Intervention of molecular breeding in water saving rice production system: aerobic rice

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Abstract

The aerobic rice system/methods developed to tackle shortage of water, is a sustainable method to enhance rice productivity. Approximately 50% of irrigation water could be saved using this system in contrast to lowland rice cultivation. The crop can be directly seeded or transplanted in dry soil in this system rather than irrigated system of rice production. Here in this review we had tried to present all the important development made in regards to aerobic rice. Many QTLs responsible for aerobic traits in rice that have been mapped already are enlisted here. Brief comparisons of aerobic rice and conventional rice, further improvements made in aerobic rice have also been discussed.

Keywords Aerobic rice · Water use efficiency · SSR markers · Marker-assisted selection · Quantitative traits loci

Introduction

Rice is one of the major cereal crops with respect to area under cultivation and total production. It was domesticated from the wild grass *Oryza rufipogon* around 10,000–14,000 years ago. Only two species (*Oryza sativa* and *Oryza glaberrima*) out of 24 in the genus *Oryza* are cultivated, while remaining are wild types. Among the cultivated species *O. sativa* is grown all over the world while *O. glaberrima* has been cultivated for the last ~ 3500 years in some parts of West Africa (Crawford and Shen 1998). *O. sativa* has two main subspecies *indica* and *japonica*. *Japonica* rice is supposed to be originated in southern India and then spread to China, Korea, Philippines (about 2000 B. C.), Indonesia, and Japan (about 1000 B.C.) (Patra et al. 2016). The other cultivated species *O. glaberrima* is supposed to be domesticated in West Africa. Although the taxonomy is still a matter of research and debate. In this respect, *O. sativa* was

shorted using isozymes and micro-satellite markers into six (*japonica*, *indica*, *aromatic*, *rayada*, *aus*, and *ashina*) and five groups (*tropical japonica*, *temperate japonica*, and *aromatic*), respectively (Glaszmann 1987; Garriss et al. 2005). Approximately 127,000 accessions and wild relatives of rice covering genetic diversity in the world have been conserved in International Rice gene bank (Chandran and Jung 2014) while National gene bank of India, ICAR-NBPGR have preserved 109,153 accessions till 2018. Germplasm collection contains high genetic diversity for the biotic and abiotic stress tolerance. Also they are well adapted to upland to lowland environmental conditions ranging from tropical to temperate zones, hence, could be used in rice improvement.

Rice is unique in its ability among cereal crops to grow in wide range of environments. These environments vary with respect to elevation, rainfall pattern, depth of flooding and drainage, hydrological status, soil type and by the adaptation of rice to agro-ecological factor. Depending on the hydrology, the rice environment can be classified into deep-water, irrigated, rainfed lowland and upland (Bouman et al. 2006). Currently, it is grown over an area 160 million ha (11% world's cultivated land) to produce 503.8 million tons (<http://www.faostat.fao.org> 2017).

As much as 90% of rice production and consumption occur in Asia, which alone occupies 89% of paddy area (<http://www.faostat.fao.org>). While, in India it is second largest producer with an estimated production of 106.1 million ton from 38.3 million ha during crop season 2015–2016

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(<http://www.indiastate.com> 2016). Irrigated paddy land supplies more than 75% of the annual rice from 79 million ha area. However, innovative technologies for rice production are highly required to overcome an increasing demand for food and water crisis in current scenarios. Under rainfed upland conditions rice is grown in unbound fields with direct-seeded method into unpuddled, unsaturated soil applying little or no fertilizers which renders the accumulation of water due to good soil drainage and uneven land surface. Irrigated lowland rice is transplanted or direct-seeded into puddle lowland fields with soaking, ploughing, and puddling (DeDatta 1981). Approximately 90% of total diverted freshwater in Asia accounts for irrigated agriculture of which more than 50% is used in rice production alone (Bouman et al. 2002). Therefore, water is precious for living organisms in the world, as people extensively using more water for household, industry, and agriculture. Its scarcity has a drastic negative impact on human life on earth.

According to United Nation convention to combat climate change (UNCCD) by 2030 around 50 percent of the human population will be facing the problem of water scarcity. As per International Water Management Institute (IWMI) agriculture accounts for 70% of the global water withdrawal increasing the burden on ground water along with industrial and environmental uses. At the same time plants frequently encounter stresses caused by both biotic and abiotic factors, which limit their genetic yield potential. Abiotic stress exposes, up- or downregulation of stress responsive elements to maintain homeostasis against stresses. Among the various abiotic stresses, heat and drought during the flowering, pollination, and grain-filling stages reduces both production and productivity in rice crop.

