Identification of Quantitative Trait Loci for Mesocotyl Length of Rice Seedling in Different Sowing Depths using Genome-Wide Association Study

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Abstract

Background: The mesocotyl length of rice seedling is a complex trait associated with the ability of seedling emerging and controlled by quantitative trait loci (QTLs). Genome-wide association study (GWAS) is a high-through QTLs mapping method and widely used to identify QTLs in the field of plant genetics.

Results: A series of rice accessions including 290 varieties from all over the world, which harbored widely genetic background, were finished whole genome re-sequencing and investigated the mesocotyl length of rice seedlings in three different sowing depths (0cm, 4cm and 6cm). The analysis of coefficient of variation (CV) showed that the rice mesocotyl length variability in the three different treatments with 0cm, 4cm and 6cm sand culture are 114.43%, 146.65% and 152.55%, respectively. The mesocotyl length of the three groups are positively correlated with each other, indicating that the variation trend is consistent despite the differences in experimental treatment conditions, which led to the different performances of the mesocotyl lengths of the same accession. After GWAS, we found There are 922 single nucleotide polymorphism (SNP) makers associated with rice seedling mesocotyl length across 20 QTL regions and covered 1246 genes.

Conclusions: In this study, we found that there are 922 SNP makers associated with rice seedling mesocotyl length across 20 QTL regions and covered 1246 genes. And we detected 23 candidate genes which maybe have effect to the mesocotyl length of rice seedling at different sowing depths

Background

Rice is one of the most important crops in the world. In traditional rice cultivation, rice is sprouted first and the fully germinated seedling is then replanted into a permanent location, termed as seedling transplanting. Compared to seedling transplanting, direct seedling is a simplified cultivation technology that has the advantages of saving labor and energy, environmental protection and higher cost efficiency. Although previously direct seedling is associated with low seedling emergence rate, difficulty in weed control and weak lodging resistance, it becomes more and more popular with significant developments in recent years(Farooq et al. 2011; Kumar and Ladha 2011; Shahi and RAU 2015; Soriano et al. 2018). For instance, in the USA, Italy and Australia, almost all rice is direct seeded(Kumar and Ladha 2011).. In Asia, more than 50% of rice is direct seeded in Sri Lanka, Malaysia and some parts of India; and the direct-seeded rice fields are also increased rapidly in China, Philippines, South Korea, Japan, Thailand and several other countries recently(Chen et al. 2018; S Marasini 2016; Sansen et al. 2019; Weerakoon et al. 2011).

Direct seedling of rice is roughly divided into paddy field direct seedling and dryland direct seedling, in which dryland direct seedling rice is particularly important for arid and semi-arid areas. Rice cultivation with direct seedling is greatly affected by sowing depth. Although increasing sowing depth within a certain range increased drought resistance and lodging resistance of rice, too deep seedling significantly

reduced seedling emergence. Previous studies have shown The length of mesocotyl at different sowing depths is positively correlated to the rice seedling emergence rate(Dilday et al. 1990; Ohno et al. 2018). Moreover, the rice mesocotyl length is also essential for its capacity to unearth and early vigor(Allan et al. 1961; Purchase et al. 1992). However, most current rice accessions are semi-dwarf accessions with short mesocotyl that showed low emergence rate when planted deeply (Turner et al. 1982; Wu et al. 2015).

Rice mesocotyl length is determined by both environmental and genetic factors. Environmental factors, such as light condition, temperature, soil moisture condition, oxygen concentration, sowing depth and exogenous hormones, can affect mesocotyl elongation(Gao et al. 2012; Hu et al. 2010; Watanabe et al. 2001; Yalan 2016). Genetic analysis showed that the length of rice mesocotyl was controlled by multiple genes, which varied from accession to accession but could be inherited stably(Redoña and Mackill 1996). There are many rice mesocotyl length quantitative trait loci which are distributed on 12 chromosomes identified by different mapping populations(Lee et al. 2012,2017; Wu et al. 2015; Yalan 2016; Zhao et al. 2018). Hyun-Sook Lee et al(Lee et al. 2012) detected 7 QTLs associated with mesocotyl length on rice chromosomes 1, 3, 7, 9 and 12 using restriction fragment length polymorphism(RELP) molecular makers by BILs population which was constructed by hybridization of rice accessions Nipponbare and Kasalath. Ya-lan Li et al(Yalan 2016) constructed the rice F3 population from the cross between the parental lines of 'Zhaxima' and 'Hanhui No. 3', and detected 11 QTLs related to rice mesocotyl length on chromosomes 1, 3, 6, 8, 11 and 12 by BSA. With the development and application of NGS and GWAS, more and more loci related to rice mesocotyl length were found precisely: Jing-hong Wu et al(Wu et al. 2015) in a GWAS research detected 7 rice mesocotyl length QTLs distributing chromosome 1,3,4,5,6,9,10 including 36 genes; Yan Zhao et al(Zhao et al. 2018) used GWAS to associate the re- sequencing data of 621 rice cultivars and the seedling mesocotyl length in the 10 cm sand-culture condition and detected 13 QTLs controlling rice mesocotyl length predicted 21 candidate genes distributing rice chromosome 2, 3, 4, 7, 8, 9, 10 and 11.

