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QTL mapping for morpho-physiological traits of rice under aerobic conditions using back cross populations

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Abstract

Restructuring the rice production system to reduce water consumption during cultivation is necessary to combat the negative impact of global climate change. The present study was conducted to identify QTLs associated with various morpho-physiological traits under aerobic production systems using back cross population. The findings showed that aerobic parent MAS26 showed significantly higher performance for most of the studied traits except grain length/breadth ratio. The studied traits showed again yield/plant revealed a positive correlation with an effective number of tillers/plants and 1000-grain weight. The composite interval mapping identified a total of 22 QTL0s for various morpho-physiological traits in BC$_1$F$_2$ (11) and BC$_1$F$_3$ (11) populations. The phenotypic variation explained by the identified QTL ranged from 9.1 to 84.0%.Grain yield/plant was associated with four QTLs on chromosomes 1, 3, and 7 with LOD values ranging from 3.31 to 8.43 explaining phenotypic variation 26.46 to 58.57%. The identification of QTL conferring improved adaptation and higher grain yield under direct seeding aerobic environment may facilitate the development of high-yielding direct-seeded rice varieties. However, QTLs identified in this study were putative and need to be further confirmed followed by validation.

Keywords: Rice, backcross, QTL, aerobic, basmati, population

Introduction

Rice is a primary source of food for about 3 billion people across the world, widely grown in tropical and subtropical regions (FAO, 2004) [14].It is water water-loving crop cultivated in 55% of the global area under irrigated conditions followed by 25% under rainfed lowland, 12% under upland, and 8% under deep water conditions. The estimates also showed that more than 75% of the annual rice supply comes from 79 million ha of irrigated paddy land. With the increasing effects of climate change and extreme weather events production of rice is affected globally. To combat the negative impact of global climate change on rice production restructuring in the production system is necessary. Among the several strategies used for reducing water consumption in rice cultivation, such as saturated soil culture on raised beds, alternate wetting and drying (Bouman and Tuong, 2001) [8], ground cover system, system of rice intensification (Stoop *et al*. 2002) [42], and aerobic rice cultivation (Bouman *et al*. 2006) [9]. Among these strategies, aerobic rice is considered to be one of the most promising strategies in terms of water-use efficiency (Tuong and Bouman, 2002) [44]. Aerobic rice system technology by scientists at IRRI has developed an “Aerobic rice” technology that aims to significantly reduce the crop’s water requirement below current levels. It is a water-saving rice production system in which potentially high-yielding, fertilizer-adapted rice varieties are grown in fertile aerobic soils that are non-puddled and have no standing water (Kreye *et al*. 2009) [25]. Such ‘aerobic rice’ varieties combine the aerobic adaption of traditional upland varieties with the input responsiveness, and yield potential of irrigated varieties (Atlin *et al*. 2006) [3]. By reducing water use during land preparation and limiting seepage, percolation, and evaporation, aerobic rice had about 51% less total water use and 32-88% higher productivity than flooded rice (Bouman 2009) [7].

The establishment of efficient molecular marker technology allowed the construction of linkage map, QTL detection, and marker-assisted selection of the target traits which greatly improved the selection efficiency and precision in rice breeding programs including the development of new water-efficient cultivars with improved root traits (Tanksley, 1989; Staub*et al*. 1996; Mohan *et al*. 1997) [43, 40, 28]. Various studies were conducted earlier to identify genomic locations associated with the aerobic cultivation of rice. QTLs for grain yield on chromosome 1(Vikram *et al*. 2011) [46], 2, 9, and 12 (Dixit *et al*. 2012) [11] were already reported. Similarly, genomic locations associated with suitable agronomic aerobic traits such as plant height, effective no of tillers, grain yield/plant, and root parameters have been previously identified (Vikram *et al*. 2011; Dixit *et al*. 2012; Sandhu *et al*. 2013; Sandhu *et al*. 2014) [46, 11, 36-37]. However, the genomic regions associated with aerobic conditions in basmati rice varieties are very limited. Basmati varieties command premium prices in the rice market due to their exquisite fragrance and grain and cooking qualities; their demand and export have increased markedly in recent years. Water scarcity and declining groundwater table in several states of India including Haryana and Punjab have posed serious challenges to Basmati rice production in this region. Keeping the above facts under consideration present study was conducted to identify genomic locations associated with aerobic conditions in the Basmati background using back cross population.

