Meta-QTL and ortho-MQTL analyses identified genomic regions controlling rice yield, yield-related traits and root architecture under water deficit conditions

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Meta-QTL (MQTL) analysis is a robust approach for genetic dissection of complex quantitative traits. Rice varieties adapted to non-flooded cultivation are highly desirable in breeding programs due to the water deficit global problem. In order to identify stable QTLs for major agronomic traits under water deficit conditions, we performed a comprehensive MQTL analysis on 563 QTLs from 67 rice populations published from 2001 to 2019. Yield and yield-related traits including grain weight, heading date, plant height, tiller number as well as root architecture-related traits including root dry weight, root length, root number, root thickness, the ratio of deep rooting and plant water content under water deficit condition were investigated. A total of 61 stable MQTLs over different genetic backgrounds and environments were identified. The average confidence interval of MQTLs was considerably refined compared to the initial QTLs, resulted in the identification of some well-known functionally characterized genes and several putative novel CGs for investigated traits. Ortho-MQTL mining based on genomic collinearity between rice and maize allowed identification of five ortho-MQTLs between these two cereals. The results can help breeders to improve yield under water deficit conditions.

Abbreviations
AIC  Akaike information content
AICs  AIC correction
AIC3  AIC 3 candidate models
AWE  Average weight of evidence
BIC  Bayesian information criterion
CGs  Candidate genes
CT  Canopy temperature
CI  Confidence interval
DRI  Drought response index
DT  Drought tolerance
GW  Grain weight
HD  Heading date
LOD  The log of odds ratio
LR  Leaf rolling
LD  Leaf drying
MQTL  Meta-QTL
MAS  Marker-assisted selection

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Rice is the world's most important staple food and it is an excellent model crop for plant genetic studies. Considering climate change scenarios and increasing water deficits, rice breeding programs have invested significant efforts into producing new rice varieties suitable for growing under reduced water inputs. Tolerance to water deficit is a highly complex trait controlled by quantitative trait loci (QTLs). QTL mapping based on bi-parental populations is strongly influenced by the choice of marker sets, parents, population size, population types and environments, hampering the transfer of QTLs and associated markers across different breeding programs. A powerful approach to circumvent this issue is Meta-analysis of QTLs (MQTL), which compiles QTL data from independent studies, locations, years and genetic backgrounds in order to detect stable and reliable QTLs. An additional benefit of this approach is the reduction of confidence intervals (CIs) in the MQTLs leading to improved genetic resolution for marker-assisted selection (MAS) and identification of candidate genes (CGs). Together, MQTL analysis may increase selection accuracy and efficiency, thus enhancing genetic gains in plants breeding programs. Several MQTL studies for drought stress have been conducted in cereals such as wheat, maize, and barley. While a recent rice MQTL study considered various traits under unstressed conditions, relatively few reports address water deficit conditions in rice: MQTL studies by Swamy et al. and Trijatmiko et al. focused on yield integrating data from 15 and 13 experiments, respectively, and Khowaja et al. and Yang et al. reported some MQTLs for plant height and heading date based on QTLs published until 2009 and 2011, respectively.

In the current study, we conducted a comprehensive genome-wide meta-analysis on QTLs reported in the last two decades controlling yield and yield-related traits in rice under water deficit conditions including Yield (YLD), grain weight (GW), heading date (HD), tiller number (TN) as well as some drought tolerance criteria. Moreover, considering the key role of root architecture in plant responses to water deficit, different root related traits including root dry weight (RDW), root length (RL), root thickness (RT), roots number (RN) and rate of deep rooting (RDR) were subjected to MQTL analyses. We further scanned refined intervals of resulting stable QTLs for CGs related to the aforementioned traits. Additionally, to evaluate transferability of information to other cereals, ortho-MQTLs were investigated based on genomic collinearity between rice and maize. Results will be applicable to improve selection for yield potential, stability and performance under water deficit conditions in cereal breeding programs.