Results

The variation of rice mesocotyl length

The analysis of CV (Table 1 & Table S1) showed that the rice mesocotyl length variability in the three different treatments with 0 cm, 4 cm and 6 cm sand culture are 114.43%, 146.65% and 152.55%, respectively. While most mesocotyl lengths in the three groups are in 0.00 ~ 0.50 cm; some are above 1.00 cm. There are 10 (the least) and 20 (the most) rice accessions whose mesocotyl lengths are in the range of 1.00 ~ 3.00 cm when cultured with a sowing depth of 4 cm and 6 cm, respectively (Fig. 1). For each rice accession, the difference in mesocotyl lengths at different sowing depths is within 1 cm. The analysis of variance (ANOVA) showed that there is significant difference in the mesocotyl length of 290 rice accessions in the three groups (Table 2) Although there was difference in the mesocotyl length for the same accession when cultured with different sowing depths, the trend of change in mesocotyl length for each accession is highly correlated to the sowing depths.

The experiments results show that there is extensive variation but similar variation pattern for the mesocotyl length of rice seedling in the 290 rice accessions. According to the experimental data, the coefficient of variation (CV) of the mesocotyl lengths in experimental rice population is large and the averages of dispersion is high. This means that the experimental rice population which we used in this study have huge genetic difference and broad representation. The mesocotyl length in the most of the experimental accessions is short. And the variation of mesocotyl length is relatively slight when the treatment condition is 4 cm. It may be because that the depth of sand was shallow, and the seedling growth may be affected by light, thus the mesocotyl elongation was limited(Feng et al. 2017; Gao et al. 2011; Kondo et al. 2010; Yalan 2016). The mesocotyl length of the three groups are positively correlated with each other, indicating that the variation trend is consistent despite the differences in experimental treatment conditions, which led to the different performances of the mesocotyl lengths of the same accession.

Population structure analysis and whole genome resequencing of 290 rice accessions

There are 115 indica rice accessions, 133 japonica rice accessions and 42 Indica japonica intermediate types in the whole 290 experimental rice accessions from all over the world (Table S2). This germplasm resource population can represent two subspecies of rice and have rich genetic background, so this population is suitable for GWAS of mesocotyl length traits in rice seedlings. The average sequencing depth in the whole genome resequencing was 10 × for the 290 rice accessions and developed 1095430 SNPs genotypes. The MSU database(Xiong et al. 2017) http://rice.plantbiology.msu.edu was used to annotate the identified variations. It is the molecular basic for GWAS.

Detection of SNPs associated with mesocotyl length in rice seedling

The EMMAX software was used to analyze the correlation between the rice seedling mesocotyl length data and the SNP data developed by resequencing in 290 rice accessions, and 922 SNPs significantly was found to be correlated with the mesocotyl length were identified (Table 3). 85, 48 and 186 SNPs (-log (P value) ≥ 8.0) were identified when cultured at dark with 0 cm sand, 4 cm sand and 6 cm sand, respectively. 6 QTL regions across chromosomes 1, 4, 8 and 10 under 0 cm sand dark culture condition; 2 QTL regions across chromosomes 7 and 8 under 4 cm sand culture condition and 4 QTL regions across chromosomes 1, 6, 7 and 9 were the distribution of associated SNP makers. Because Bonferroni correction can be conservative, it may result in the probability of producing false negatives. Therefore, we identified the SNP makers associated with rice mesocotyl length again with the -log(P value) ≥ 7.0. And under 4 cm and 6 cm sand culture conditions, we newly identified 172 and 428 SNP makers, respectively. 172 SNP makers were across 2 QTL regions distributed in chromosomes 6 and 9. 428 SNP makers were in across 5 QTL regions distributed in chromosomes 1, 6, 7 and 12. The Manhattan plots of p-values analyzed the SNP makers associated with rice seedling mesocotyl length showed the visible loci in chromosomes (Fig. 2&3).