Rice production and water requirement

Lowland rice requires flooded irrigation system, it is grown either by transplanting or direct seeding methods (Bouman and Tuong 2001; Cantrell and Hettel 2005). It contributes the most part of rice production but on the other hand uses huge amount of water and labor. Being water-lusty, crop rice requires 3000–5000 liters of water to produce 1 Kg of rice. Approximately, 2 mha of irrigated dry-season rice and 13 mha of its irrigated wet-season rice in Asia may experience “physical water scarcity” (17 million ha) and “economic water scarcity” (22 million ha) by 2025 (Bouman et al. 2002). The main reasons for decline in water level are of diverse origin including over-exploitation of ground water and increased competition from urban and industrial development, etc. Global warming, pouring of industrial waste in rivers, adverse climatic changes, over-pumping of ground water causing aquifer resources to decline, etc, are main reasons behind high cost of water (Tuong and Bouman

2003). As rice requires huge amount of water, its scarcity is worsening the sustainability of irrigated rice ecosystem (Tuong and Bouman 2003).

About 30% of total rice area is under irrigated watering system and accounting for the use of 50% irrigation water, hence, it is an appropriate target for water conservation. Transplanting method of rice production is a traditional method that requires repeated puddling, affects soil physical properties by reducing soils aggregates, permeability in sub-surface layers and forming hard-pans at shallow depths which enhanced the requirement of energy for land preparation in succeeding crops (Singh et al. 2014). Previous studies showed 10% reduction in water inputs of irrigated rice could save 150,000 million m³ water which corresponds to approximately 25% of the total freshwater used globally in non-agriculture sectors (Klemm 1999).

Aerobic rice: a water saving technology

The term “Aerobic rice”, was used for the first time by International Rice Research Institute (IRRI). It is method of rice cultivation where seeds are sowed directly in well-tilled and leveled fields with the uniform slop without puddling. In this system of cultivation aerobic condition is maintained by avoiding standing water throughout the crop season. The crop calendar for cultivation of aerobic rice has been presented in Fig. 1. The varieties of this production system contain the characteristics of upland varieties grown on non-flooded sloping islands (drought tolerance) and lowland varieties grown in irrigated, flooded fields (high-yielding traits). This system of rice cultivation is best suited for the areas where availability of water is very limited and frequently encountered with drought stress.

Drought can be defined as the conditions of physical deficit of water where the demand of water exceeds the supply, for example the rate of transpiration increases, the availability of water near root decreased etc. Normally rice requires fully puddled conditions, which, if unavailable, can be considered as drought. Aerobic rice are special type in term of water use, they do not require the puddled condition and hence can be grown in wheat-like conditions. Drought tolerance can be defined as the ability of plant to produce up to its maximum potential even if the desirable water requirements are not met whereas aerobic rice is a type of rice where the total requirement of water has been decreased up to some extent to save amount of water used as a input. Drought tolerance and aerobic rice are two different things as aerobic rice may feel drought if the desirable amount of water is not provided. Approximately 46 mha rainfed rice area in Asia is affected by drought stress, where rice is the main food for subsistence (Pandey et al. 2007). Rice has semi-aquatic evolutionary properties therefore it has relatively less adaptation

Fig. 1 Crop calendar of direct-seeded aerobic rice. (Source: Rice Knowledge bank IRRI)

to water-limited conditions but very sensitive to conditions of drought stress (Lafitte et al. 2002). Due to its sensitivity towards drought stress, global rice production faces reduction of approximately 18 million tons annually (O'Toole 1982). Aerobic cultivation system of rice is considered as suitable for enhancement of yield potential (improved upland rice) and drought tolerance (improved lowland rice) with responsiveness towards high input used and tolerance to occasional flooding (Bouman and Tuong 2001).

In aerobic system of rice cultivation plants are relatively wide which enables them to establish and flourish well. Depending on the water holding capacity of soil, crop is irrigated once in 5–10 days interval. The varieties used in this system have ability to grow faster under moisture content at or below the field capacity in the soil, with the moderate application of fertilizers sufficiently produce 4–6 tons/ha by saving as much as 50% of irrigation water as compared to lowland conditions (George et al. 2002; Kato et al. 2009; Parthasarathi et al. 2012).