Materials and Methods

Plant material

A total of twenty-one (BC_1F_2, and BC_1F_3) back cross plants population derived from PUSA1121 x MAS26/MAS26 were used in the study. The genotype MAS26 is an aerobic indica rice variety developed at IRRI, Manila, Philippines. While, PUSA1121 is a premium Basmati rice variety developed at IARI, New Delhi. Both varieties were developed at Punjab Agricultural University Ludhiana. The details of the parents and crossing were presented in Meena *et al*. 2020 [52].

Phenotyping

Phenotyping was done in the field and net house conditions. The crop was raised during the Kharif season of two growing season/years in the net house of the Department of Molecular Biology, Biotechnology and Bioinformatics, CCS Haryana Agricultural University, Hisar, and in the field at CCS HAU Rice Research Station, Kaul (Kaithal), which falls under semi-tropical regions if North India. Selected promising lines derived from the various crosses were evaluated in a further generation. All recommended agronomic practices were followed for raising a good crop. Seeds were grown in rows of 2.5m in length (3 rows each) in the field with plant-to-plant spacing of 15cm and row-to-row spacing of 20cm. All recommended agronomic practices were followed for raising a good crop. The evaluation of back cross populations was performed as given in Meena *et al.* 2020 [52]. The data were recorded for Plant height (cm), Effective number of tillers per plant, Panicle length (cm), Grain yield per plant (g), 1000-grain weight (g), and Length/Breadth ratio. The data were subjected to statistical analysis using CROPSTAT 7.2 (available at http://bbi.irri.org/products) and SPAR 2.0.

Genotyping

Genomic DNA was isolated using the CTAB method of Saghai-Maroof *et al.* (1984) [34]. DNA quantity was estimated by ethidium bromide staining on 1% agarose gels using a standard containing 100 ng/µl genomic DNA. PCR amplification, denaturing polyacrylamide gel electrophoresis, and silver staining were essentially carried out as described earlier by Jain *et al*. (2006) [53]. A total of 604 SSR markers widely distributed on 12 rice chromosomes were used in the study of the parental polymorphism. Out of 604 SSR markers, 60 were found to be polymorphic and were used to genotype the selected BC_1F_2 and BC_1F_3 populations. The markers were obtained based on published rice genome maps (IRGSP 2005) [19] and their physical position (Mb) on the indica genome (www.gramene.org) was used as a reference. QTL analysis was performed using QTL Cartographer v2.5 (Wang *et al.* 2010) [54]. Before QTL analysis, single marker analysis was performed to identify significant genetic markers associated with phenotypic traits. The trait settings for CIM were done using model 6, forward and backward stepwise regression with a threshold of P/0.05 to select cofactors, window size 10, and 3cM walking speed along chromosomes. QTLs were verified by LOD scores compared to an empirical genome-wide significant threshold calculated from 500 permutations for P/0.05. LOD scores and coefficients of determination were estimated by CIM for each QTL. Map and QTL graphics were drawn using the software Map Chart v2.1.

Results

Phenotyping

In the present study parents as well as BC_1F_2 and BC_1F_3 populations showed high variations for all the physio-morphological traits under aerobic field conditions (Table 1). The aerobic parent MAS26 showed higher performance for effective tillers/plants, panicle length, 1000-grain weight, and grain yield per plant for both BC_1F_2 and BC_1F_3 populations. While parent PUSA1121 showed higher performance for the L/B ratio in both populations. In the case of plant height parent MAS26 was higher in BC_1F_3 and PUSA1121 was higher in BC_1F_2 population. Similarly, plant height ranged from 84 to 125cm with 99.8cm and75 to 135cm with 106.3cm in BC_1F_2 and BC_1F_3 populations, respectively.The number of effective tillers per plant ranged from 6 to 17 in the BC_1F_2 population while it ranged from 6 to 20 in the BC_1F_3 population. Grain yield/pant ranged from 8.4 to 20.1g in BC_1F_2 and 6.3 to 27.5 g in BC_1F_3 population. Likewise, 1000-grain weight (g) ranged from 14.2 to 26.7 in BC_1F_2 and 8.6 to 28.1 g in the BC_1F_3 population with a mean of 21.51 and 19.7 g, respectively. Similarly, other studied traits showed a significant variation among both the back cross populations. The frequency distribution curves for various physio-morphological traits of BC_1F_2 and BC_1F_3 populations and parental rice genotypes are shown in Figure 1. The frequency distribution indicated that both the back cross populations showed positive as well as negative transgressive segregants.