The comparative analysis of associated SNP makers in three different culture conditions

There were total 8 chromosomes were identified the SNP makers associated with rice seedling mesocotyl length in three different culture conditions. And there were identified 85, 220 and 614 SNP makers (-log (P value) ≥ 7.0) associations under 0 cm, 4 cm and 6 cm sand culture conditions, respectively. And the comparative analysis of the QTL regions in three different culture conditions showed that there was no overlap among 0 cm,4 cm or 6 cm sand culture conditions, but there were three overlap regions between 4 cm and 6 cm sand culture conditions. The overlap regions were distributed in chromosomes 6, 7 and 9. The length of regions was 297.472Kb、253.012Kb、312.368Kb, respectively. The repetitive SNP maker number in three overlap regions was 112, 9 and 5, respectively.

These results showed that there were wide differences in SNP makers associated with rice seedling mesocotyl length among three culture conditions. For each culture conditions there were many specific SNP makers, although there were some overlapped SNP makers between 4 cm and 6 cm sand culture conditions. It indicates that there are multiple genes controlling rice seedling mesocotyl length, and rice seedling mesocotyl length is sensitive to environmental influences.

Identification of candidate genes for seedling mesocotyl length

There are 922 SNP makers associated with rice seedling mesocotyl length across 20 QTL regions and covered 1246 genes. There are little genes known the functions among these genes, and most of these genes are annotated as the unknown expressed protein or putative protein in http://rice.plantbiology.msu.edu (Xiong et al. 2017). And some of these genes are annotated as the regulated genes of growth and development or transcription factors.

For 6 cm sand culture condition, there were 7 QTL regions associated with seedling mesocotyl length. And total 11 SNP makers was located in *qML_{6cm}6-1* covered 1687.342 kb(6610901–8298243) region in Chr6. The *qML_{6cm}6-1* includes 2 GDSL-like lipase/acylhydrolase genes*(LOC_Os06g12410, LOC_Os06g14630)*and 1 growth regulator related protein gene*(LOC_Os06g13215).* Moreover, there were 173 SNP makers located in *qML_{6cm}6-2*(Chr6:27582320–28071845) covered 489.525 kb region including a MYB gene*(LOC_Os12g39640)* and 2 Auxin-responsive Aux/IAA gene family member genes *OsIAA30(LOC_Os12g40890), OsIAA3（LOC_Os12g40900）*.

For 0 cm sand dark culture condition, 6 QTL regions were identified associated with seedling mesocotyl length. In *qML_{0cm}8*, there are 28 SNP makers located in 363.334 kb region (Chr8:25706134–26069468) covered 66 candidate genes including an auxin response factor *OsARF21(LOC_Os08g40900)*. And there were 2 OsWAK receptor-like protein kinase genes *(OsWAK34, OsWAK33)* found in *qML_{0cm}4* and 3*(OsWAK95, OsWAK96, OsWAK97)* in *qML_{0cm}10-1.* Furthermore in *qML_{0cm}10-1*, an OsWAK receptor-like cytoplasmic kinase gene*(OsWAK98, LOC_Os10g02360)* and an oxidoreductase, aldo/keto reductase family protein gene*(LOC_Os10g02380)* were identified.

GDSL-like lipase/acylhydrolase genes are mainly expressed in the root of rice seedlings and possibly regulate the cell elongation as well as extracellular matrix. *EGR1* with a GDSL-motif domain was as a negative regulator of coleoptile elongation in the context of recent findings on the impact of JA on light