### Results and discussion

#### Distribution of yield and yield-related QTLs under water deficit conditions on the rice genome

In order to discover consensus genomic regions associated with YLD, PH, TN, HD, GW, RDW, RL, RT, RN and RDR and some drought tolerance-related traits including drought response index (DRI), relative water content (RWC), canopy temperature (CT), leaf rolling (LR), leaf drying (LD) under water deficit conditions in rice, we compiled a total of 563 QTLs derived from 67 QTL populations (57 studies) reported from 2001 to 2019 (Table 1; Fig. 1A). The number of QTLs for each trait and their distribution on 12 rice chromosomes are shown in Fig. 1A,B. The chromosome 1 harbored the highest number of QTLs for all studied traits with 241 initial QTLs (93%) were successfully projected on the reference map (Table 2). Consequently, chromosome 1 had the highest (83) and chromosome 5 and 10 had the lowest (21) number of projected QTLs. The meta-analysis greatly summarized the total number of projected QTLs from 527 to 61 MQTLs (11.5%; Fig. 1B,C) supported by at least two QTLs deduced from different populations and considerably reduced the respective confidence intervals (CI) in comparison to the initial QTLs (Table 3). Therefore, MQTL analysis can efficiently confine the number of QTLs and narrow down the genomic regions controlling different traits.

#### Detected MQTLs and their distribution on the rice genome

A total of 527 QTLs out of the 563 initial QTLs (93%) were successfully projected on the reference map (Table 2). Chromosome 1 had the highest (83) and chromosome 5 and 10 had the lowest (21) number of projected QTLs. The meta-analysis greatly summarized the total number of projected QTLs from 527 to 61 MQTLs (11.5%; Fig. 1B,C) supported by at least two QTLs deduced from different populations and considerably reduced the respective confidence intervals (CI) in comparison to the initial QTLs (Table 3). Therefore, MQTL analysis can efficiently confine the number of QTLs and narrow down the genomic regions controlling different traits.