The correlation coefficients of BC_1F_2 and BC_1F_3 populations showed significant positive correlations between plant height with panicle length, 1000-grain weight, grain yield/plant, and L/B ratio (Table 2). During both crop seasons, grain yield/plant revealed a positive correlation with an effective number of tillers/plants and 1000-grain weight. While during first year it showed a significant positive correlation with the L/B ratio.

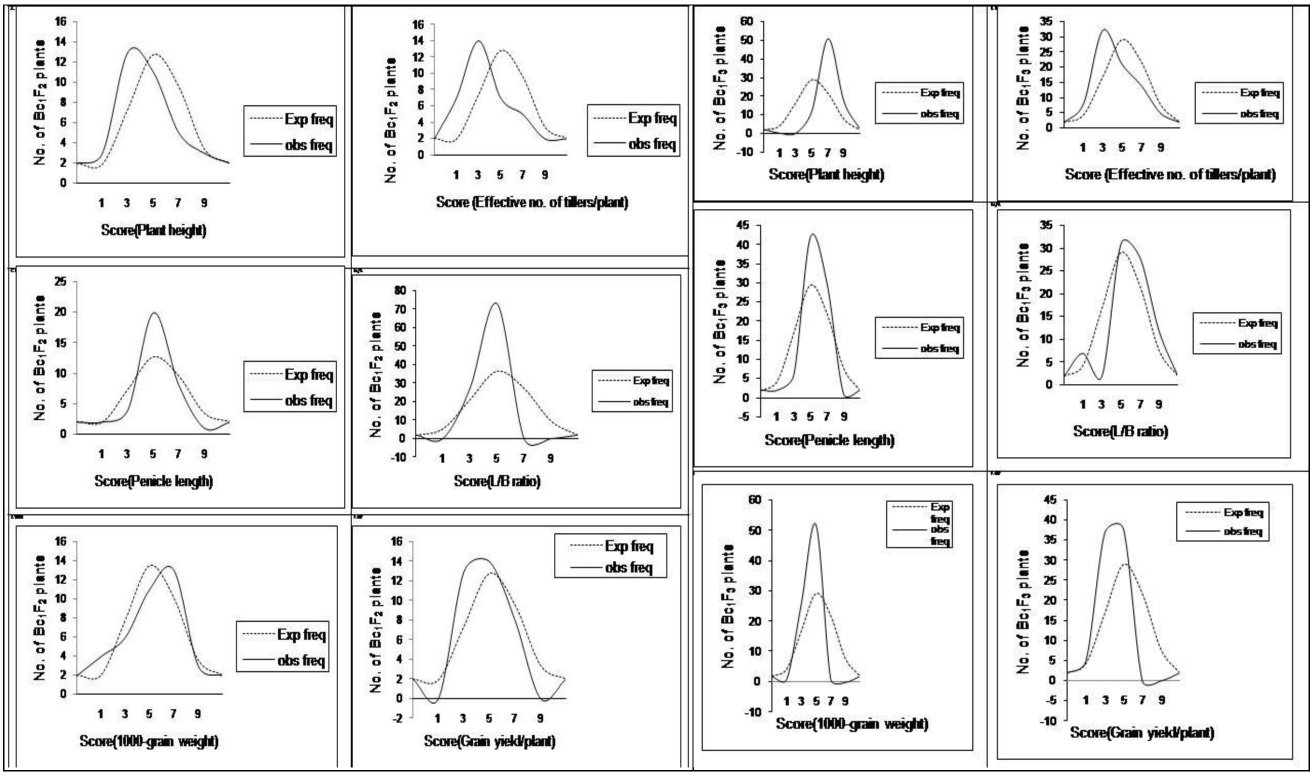

Fig 1: Frequency distribution curves for physio-morphological and traits of (a) BC1F2 and (b) BC1F3 plants PUSA1121 x MAS26 populations grown under aerobic conditions in the field