signaling(GER1, a GDSL Motif-Encoding Gene from Rice is a Novel Early Light- and Jasmonate-Induced Gene). The main function of MYB family transcription factors was the regulator of secondary metabolism and Cellular morphogenesis, and MYB family transcription factors were expressed in different tissues and organs at different development stages of rice(Hande et al. 2017; Slabaugh et al. 2011). *OsSAUR25* and *OsSAUR26* are the member of the SUAR gene family which is as part of the primary auxin response in plants and involved in plant growth by regulating auxin synthesis and transport(Xihua et al. 2017; Chen et al. 2014; Kant and Rothstein 2009; Niek et al. 2018; Spartz et al. 2012). *OsIAA30* and *OsIAA3* are expressed in different tissues and organs at different development stages of rice especially highly expressed in the root of seedling, as reported that these two genes take part in the signal transduction of auxin(Jie et al. 2018; Nakamura et al. 2010). The genes in the wall-associated kinase (WAK) gene family have important function in plant growth and development such as signal transduction, Resistance of pathogens, response to mineral element and cell elongation(Shibo Zhang 2005). In rice, the genes of OsWAK receptor-like protein kinase are expressed in different tissues and organs at different development stages, *OsWAK1* is part in the defense of plant disease(Li et al. 2009); and *OsWAK11* is regulated by Aluminum (Al), Copper (Cu) and Sodium (Na)(Wei et al. 2014). But the function of six *OsWAK* genes in our associated QTL regions is not clear. And aldo/keto oxidoreductase gene is expressed the leaf and radicle, part in the regulation of cell elongation(Hur et al. 2009).

Taken together, based on our results and previous publications, we detected 23 candidate genes which maybe have effect to the mesocotyl length of rice seedling at different sowing depths(Table 4)(Kutschera and Wang 2016; Huizhen et al. 2018; Qi et al. 2013; Wang et al. 2007).

Discussion

The advantages and disadvantages of GWAS of rice seedling mesocotyl length trait

GWAS, based on whole genome re-sequencing, is the crucial method to identify locus of target trait due to its high throughput and resolution. The resolution of GWAS can even reach the single gene level. However, GWAS requires a large sample size and sufficient sequencing depth to ensure the accuracy of the analysis. In this study, we re-sequenced 290 rice accessions with the ~ 10X sequencing depth. The re-sequencing materials in this study were rich in genetic background from all over the world which covered both indica and japonica (about 1:1). For the sample size, sequencing depth and genetic variation, our materials meet the requirements of GWAS. But on the other hand, the regulation of rice seedling mesocotyl length is complex because it is controlled by multiple genes and is sensitive to environmental factors. For these reasons, we still may have missed some SNP makers associated with rice seedling mesocotyl length.

The comparative analysis of QTLs associated the trait of rice seedling mesocotyl length

In the previous study, researchers had identified some QTLs and genes associated with the trait of rice seedling mesocotyl length distributed in all over 12 chromosomes of rice(Lee et al. 2012,2017; Wu et al.

2015; Yalan 2016; Zhao et al. 2018) (Table 3). In this study, we had identified 922 SNP makers association covered 20 QTL regions with 1246 genes across 8 chromosomes including Chr1, 4, 6, 7, 8, 9, 10 and 12. And in our detected QTL regions, 4 QTLs (*qML_{6cm}1-3, qML_{4cm}9, qML_{6cm}9, qML_{6cm}12-2*) are adjacent or partially overlapping with 3 QTLs (*qMel-1*,*qMel-9*,*qMel-12)* which had been reported in the study of Hyun-Sook Lee et al(Lee et al. 2012) (Table 3). 8 QTLs (*qML_{0cm}1-1,qML_{0cm}1-2, qML_{4cm}6, qML_{4cm}7, qML_{6cm}6-1, qML_{6cm}6-2, qML_{6cm}7-2, qML_{6cm}12-2*) in Chr1, 6, 7 and 12 are adjacent or partially overlapped with 6 QTLs and in the study of Ya-lan Li et al(Li 2016). There are 6 QTLs (*qML_{0cm}1-2, qML_{0cm}4, qML_{4cm}6, qML_{6cm}6-2, qML_{4cm}9, qML_{6cm}9*) in our study being adjacent with the QTLs in Jing-hong Wu's(Wu et al. 2015) study. And *qML_{6cm}1-3* in the Chr1 is adjacent with *GY1*(Xiong et al. 2017), a gene functions at the initial step of jasmonic acid (JA) biosynthesis to repress mesocotyl and coleoptile elongation in etiolated rice seedlings, cloned in rice accession Kasalath (Table 3).