Root characteristics, such as density, length, and thickness and greater root penetration are important traits for aerobic rice varieties (Yadav et al. 1997). It was considered as promising rice cultivation system under water scarcity. Deep root in aerobic rice varieties is one of the key traits;

it enables plant to withstand well by higher absorption of ground water which eliminates the need of water logging and decrease methane emission (Clark et al. 2000). The root system in aerobic rice grows deeper as compared to conventional rice (Sunil and Shankaralingappa 2014). Due to deeper roots in aerobic rice, water input is 50% lower and water productivity is 60% higher than lowland transplanted rice (Subramanian et al. 2008).

Likewise, aerobic system of rice cultivation had 51% less water use with 32–88% higher productivity during land preparation by limiting seepage, percolation, and evaporation than flooded rice (Atlin et al. 2006; Bouman et al. 2006). Atlin et al. (2006) observed that both irrigated high-yielding rice varieties and aerobic types yielded approximately 4 t/ha under lowland conditions. In non-stress upland environment, aerobic rice varieties significantly out-yielded all other types and recorded significantly more panicles than traditional upland varieties with higher water use efficiency compared to normal method of planting. Thus this approach could save up to 55–60% of irrigation water; a concomitant reduction in productivity by 35–40% (Bouman et al. 2005). The reduction in sink size associated with a dramatically reduced spikelet number per unit land area (20,000–24,000/m²) was identified as the major limitation of aerobic cultivation (Tables 1, 2, 3).

Table 1 A hypothetical comparative analysis of water use in aerobic and conventional rice field

Parameters	Aerobic rice	Conventional rice
Puddling	–	10–15 l/m ² (i.e., 3000–4000 l/kg of rice)
Irrigation efficiency	60–80%	–
Evaporation	100 mm	200 mm
Transpiration	400 mm	400 mm
Seepage and percolation	Minimal	500–1000 mm
Total	500 mm + irrigation	1100–1600 mm + 3000–4000 l/kg

Table 2 Comparison between cultural conditions in both aerobic and conventional rice

Parameters	Aerobic rice	Conventional rice
Land preparation	No leveling required	Land should be leveled
Seedling	Not required	Required
Seed rate	Generally low	Comparatively high
Water saving	Yes	Most demanding in terms of water
Culturing condition	Aerobic	Puddled
Soil structure	Maintained	Disrupted
Methanogenesis	No methanogenesis	Methanogenesis occurs
Cost of cultivation	Lower than conventional	Comparatively high
Weed infestation	High	Low

Table 3 List of various water-saving varieties of rice released throughout the world

Variety	Country	Grain yield (t/ha)	Irrigation method	Year
Lemont	Australia	8.6	Sprinkler	1989
Suweon 290	Japan	8.8	Rainfed	1994
9516	China	8.4	Flush irrigation	1999
Apo (IR55423-0)	Philippines	5.7	Aerobic	2001
HD 502	China	5	Aerobic	2003
HD 297	China	4.8	Aerobic	2003
HD 277	China	4.5	Aerobic	2003
MAS 946-1	India	5.5–6	Aerobic	2007
Takanari	Japan	11.4	Sprinkler	2007
NERICA5	Japan	8.1	Rainfed	2007
MAS 26	India	5.5–6	Aerobic	2008
MAS ARB25	Philippines	5.5	Aerobic	2008
MAS 25	India	5.5	Aerobic	2008
YTH323	Japan	5.1	Sprinkler irrigation	2009
CR Dhan 200	India	4.5–5	Aerobic	2012
CR Dhan 201	India	4	Aerobic	2014
CR Dhan 202	India	4	Aerobic	2014
CR Dhan 203	India	4.05	Aerobic	2014
CR Dhan 204	India	4.8–5.6	Aerobic	2014
CR Dhan 205	India	4.5	Aerobic	2014
CR Dhan 206	India	3.95	Aerobic	2014
CR Dhan 207	India	3.7	Aerobic	2016
CR Dhan 209	India	4.07	Aerobic	2016

To overcome the water scarcity, China Agricultural University developed special aerobic rice varieties called “Han Dao” (HD297, HD277, and HD 502) which are widely grown by farmers. Usually there is a yield penalty in aerobic rice when compared to conventional rice. However, with the yield of 3.5 to 5.0 tons/ha with 450–650 mm water input in comparison to lowland rice Han dao 502 and Han dao 297 were identified as the most promising varieties (Xue et al. 2008). The deeper roots and strong root morphology were various traits which were exploited for development of aerobic rice with decreased yield penalty. Many aerobic varieties Han Dao 297 (Mujiao78-595 × Khaoman), Han Dao 277 (Qiuguang × Ban Li) and Han Dao 502 (Qiuguang