Genotyping

In the present study 71 and 63 SSR markers showing parental polymorphism were used to screen BC$_1$F$_2$ and BC$_1$F$_3$, respectively. The parent PUSA1121 showed 51 and 48.3% alleles while parent 49.0 and 51.7% alleles were from MAS26 in BC$_1$F$_2$ and BC$_1$F$_3$, respectively. In our study similarity coefficient of BC$_1$F$_2$ and BC$_1$F$_3$ was 0.44 and 0.51, respectively. The cluster analysis showed that the back cross population was interspersed between the two parental lines with the distribution of most plants towards MAS26 in both generations (Supplementary Figure 1).

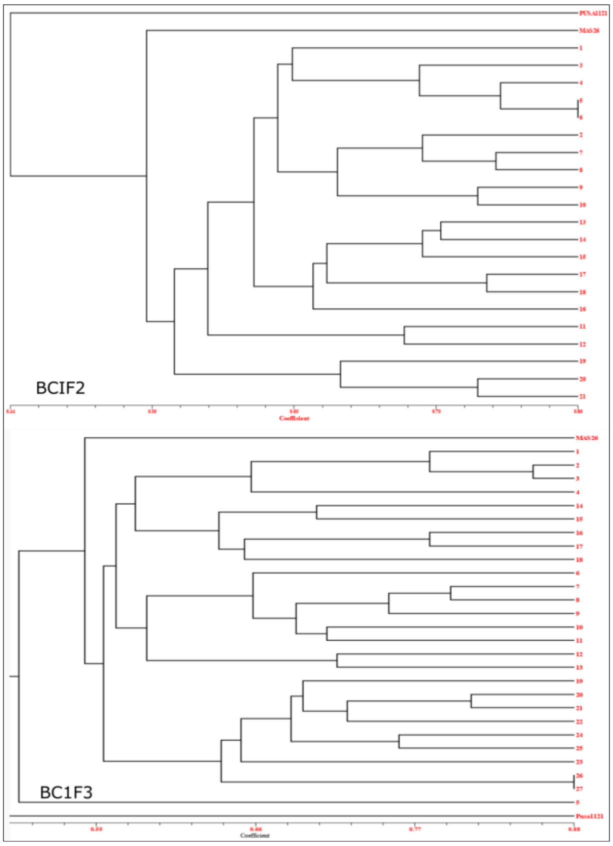

Fig 2: Dendrogram (NTSYS-pc) displaying diversity among BC1F2 Plants 21 & 27 (PUSA1121 x MAS26) BC1F3 plants (grown in field) using allelic diversity data at 71 & 63 SSR loci

The composite interval mapping showed a total of 22 QTLs for various morpho-physiological traits in BC_1F_2 (11) and BC_1F_3 (11) (Table 3 and Figure 2). The phenotypic variation explained by the identified QTL ranged from 13.0 to 62.3% in BC_1F_3 and 9.1 to 84.0% in BC1F2. Out of four QTLs identified for plant height, two QTLs (*qPH11.1* and *qPH11.2*) were mapped at positions of 54.9 and 70.4 cM on chromosome 11 respectively in BC_1F_2 while another two QTL (*qPH10.1* and *qPH10.2*) were mapped at position of 62.5 and 78.8 cM on chromosome 10 in BC_1F_3, respectively. The phenotypic variation explained by the QTL associated with plant height ranged from 22.34 to 56.12%. Panicle length was associated with the six QTLs, out of them four QTLs (*qPL2.1*, *qPL2.2*, *qPL7.1*, and *qPL11.1*) were identified in BC_1F_2 while two QTLs (*qPL10.1* and *qPL10.2*) were identified in BC_1F_3 on chromosomes 2, 7, 11 and 10, respectively. The phenotypic variation explained by these QTLs ranged from 13.01 to 84.04%. Grain yield/plant was associated with four QTLs, three inBC_1F_3 (*qGYP3.1*, *qGYP3.2*, and *qGYP7.1*) and a single in BC_1F_2 (*qGYP1.1*) on chromosomes 3, 7, and 1, respectively explaining phenotypic variation ranged from 26.46 to 58.57%. Similarly, four QTL (*qLB2.1*, *qLB2.2*, *qLB10.1*, and *qLB11.1*) were identified for grain length/breadth ratio at map positions of 36.8, 96.9, 51.3, and 39.9 cM on chromosomes 2, 10 and 11, respectively in BC1F2 while two QTLs for grain length/breadth ratio (*qLB3.1* and *qLB3.2)* at map positions of 124.2 and 153.2 cM on chromosomes 3were detected in BC1F3. Two QTLs for the effective number of tillers/plants (*qENT3.1* and *qENT3.2*) at map positions of 132.2 and 151.2 cM on chromosome 3. Most of the QTLs identified had higher LOD scores (4.43–11.46). Thirteen of these QTL had negative values for additive effect indicating that the favoring alleles were from the PUSA1121 parent while the positive additive effect indicated that favorable alleles were from MAS26.

