *qDTY 1.2* | 1 | RM259–RM315 | Kali Aus | MTU1010 |
| *qDTY 1.3* | 1 | RM488–RM315 | Kali Aus | IR64 |
| *qDTY 2.1* | 2 | RM521- RM324 | Apo | Swarna |
| *qDTY 2.2* | 2 | RM211-RM263 | Kali Aus | MTU1010 |
| *qDTY 2.3* | 2 | RM263–RM573 | Kali Aus | IR64 |
| *qDTY 2.4* | 2 | S2\_16924409–S2\_17554671 | Aus196 | IR11N121 |
| *qDTY 3.1* | 3 | RM520- RM416 | Apo | Swarna |
| *qDTY 3.2* | 3 | RM231 - RM517 | IR77298-5-6-18 | Sabitri |
| *qDTY 3.3* | 3 | S3\_2686581–S3\_2727277 | Dular | Swarna |
| *qDTY 4.1* | 4 | RM335-RM518 | Aday Sel | IR64 |
| *qDTY 6.1* | 6 | RM19367 and RM3805 | Apo | Swarna |
| *qDTY 6.2* | 6 | RM121-RM541 | IR55419- 04 | TDK1 |
| *qDTY 6.3* | 6 | S6\_14604291- S6\_15072250 | Dular | Swarna |
| *qDTY 8.1* | 8 | RM80 and RM230 | Dular | IR64 |
| *qDTY 9.1* | 9 | RM566-RM24350 | Aday Sel | IR64 |
| *qDTY 10.1* | 10 | RM216-RM304 | N22 | MTU1010 |
| *qDTY11*.*2* | 11 | S11\_23405441-S11\_25462601 | Aus196 | IR11N121 |
| *qDTY 12.1* | 12 | RM28048- RM511 | Vandana | Way Rarem |