In this study, we have detected 23 candidate genes possibly associated with the trait of rice seedling mesocotyl length. These 23 candidate genes cover 6 chromosomes including Chr4, 6, 7, 8, 10, and 12. In the Chr7, we have identified a QTL (*qML_{6cm}7-1*) which is adjacent with *qFML7-2* and overlap *qFML7-3*, two QTLs identified by Yan Zhao(Zhao et al. 2018). And that both we have predicated a gene *LOC_Os07g24010*, a functionally unknown hypothetical protein (Table 4).

There are 8 of 20 QTLs associated with the trait of rice seedling mesocotyl length in our study that are newly identified and no intersection nor adjacent with reported QTLs. These 8 newly identified QTLs may be some marginal effects specific locus in our population. In our study, the candidate genes predicted to be associated with the trait of rice seedling mesocotyl length had a low repetition rate with the results predicted by previous study. On the one hand, that's because of the difference in experimental population, on the other hand, the trait of rice seedling mesocotyl length is susceptible to environmental influences. Thus, it is complex to investigate the QTLs controlled rice seedling mesocotyl length.

Breeding application

Rice direct sowing maybe become the trend of rice cultivation techniques for saving the cost of labor and reducing the working procedure. Rice seedling mesocotyl length is an important trait for rice direct sowing. In the process of rice direct sowing, the longer mesocotyl in rice seedling, the higher rate of seedling emergence is. In our study, we had identified 20 QTLs and a series of genes associated with the trait of rice seedling mesocotyl length in natural population by GWAS. And some of these QTLs are overlap or adjacent with previous reported study, that indicates the credibility of our results. For breeders, eight newly identified QTLs in our study may facilitate to develop new strategies for improving the ability of rice direct sowing.

Conclusion

In our study, we had cultivated 290 rice accessions in three different conditions (0 cm dark; 4 cm sand and 6 cm sand growing conditions). In three growth conditions, we had detected 14, 10 and 20 rice accessions which have more than 1 cm rice seedling mesocotyl, respectively. And there are total 10 rice

accessions having more than 1 cm seedling mesocotyl in all the culture conditions. Moreover, we had identified 922 SNP makers associated with the trait of rice seedling mesocotyl length and hit 1246 genes. After bioinformatic analysis, we had got 23 candidate genes. It would be a reference for the next work of gene mapping and cloning.

Methods

Planting and growth condition

290 rice accessions (Table.S2) were used as GWAS population, in which 220 accessions were selected from International Rice Research Institute (IRRI); and the other 70 accessions were from Institute of Genetics and Developmental Biology, Chinese Academy of Sciences. These accessions are from all over the world and have the extensive genetic background. The experiments were carried out in Sichuan Agricultural University, Chengdu, China. 100 healthy ripe seeds were selected for each accession and sterilized with 3% hydrogen peroxide. The seeds were then put into 28℃ water for 36 hours to sprout. Each accession was transported in three float tray holes (20 sprouting seeds/ hole). For each accession, there were three individual float tray holes and every hole covered with different depths of sand (0 cm, 4 cm, 6 cm). The float trays were placed in constant temperature rooms at 22 ℃ with 65% air humidity for 12 days. And the 0 cm float trays are shading treatment; the others sapper-light conditions are 14 h light and 10 h dark in a single day.

Evaluation of rice mesocotyl length

After 12 days of cultivation, the length of the mesocotyl was measured with the millimeter scale. 20 seedlings were measured in each single float tray hole.

Whole genome sequencing, SNP calling and Genotyping

Whole genome re-sequencing was performed for 290 rice accessions by using Illumina hi-seq sequencing system. Briefly, paired-end sequencing with 125–150 bp reading length (~ 10 × coverage) was carried out according to the Illumina standard sequencing method(J et al. 2014). The clean data for GWAS was obtained by removing the splices and inferior quality reads in the raw data. Clean reads were mapping to Rice Annotation version of 7.0 of accession Nipponbare from Michigan State University (http://rice.plantbiology.msu.edu/cgi-bin/gbrowse/rice/) with the BWA-MEM algorithm(Li 2013). The BAM files were then sorted using SAMtools software, and only reads with q value less than 10^{-30} were retained(Rajeshwari and Sarkar 2005). Next, SNP was called using GATK UnifiedGenotyper (v3.4–46) (Van der Auwera GA et al. 2013). The SNPs marked “PASS” by VCFtools software were kept. Only SNPs with missing rate lower than 0.2 and minor allele frequency (MAF) higher than 0.05 were used for genome-wide association study (GWAS).