× Hongkelaoshuya) have been developed using combination breeding which showed stronger drought tolerance, reduced plant height, increased lodging resistance, erect upper leaves, higher yields, stronger resistance to blast and better grain quality (Zhao et al. 2010). IRRI has also initiated research on tropical aerobic rice system and identify some lowland variety (Magat) and upland genotypes (APO and CT 6510-24-1-2) which perform well under aerobic conditions particularly in tropical area, can be beneficial for over 37 mha of water short irrigated lowland and 40 mha of rainfed lowland and uplands (seasonal rainfall: 600–800 mm) in Asia (Bouman et al. 2002). Several aerobic rice varieties such as MAS946-1, MAS25, MAS26 and MAS946 has been

developed by University of Agricultural Sciences, Bangalore in India using the upland paddy and high-yielding rice germplasm however, MAS 946-1 variety which is suitable for dry sowing with scheduled irrigations was widely accepted among the farmers (Gandhi et al. 2012). Aravind et al. (2015) developed RILs from interspecific cross between *indica* and *japonica* lines (IR50×Moroberekan) and found eight elite lines (IM036, IM095, IM090, IM014, IM167, IM039, IM192 and IM176) for aerobic conditions in wet season and two lines (IM192 and IM176) under rain fed conditions.

Improvement of rice genotypes tolerance to water limitation conditions could also enhance by combined selection for water acquisition and high cellular level tolerance (Raju et al. 2014). Root architectural plasticity and adaptability (yield stability) of two mapping population (Aus276/3 and MTU1010 and Kali Aus3 and MTU1010) has been evaluated under direct-seeded upland and transplanted lowland with stress and non-stress conditions of drought and identified good root architectural plasticity in 13 and 21 lines in Aus276 population and Kali Aus population, respectively (Sandhu et al. 2016).

Enhancement of quality of aerobic rice

High production along with grain quality of the produce has always been an important consideration in rice breeding programmes worldwide (Khush and Juliano 1991). The development of high-quality rice varieties (aromatic rice) is gaining high interest among rice breeders because of their aroma, flavor, texture and high market value as compared to non-aromatic rice varieties. There are two types of quality rice, fragrant rice varieties have a copy of the gene encoding *BAD2* which contains the deletions and SNPs generate a premature stop codon that presumably disables the *BAD2* enzyme; however, other non-fragrant rice varieties possess functional copy of gene encoding *BAD2* (Bradbury et al. 2005). Another is *japonica* rice which contains *frg* gene for aroma (Bourgis et al. 2008). The total three SNPs in exon 7 of the gene encoding betaine aldehyde dehydrogenase 2 (*BAD2*) and *frg* gene in on chromosome 8 of generated through eight base pair deletion are likely cause of fragrance in Jasmine and Basmati rice (Bradbury et al. 2005; Bourgis et al. 2008). Increased level of 2-acetyl-1-pyrroline (2AP) has been associated with the flavour and fragrance of Basmati and Jasmine rice types (Ramaratnam et al. 1983; Yoshihashi 2002). These jasmine and basmati rice could be used to improve the aerobic rice through combination breeding. Keeping in view the decrease in the fresh water availability for rice production, Basmati rice (most desirable rice) is also needed to be incorporated with aerobic characters. The use of DNA markers and marker-assisted selection

along with conventional breeding will be an effective tool to achieve the target.

Various efforts of improvement of basmati characteristics in aerobic rice have been initiated by the development of Pusa Basmati-1 (world's first high-yielding semi-dwarf basmati variety) released by India in 1989. This efforts simultaneously initiated the consistent breeding programmers for the development of high-yielding Basmati/aromatic hybrids and varieties (Pusa Sugandh 4, Pusa Basmati 1121, Basmati 370, Improved Pusa Basmati 1, Pusa Basmati 6, Dehradun Basmati, Pusa Sugandh 2, Pusa Sugandh 3, Pusa Sugandh 5 and hybrid Pusa RH10, Super Basmati, Punjab Basmati, Taraori Basmati and Haryana Basmati-1) following crossing between traditional Basmati and high-yielding *indica* rice varieties. Breeding program to transfer aerobic rice traits form newly developed aerobic rice (MAS25 and MASARB25) to high-yielding *indica*/basmati rice varieties has been initiated (Improved Basmati 370, Pusa1460, PAU201, HBC19 and Pusa1121) at IRRI, Manila, Philippines; CCS HAU, Haryana and UAS Bangalore India. Consequently, duration of traditional basmati varieties has also been reduced from 160 days to 115–140 days with enhancement of productivity from 2.5 tons/ha to 6 to 8 tons/ha. Overall, as a result of these efforts earning from the export of basmati rice has gone up from Rs. 294 crores in 1990–1991 to Rs. 22,000–22,500 crores in 2016–2017 (<http://www.apeda.gov.in>).