Discussion

Aerobic rice is specifically developed rice that combines drought tolerance of upland rice with yield potential of lowland rice, considered improved upland rice. The development of aerobic rice could reduce the negative impact of global climate change. Therefore present study was focused on the identification of QTL associated with traits of aerobic cultivation. In the present study grain yield of BC_1F_2 and BC_1F_3 populations ranged between 8.4 –20.1g and 6.3–27.5 g, respectively. The parental line MAS26 showed higher performance for most of the studied traits as compared to the PUSA1121. Previous reports also suggested the yield potential and yield stability of the aerobic rice varieties (Kanbar *et al*. 2009; Babu *et al*. 2011) [22, 4]. It has been also reported that the performance of aerobic rice genotypes i.e. MAS26 could be declined by 13.4-20.1% under submerged conditions while under aerobic conditions the yield of lowland Basmati rice varieties i.e. PUSA1121 could decline by 23–27% (Sandhu *et al*. 2012) [35]. Earlier reports also suggested the higher performance of aerobic rice genotypes for tillers hill-1,longer root length, higher root and shoot dry weight hill-1 compared to the traditional method of planting (Gani *et al*. 2002; Xiaoguang *et al*. 2005; Kato *et al*. 2009;Kato *et al*. 2009) [15, 50, 23, 24]. Similarly, the association among the traits under aerobic conditions showed a positive and significant association with grain yield per plant (Akhtar *et al*. 2011; Yadav *et al*. 2011; Seyoum *et al*. 2012) [1, 51, 55] as in our study. Nagaraju *et al.* (2013) [29] also reported that the number of grains per panicle, total number of productive tillers per plant, kernel L/B ratio, and panicle length showed a highly significant positive association with grain yield per plant. Ramesha *et al*. (2010) [31] observed that grain yield was positively correlated with the number of effective tillers per plant, panicle length, spikelet fertility, and thousand-grain weight. While increased root length allows roots to penetrate hard pans characteristic of some lowlands, root thickness, and density improve water uptake by producing more and larger root branches. Similarly, grain yield per plant had a significant positive correlation with biological yield per plant, plant height; number of spikelets per panicle, and panicle length are important plant traits that should be considered when any breeding program for higher paddy yield (Reddy *et al*. 2013; Kumar *et al*. 2014; Rani *et al*. 2017) [33, 26, 32]. Similarly, grains per panicle showed a highly significant and positive association with 1000 grain weight at both the genotypic level and phenotypic level. This was earlier found in aerobic conditions by Sankar *et al.* (2006) [38]. The criterion for a character to be an index of drought tolerance/aerobic adaptation is that it has a positive significant correlation coefficient with grain yield under water stress (Prakash and Anandan, 2012) [30].

In this study, SSR-based polymorphism was worked out between aerobic and Basmati rice varieties showing backcross populations were interspersed between the parental rice genotypes. The populations were skewed towards the respective aerobic rice parent which is also clear from frequency distribution curves for the majority of agronomic and root traits. However, it must be noted that the contribution of alleles from the aerobic rice parents varied between 49.1 to 51%indicating that the contribution of equal alleles at similar frequency in this population. The previous studies also indicated clustering or grouping of Basmati rice varieties in a different group than lowland and aerobic *indica* rice (Glaszmann 1987; Jain *et al*. 2004; Sandhu *et al.* 2012) [17, 20, 35]. The finding suggested that aerobic rice varieties were developed from different *indica*x upland rice crosses and may have differential levels of genetic content from the recurrent *indica* and donor upland rice varieties. The previous study also indicated that Indian aromatic and quality germplasm is genetically distinct from other groups within O. sativa and is the product of a long independent pattern of evolution (Jain *et al*. 2004) [20].