GWAS

GWAS for mesocotyl length of rice seedlings was conducted by using EMMAX (mixed linear model). The population structure matrix was obtained by EIGENSOFT (version 6.0.1) for Principal component analysis (PCA). In order to minimize the impact of strongly linked genomic regions on PCA analysis, SNPs for PCA analysis were filtered using PLINK parameter -indep-pairwise 50 5 r2. Kinship matrix was obtained by emmax-kin-intel tool in EMMAX software. Bonferroni correction method was used to correct the p values of each SNP loci obtained from the association analysis, and a threshold of 0.05 was used to screen the significantly correlated SNP loci.

Abbreviations

QTL: Quantitative trait loci; CV: Coefficient of variation; GWAS: Genome-wide association study; SNP: Single nucleotide polymorphism; ANOVA: The analysis of variance; ML: Mesocotyl length.

Declarations

Ethical Approval and Consent to participate

Not applicable

Consent for publication

Not applicable

Availability of supporting data

The datasets supporting the conclusions of this article are included within the article and its additional files.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

CHY, SGL and YPW conceived and designed the experiments. XJT, QG, YHL, YL, and HW performed the experiments. CHY, HW, PQ, BT, WLC, HY, BTM, XXL, CZL, SGL and YPW analyzed the data. HW wrote the manuscript. All authors have read and approved the final manuscript.

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Tables

Due to technical limitations, table xlsx is only available as a download in the Supplemental Files section.

Figures

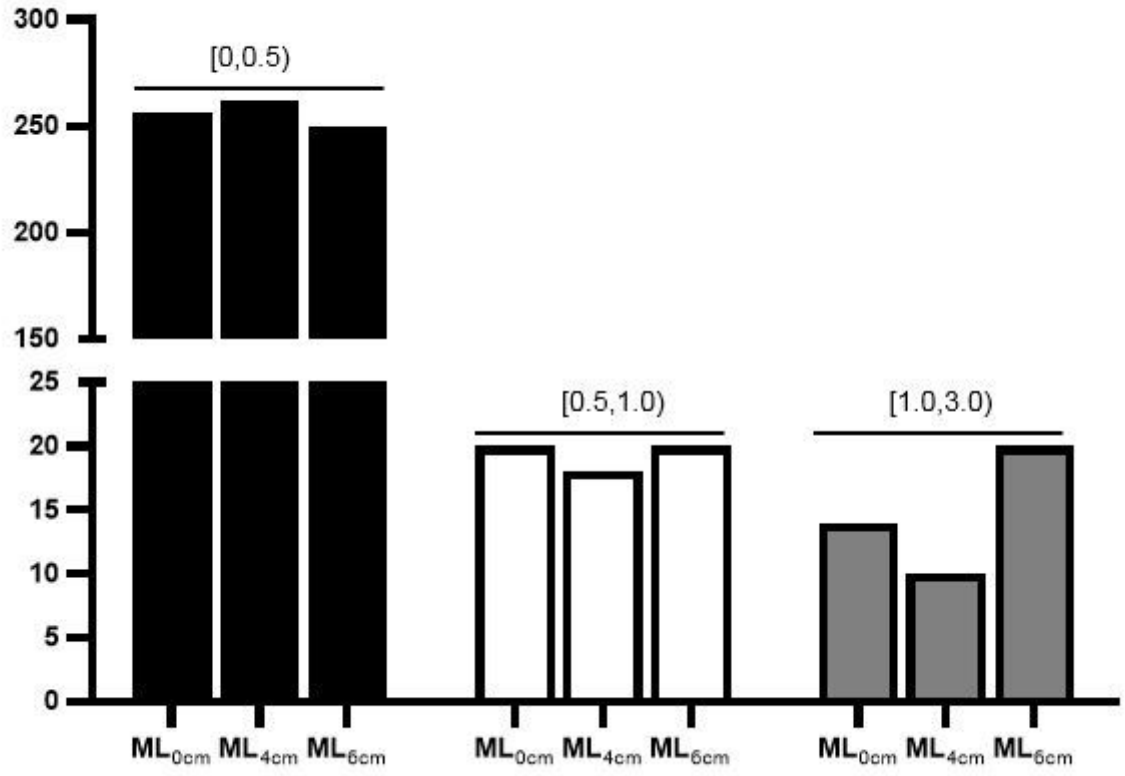

Figure 1

The mesocotyl length of 290 rice accesssions were classified under three different sowing depth. The group in black border and black fill is the number of rice variety whose mesocotyl length between 0-0.5cm in three different sowing conditions; the group in black border and white fill is the number of rice variety whose mesocotyl length between 0.5-1.0cm in three different sowing conditions; and the group in black border and gray fill is the number of rice variety whose mesocotyl length between 1.0-3.0cm in three different sowing conditions.