Mapping of water-saving traits

Genetic diversity is the key for the genetic enhancement of crop plant while, molecular markers are valuable tools for genetic analysis in breeding programs (Tanksley 1993). Mapping QTLs and introgression (marker-assisted selection) of the target traits can greatly improve the selection efficiency and precision in rice breeding program. Molecular marker technology can help in identification of suitable parental lines, diversity and pedigree analysis and introgression of desirable traits without altering the genetic background of the recipient parent. Advancement in molecular marker technology boost the genetic improvement in crop plants by providing opportunity to dissect variation in quantitative traits and to identify genomic locations (QTL) associated with these complex traits.

To identify the quantitative trait loci of complex traits based on linkage molecular markers, particularly the microsatellite markers (SSRs), have been widely used. The high specificity and multiplexing potential of the microsatellite markers (SSRs) makes them more preferable for high-throughput mapping, genetic analysis and marker-assisted plant improvement strategies. Mapping of QTL for traits promoting aerobic cultivation of rice has gained momentum

in the last decade. Previously a major genomic location associated with grain yield between markers RM11943–RM431 on chromosome 1 has been identified using three F3:4 mapping populations derived from cross of N22 (drought tolerant *aus* cultivar) with Swarna, IR64 and MTU1010 (Vikram et al. 2011). Four QTLs viz., *qDTY_{2.1}*, *qDTY_{2.2}*, *qDTY_{9.1}* and *qDTY_{12.1}* of grain yield under drought stress and non-stress conditions has been identified in chromosomes 2 (two), 9 (one) and 12 (one), respectively (Dixit et al. 2012). More than 40 QTLs have been identified using MASARB25/Pusa Basmati 1460 and HKR47/MAS26 derived population for grain yield under aerobic conditions (Sandhu et al. 2013). In the last two decades, a good progress has been made towards linkage mapping of traits promoting adaptation to aerobic soils (Sandhu and Kumar 2017). The summary of the major QTL reported earlier is given in Table 4.

Development of high-yielding aerobic rice may be significantly affected by the characteristics of root. The double haploid population of IR64/Azucena was evaluated under low moisture stress and non-stress conditions for root-related traits and identified QTLs for root-penetration (four), root thickness (four), penetrated root number (two) and total root number (two) explaining 84–16.4% phenotypic variations (Zheng et al. 2000). Most of these identified QTL were consistent and could be used for marker-assisted selection deep and thick roots with high root-penetrating ability. It is also identified that loci associated with grain yield and related traits were non pleiotropic in nature with desirable root traits under low-moisture stress conditions particularly at vegetative stage, thus there is high possibility of combining higher grain yield with desirable root traits for the enhancement of rice production under low moisture stress (Venuprasad et al. 2002). The QTLs for dry root weight has also been identified under drought stress conditions explaining 20.7–30.8% phenotypic variation (Lang et al. 2013). Fourteen traits (grain yield-related traits, root traits, and agronomic traits) associated with 35 QTL were identified on chromosomes 1, 2, 5, 6, 8, and 9 using mapping populations derived from crosses between MASARB25 and Pusa Basmati 1460 and nine traits were associated with 11 QTL using mapping population derived from cross between HKR47 and MAS26 on chromosomes 1, 2, 8, 9, 10, 11 and 12 at the same time numbers of breeding lines with high yield, root length, biomass, length, breadth ratio and Pusa Basmati 1460 specific alleles in the homozygous or heterozygous conditions at the *BAD2* locus have been identified which could serve as suitable material for the development of stable aerobic Basmati rice (Sandhu et al. 2014). Likewise, 26 QTL for 23 traits and 20 QTL for 13 traits were identified using BC2F4 populations derived from the cross between Aus276/3 and IR64 and Aus276/3 and MTU1010, respectively. However, four QTL *qGY_{1.1}*, *qGY_{6.1}*, *qEVV_{9.1}*, and *qGY_{10.1}* mapped on chromosomes 1, 6, 9, and 10 were consistent in both the populations which