The present studyidentifies QTL for grain yield, plant height, effective tillers/plants, panicle length, and grain L/B ratio usingcomposite interval mapping analysis. QTLs identified for plant height were mapped on chromosomes 10 and 11explaining 22.34 to 56.12% phenotypic variation. Previously many SSR markers have been reported to be linked to QTL promoting aerobic adaptation in rice such as yield under drought (Venuprasad *et al*. 2009; Vikram *et al.* 2011) [45, 46], root length (Steele *et al*. 2007) [41], basal root thickness and root dry weight (Kanbar and Shashidhar, 2004) [21].Similarly, four QTLs, *qGYP1.1, qGYP3.1, qGYP3.2,* and *qGYP7.1* were identified in the present study using back cross population explained phenotypic variation ranging from 26.46 to 58.57% on chromosomes 1, 3, and 7. Earlier, QTL for grain yield in rice has been reported on chromosomes 2, 3, 5, 7, and 9 (Wan *et al*. 2006; Song *et al*. 2007; Weng *et al*. 2008) [47, 48].Several of the QTL identified for GY in the present study have also been previously reported to be consistent across different mapping populations and conditions (Ghimire *et al*. 2012; Vikram *et al*. 2011; Sandhu *et al*. 2013; Dixit *et al*. 2012) [16, 46, 36, 11]. Several QTLs for grain yield under drought stress have been reported for both upland and lowland rice (Bernier *et al*. 2007; Venuprasad *et al*. 2009) [5, 45]. Dixit *et al*. (2014) [10] identified three QTL–*qDTY3.1* (RM168-RM468), *qDTY6.1* (RM586 – RM217), and *qDTY6.2* (RM121 – RM541) for grain yield under drought. QTL, *qDTY3.1,* and qDTY6.1 showed consistent effects across seasons under lowland drought-stress conditions. In the present study, two QTLs, *qGY3.1*, and *qGY3.2*, for grain yield on chromosome 3 were mapped for grain yield on chromosome 3. The QTLs *qLB2.1*, *qLB2.2*, *qLB3.1*, *qLB3.2*, *qLB10.1*, and *qLB11.1*for grain length/breadth ratio on chromosomes 2, 3, 10, and 11 in the present study explained 9.16 to 56.31% phenotypic variation. Major QTL for grain length has also been reported earlier on chromosomes 1, 2, 3, and 6 (Aluko *et al*. 2004; Fan *et al*. 2006) [2, 13].Lou *et al*. (2009) [27] reported that the two QTL on Chromosome 3 and 6 for grain length. Wan *et al*. (2006) reported the six main effects of QTL for grain length in four environments on five rice chromosomes (2, 3, 5, 7, and 9) with LOD values between 7.30 and 28.94. Among them, *qGL-3a* was consistently detected in these four environments and mapped to the interval C80–C1677 in the centromeric region of chromosome 3 (Harushima *et al*. 1998) [18]. A comparative sequencing study between short and long-grain varieties showed that the second exon of the putative grain length gene GS3 has a nonsense mutation that is found in long-grain varieties (Fan *et al*. 2006) [13]. On the other hand, a loss of function mutation in GW2, a QTL located on chromosome 2, affects the grain width and weight (Song *et al*. 2007) [39]. Sixteen QTL were mapped on Chr 1, 2, 3, 6, 7, and 9 for grain quality in RIL populations derived from *indica* x japonica crosses (Lou *et al*. 2009) [27].

The identification of QTL conferring improved adaptation and higher grain yield under direct seeding aerobic environment may facilitate the development of high-yielding direct-seeded rice varieties. The QTLs identified in this study were based on only two-year data; they are putative QTLs and need to be further confirmed. The present study involved a lower size of the population and a lower number of SSR loci and molecular analyses may have missed several large-effects QTL promoting aerobic adaptation. However, the identified QTL in this study could incorporated into future introgression work to improve rice yield under dry direct-seeded drought conditions after validation.

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