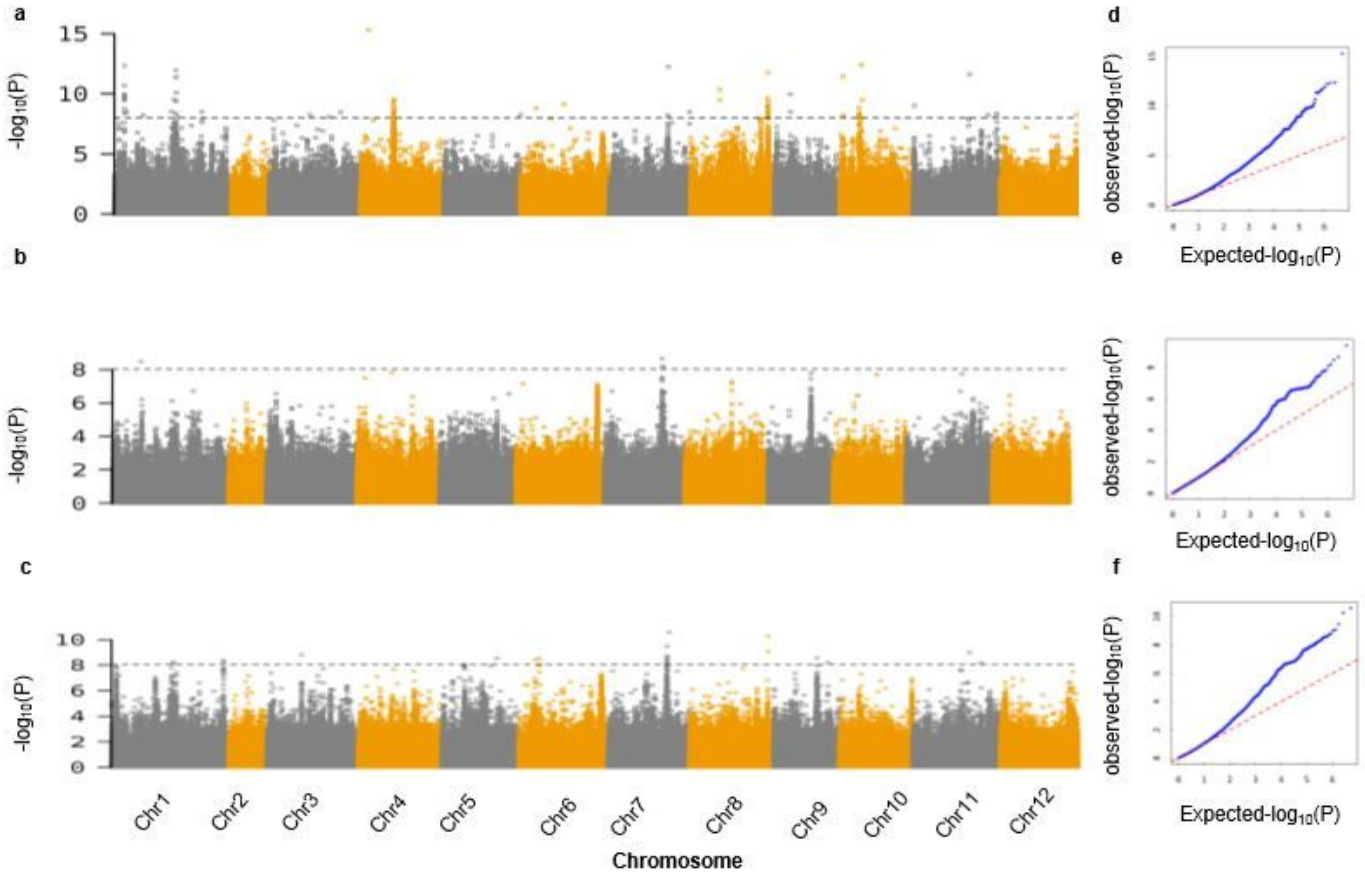

Figure 2

Manhattan plots of GWAS mapping for mesocotyl lengths. Manhattan plots of GWAS mapping for mesocotyl lengths measured in 0cm sand culture (ML0cm,a) in dark germination and in 4cm,6cm sand culture (ML4cm,b, ML6cm,c) and Quantile-Quantile plots for (ML0cm ,d) , (ML4cm,e)and(ML6cm,f).