were linked with markers RM147, RM167, and RM215 could be used for marker-assisted selection to select suitable genotypes. It has also been emphasized that development of varieties for aerobic condition can be accelerated by selecting suitable traits like seedling emergence, early vegetative vigour, nutrient uptake, nodal root number, and root hair length and density under rainfed conditions (Shahriar et al. 2014; Sandhu et al. 2015). The genomic location on chromosome 8 within the region of 24.9 cM distance six QTL associated with various grain yield and root traits, explaining the phenotypic variation ranged from 13.7 to 27.3% have been identified using F2 population derived from HKR47 cross between (high-yielding low-land *indica* rice) and MAS26 (aerobic adopted rice) (Kharb et al. 2015). The QTL for higher grain yield, better root length/biomass under managed aerobic condition has also been identified on chromosome (Kharb et al. 2016). Several QTL for basal root thickness, root number, root length and root biomass has been identified using double haploid population derived from cross between upland and lowland *japonica* rice in three different environments (Li et al. 2005). Two mapping populations derived from Aus276/MTU1010 and Kali/Aus276 populations were evaluated for root architectural plasticity and adoptability and identified three genomic locations as hot spots for root architectural plasticity grain yield-related traits could be used for development of aerobic rice using marker-assisted selection (Sandhu et al. 2016).

Marker-assisted selection for traits promoting aerobic adaption in rice

Development of aerobic rice could be accelerated by selecting suitable agronomic traits such as grain yield and component traits, physiological and root traits. To achieve yield stability in aerobic rice, strategic selection for large and deep root system is important. However, selection for deep root system is very difficult therefore marker-assisted selection provides the best opportunity. Breeding lines suitable for poor environment in specific locations were identified by pyramiding the QTL (*qRT11-7* × *qRT18-1* + 7–17) plant height and seed yield and total biomass and maximum root length (*qRT11-7* × *qRT18-1* + 7–32) (Selvi et al. 2015). Pyramiding of grain yield, physiological traits and root traits were performed under two different regimes of water and identified genotypes with high yield (*qRT2* + 9–19–3), high water use efficiency (WUE) (*qRT* 1 + 7–16–4), maximum root length (*qRT* 1 + 7–18–4), maximum root number (*qRT* 1 + 7–19) and high root volume (*qRT* 2 + 7–10–4) in a set of 22 NILs and 94 pyramided lines (Palanog et al. 2014). The breeding line MR219 has been developed by pyramiding the QTL associated with grain yield (*qDTY_{2.2}*, *qDTY_{3.1}* and *qDTY_{12.1}*) which performed more than 1500 kg/

Table 4 Summary of major QTL reported earlier for traits promoting aerobic adaptation