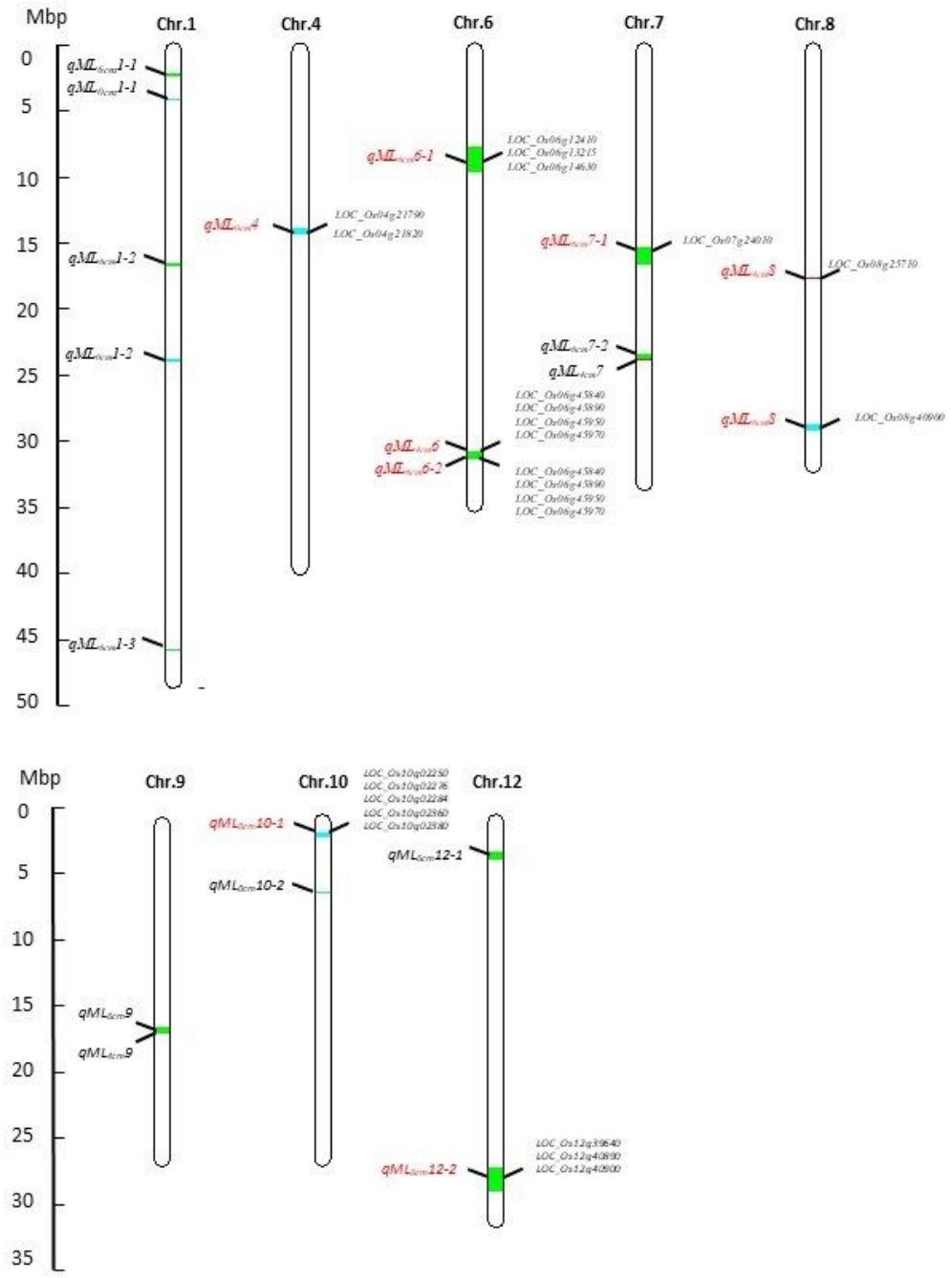

Figure 3

QTLs chromosome distribution of mesocotyl length in rice seedlings.

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