QTL	Chromosome	Interval/markers name	References
qDTY _{1.1}	1	RM431–RM104	Ghimire et al. (2012)
qDTY _{1.2}	1	RM259–RM315	Bernier et al. (2009), Sandhu et al. (2014)
qGY _{1.1}	1	RZ513–RZ613	Martinez (2006)
qPH _{1.1}	1	RM315–RM431	Bernier et al. (2009), Sandhu et al. (2014)
qDTY _{1.3}	1	RM263–RM573	Bernier et al. (2009), Sandhu et al. (2014)
qPL _{1.1}	1	RM1282–RM220	Marathi et al. (2012)
qPL _{1.1}	1	RM495–RM577	Meena et al. (2018)
qDTY _{2.1}	2	RM327–RM262	Venuprasad et al. (2008)
qPL _{2.1}	2	RM3732–RM324	Marathi et al. (2012)
qDTY _{2.2}	2	RM236–RM279	Yadaw et al. (2013)
qDTY _{2.2}	2	RM211–RM263	Sandhu et al. (2013)
qDTY _{2.1}	2	RM263–RM573	Sandhu et al. (2014)
qDTY _{2.3}	2	RM211–RM250	Palanog et al. (2014)
qDTY _{2.3}	2	RM263–RM573	Bernier et al. (2009), Venuprasad et al. (2009), Sandhu et al. (2014)
qDTY _{2.2}	2	RM211–RM263	
qDTY _{2.1}	2	RM324–RM263	
qDTF _{2.3}	2	RM450–RM250	
qYLD _{2.1}	2	RM3732–RM7144	Marathi et al. (2012)
qDTY _{3.1}	3	RM520–RM16030	Venuprasad et al. (2009)
qPL _{3.1}	3	RM3766–RM157A	Marathi et al. (2012)
qPL _{3.1}	3	RM569–RM517	Meena et al. (2018)
qDTY _{3.1}	3	RM168–RM468	Dixit et al. (2014)
qDTY _{3.2}	3	RM569–RM517	Yadaw et al. (2013)
qDTY _{3.2}	3	RM20–RM22	Vikram et al. (2011)
qGL _{3.1}	3	RM6283–RM16	Lou et al. (2009)
qGL _{3a}	3	RMw357–RMw353	Wan et al. (2006)
qGY _{3.1}	3	RG100	Martinez (2006)
qGL _{4b}	4	RM5586–RM3524	Kato and Okami (2011)
qGY _{5.1}	5	RM13	Martinez (2006)
qGY _{6.1}	6	RM217	
qDTY _{6.1}	6	RM589–RM204	Venuprasad et al. (2012)
qGL _{6.1}	6	RM588–RM540	Lou et al. (2009)
qDTY _{6.1}	6	RM586–RM217	Dixit et al. (2014)
qDTY _{6.1}	6	RM212–RM541	
qDTY _{6.2}	6	RM121–RM541	
qLB _{7.1}	7	SSR	Redoña and Mackill (1998), Rabiei et al. (2004)
qGL _{7.1}	7	SSR	Wan et al. (2006)
qGL ₇	7	RID711–RM6389	Bai et al. (2010)
qPH _{8.1}	8	RZ333–RZ562	Xiao et al. (1995)
qYPP _{8.1}	8	RM547–RM72	Kharb et al. (2016)
qPH _{9.1}	9	RZ9106–RZ777	Li et al. (1995)
qPH _{9.1}	9	17141056–18060875	Lu et al. (2009)
qDTY _{9.1}	9	RM105–RM434	Mallikarjuna et al. (2014)
qGY _{9.1}	9	RM215	Martinez (2006)
qGY _{9.2}	9	RM242	
qGY _{10.1}	10	RM10030–RM228	Zhao et al. (2010)
qDTY _{10.1}	10	RM216–RM304	Vikram et al. (2011)
qPH _{10.1}	10	G1082–G291	Lu et al. (1997)
qDTY _{10.2}	10	RM269–G2155	Mallikarjuna et al. (2014)
qPH _{11.1}	11	RG118	Zhuang et al. (1997)

Table 4 (continued)

QTL	Chromosome	Interval/markers name	References
qTGW _{11.1}	11	RM287–RM21	Kharb et al. (2016)
qENT _{11.1}	11	RM26245–RM202	
qGL _{11.1}	11	SSR	Li et al. (1995), Wan et al. (2006), Amarawathi et al. (2008)
qGY ₁₁	11	RZ537–RZ900	Martinez and Thome (2001)
qGY _{11.1}	11	RM287–RM26775	Zhao et al. (2010)
qTGW ₁₁	11	RM287–RM26775	
qDTY _{12.1}	12	RM28166–M28199	Mishra et al. (2013)
qDTY _{12.1}	12	RM280–RM28166	Bernier et al. (2009)
qGY _{12.1}	12	R901	Martinez (2006)
qGY _{12.2}	12	G1112	
Badh2	8	nksbadh2	Li et al. (1995), Bradbury et al. (2005), Kovach et al. (2009)

DTY drought yield, *GY* grain yield, *PH* plant height, *ENT* effective number of tillers, *PL* panicle length, *TGW* 1000 grain weight, *YPP* yield per plant, *LB* grain length/breadth ratio, *GL* grain length

ha under drought stress condition (Shamsudin et al. 2016). Steele et al. (2007) used 22 NILs to pyramid five targeted segments associated with root traits and identified increase in root length under irrigated and drought stress environment in some of the lines. Marker-assisted back crossing identified these lines contained genetic segment from chromosome 9 and linked with marker interval RM242 to RM201. Strategies of marker-assisted selection are cost-effective techniques and suitably complemented the conventional breeding methods by enhancing the efficacy and precision to identify the genetic purity in aerobic rice improvement programme (Singh et al. 2011). While, marker-assisted back-cross breeding (part of marker-assisted selection) enables to precise transfer of desirable segment from donor with minimum linkage drag to recurrent parent provides a great opportunity for precise transfer of desirable donor segment by minimizing the linkage drag into a recurrent parent.

Sandhu et al. (2018) applied marker-assisted recurrent selection to accumulate the positive alleles responsible for aerobic adaptation, hence improving the grain yield in lowland-adapted popular rice variety Samba Mahsuri under reproductive-stage drought. Similarly QTL analysis in progenies derived from cross between *Dular* (drought-tolerant) and IR64-21 (drought susceptible) lines revealed three major consistent-effect QTLs for grain yield (qDTY1.1, qDTY1.3, and qDTY8.1) under non-stress and reproductive-stage drought stress conditions, and 2 QTLs for root traits (qRT9.1 for root-growth angle and qRT5.1 for multiple root traits, i.e., seedling-stage root length, root dry weight and crown root number) (Catolos et al. 2017). Kumar et al. (2018), Rani et al. (2017), Kumar et al. (2017) used markers already reported to be linked with adaptation in aerobic environment to select the putative progenies in F₃ and F₄ generations. Meena et al. (2018) developed F₃ and F₄ population derived from MAS25 (aerobic rice) × IB370

(lowland basmati) and analyzed them for different physiological traits under aerobic conditions. They reported important QTLs responsible for adaptation in aerobic environment, e.g., qPL1.1, qLB1.1, qPL3.1 which may be useful for marker-assisted pyramiding into lowland rice to enhance aerobic adaptation.

Problems in aerobic rice

In general all the problems that results decrease in yield, whether biotic or abiotic are called to be soil sickness. The major problems of aerobic rice field are listed here:

1. Weed infestation

Weeds are the major constraint in the success of aerobic rice (Singh et al. 2008a). Problem is so devastating that it can causes the loss in yield up to 70–80% (Hussain et al. 2008). The weed diversity in case of aerobic rice is completely different from that of conventional rice. The cultivation conditions of aerobic rice, e.g., high moist condition are favourable for weed germination. Soil solarisation, stale seed bed, mulching, proper fertilizer application, integrated weed management etc. are some important strategies to overcome high weed problem in aerobic rice. All these methods are described in detail by Jabran and Chauhan (2015).

2. Nematode infestation

The unpuddled condition in aerobic rice leads to infestation of nematodes, which is one of the major problems occurring in aerobic rice field (Kreye et al. 2009). Root knot nematodes may cause yield loss by 12–80% (Padgham et al. 2004).

3. Nutrient availability

The soil in aerobic rice field had comparatively high pH than in conventional puddled field due to absence of phenomenon known as soil acidification Xiang et al. (2009). This leads to liming of oxisol, ultimately leading to iron deficiency in aerobic soil (Fageria 2001). Hence the interaction between nutrient availability of water and nutrient uptake is important. In puddled conditions soil is buffered somewhere around neutral pH and most of the nutrient are easily accessible to plant at this range. With the pH increases, availability of nutrients such as P, Fe, Zn and Mn becomes less available for plant uptake (Dobermann and Fairhurst 2000).

Clearly the problems in aerobic rice field such as weed problem, nematode infestation and nutrient availability are due to the type of cultivation method. These problems can mainly be solved by a good cultivation package and practices like proper identification of weed and application of weedicide and nematicide. Hence overall an integrated methodology comprising of a holistic approach for manure application, nutrient use, weed management etc is recommended. Hence in broader sense biotechnological intervention will be less useful in eliminating the drawbacks of aerobic rice. Although much work in term of development of nematode resistance plant (reviewed by Fuller et al. 2008) and improvement of nutrient uptake (reviewed by López-Bucio et al. 2003) have already been done which can be directly applied to aerobic rice.

Future prospective

Enormous works have been done throughout the world for dissecting the complex aerobic trait in rice. Very important QTLs have been reported and mapped within fine intervals, even molecular characterization of many such QTLs has also been done. With availability of such large information there is a need to characterize each QTL in term of genes present, so that they can be exploited for transgenic approach. Even marker-assisted pyramiding of QTLs responsible for important traits such as root length, grain weight, number of tiller, number of grain needs to be done to develop a water efficient but at the same time high-yielding cultivar.

Conclusions

Available literature related to the water scarcity and rice production, aerobic rice, linkage mapping and molecular breeding for water-efficient aerobic rice have been reviewed and presented various causes to increase or decrease aerobic rice yield and yield-related attributes. The finding indicated that there is a urgent need to enhance productivity of land

with water productivity (high yield from every drop of water used) particularly in rice cultivation. To overcome the challenges of water scarcity, agricultural scientists were developing water-efficient rice (aerobic). At the same time several strategies are used for reducing water consumption in rice cultivation, such as saturated soil culture on raised beds, etc.; however, development of aerobic rice is the most effective strategy in terms of efficient use of water.

Compliance with ethical standards

Conflict of interest We declare that the authors of this paper have no conflicting interests.

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