The number of MQTLs per chromosome ranged from two (chromosome 10) to nine (chromosomes 1 and 9) with an average of 5.08 MQTLs (Fig. 2; Table 3; Additional file 1). Chromosomes 1 and 9 with nine MQTLs and...
| Ref no. | Number of QTL | Parents of population | Population type | Population size | No. of markers | Map density (cM) | Marker type | Trait(s) | References |
|--------|--------------|-----------------------|----------------|----------------|--------------|----------------|-------------|----------|------------|
| 1      | 1            | Caiapo × IRGC105491   | BC             | 300            | 718          | 2.49           | SSR, RFLP  | HD, PH, GW |            |
| 2      | 1            | IR58821 × IR52561     | RIL            | 183            | 178          | 5.29           | RFLP, AFLP | RT       |            |
| 3      | 1            | Bala × Aucena         | RIL            | 205            | 6969         | 0.20           | RFLP, AFLP, SSR | RT, RL, RN |            |
| 4      | 1            | CT9993 × IR62266      | DH             | 220            | 399          | 5.49           | RFLP, AFLP, SSR | YLD, HD, PH, RWC, CT, LR, LD |            |
| 5      | 1            | JAC65 × Co39          | RIL            | 96             | 117          | 10.20          | RFLP       | RL, RT   |            |
| 6      | 1            | Zhenshan 97 × Ming-ghu 63 | RIL          | 241            | 208          | 8.05           | SSR, RFLP  | YLD, GW   |            |
| 7      | 1            | Milyang23 × Akihikari | RIL            | 191            | 182          | 6.56           | RFLP       | TN       |            |
| 8      | 1            | IR1552 × Aucena       | RIL            | 96             | 117          | 11.01          | RFLP, AFLP, SSR | RL, RN   |            |
| 9      | 1            | Zhenshan 97 × Ming-ghu 63 | RIL          | 241            | 208          | 8.05           | SSR, RFLP  | PH, TN, HD |            |
| 10     | 1            | CT9993 × IR62266      | DH             | 220            | 182          | 4.19           | RFLP, AFLP, SSR | YLD, HD, PH |            |
| 11     | 1            | Yuefu × IRAT109       | DH             | 116            | 4662         | 0.23           | SSR, RFLP  | RT, RN, RL, RDW |            |
| 12     | 1            | ZenShan 97B × IRAT109 | RIL            | 187            | 339          | 2.99           | SSR        | YLD, GW   |            |
| 13     | 1            | ZenShan 97 × IRAT109  | RIL            | 180            | 683          | 2.45           | SSR        | HD, DRI, LR, LD |            |
| 14     | 1            | Bala × Aucena         | RIL            | 177            | 592          | 0.58           | RFLP, AFLP | PH, HD, LD |            |
| 15     | 1            | Akihikari × IRAT109   | BC             | 106            | 2506         | 0.23           | SSR        | RDW, RL  |            |
| 16     | 1            | IR62266 × IR 52,561   | RIL            | 148            | 231          | 5.43           | RFLP, AFLP | YLD, GW, PH, HD, CT, LR, LD |            |
| 17     | 1            | IR64 × Aucena         | BC             | 323            | 944          | 0.27           | SSR, RFLP  | RL, RT   |            |
| 18     | 1            | ZenShan 97B × IRAT109 | RIL            | 182            | 6969         | 0.20           | SSR        | RDR, RL  |            |
| 19     | 1            | Otomemochi × Yumenohata-mochi | RIL | 98             | 2187         | 0.25           | SSR        | RDW, RN, RL |            |
| 20     | 1            | Taichung 189 × Milyang 23 | F2           | 100            | 718          | 2.49           | SSR        | YLD, GW, PH |            |
| 21     | 1            | CT9993 × IR62266      | DH             | 220            | 154          | 5.14           | AFLP       | YLD, HD   |            |
| 22     | 1            | Vandana × Way Rarem  | F2             | 436            | 112          | 12.37          | SSR        | YLD, PH, HD |            |
| 23     | 1            | IRAT109 × Yuefu       | RIL            | 120            | 6969         | 0.25           | SSR        | RT       |            |
| 24     | 1            | Yuefu × IRAT109       | RIL            | 120            | 6969         | 0.25           | SSR        | RT, RN, RL |            |
| 25     | 1            | CT9993 × IR62266      | DH             | 220            | 207          | 4.96           | RFLP, AFLP | YLD, HD, PH, LD, RWC |            |
| 26     | 1            | Kinandang Patong × IR64 | F2           | 117            | 1694         | 0.20           | SSR, STS   | RT       |            |
| 27     | 1            | Zhenshan 97 × IRAT109 | RIL            | 180            | 344          | 2.69           | SSR        | PH       |            |
| 28     | 1            | IR64 × Aucena         | DH             | 96             | 110          | 9.50           | RFLP, SSR  | RL       |            |
| 29     | 1            | Norungan × IR64       | RIL            | 380            | 126          | 7.61           | SSR        | YLD, GW, PH, TN, LR, RWC |            |
| 30     | 1            | IR20 × Nootripathu    | RIL            | 250            | 24           | 14.90          | SSR, RAPD, EST | PH, TN, CT, LD, LR |            |
| 31     | 2            | Yuefu × IRAT109       | BC             | 430            | 4475         | 0.23           | SSR        | RT       |            |
| 32     | 1            | Yuefu × IL255         | F2             | 304            | 7            | 2.95           | SSR        | RT       |            |
| 33     | 1            | CT9993 × IR62266      | DH             | 135            | 399          | 5.49           | SSR, AFLP, RFLP | YLD, HD, GW, PH, TN, DRI |            |
| 34     | 1            | IR64 × Kinandang Patong | RIL          | 117            | 406          | 0.33           | SSR, STS   | RDR      |            |
| 35     | 1            | CT9993 × IR20         | BC             | 234            | 577          | 0.24           | SSR        | RT       |            |
| 36     | 1            | Teqing × Binam       | BC             | 77             | 718          | 2.49           | SSR        | YLD, GW, PH |            |
| 37     | 1            | OM1490 × WAB880       | BC             | 229            | 133          | 11.06          | SSR        | YLD, HD, PH |            |
| 38     | 2            | HKR47 × MAS26         | F2             | 94             | 74           | 13.26          | SSR        | YLD, PH, TN |            |

Continued
Out of the total number of 61 MQTLs, we detected 10 MQTLs for YLD, five MQTLs for GW, seven MQTLs for HD, 10 MQTLs for PH, two MQTLs for TN, four MQTLs for RT, six MQTLs for RT, four MQTLs for RL, five MQTLs for RN and three MQTLs for RDR. These MQTLs were stable across different environments and genetic backgrounds. MQTL-PH7 and MQTL-RL2 involving the highest number of initial QTLs (6) were considered as the most stable QTLs (Table 3; Additional file 1). Among the identified MQTLs, four MQTLs for HD (MQTL-HD3, MQTL-HD4, MQTL-HD5 and MQTL-HD6) and three MQTLs for YLD (MQTL-YLD2, MQTL-YLD7 and MQTL-YLD10) overlapped with previously reported MQTLs under drought conditions in rice. To the best of our knowledge this is the first MQTL analysis for GW, TN and DT in rice.

A total of 10 MQTLs were detected in the same chromosomal regions with similar yield and yield-related traits under well-water condition in rice. This indicates the same loci might control aforementioned traits under both water deficit and well-water conditions (Additional file 2). They include five MQTLs for PH (MQTL-PH2,

| Ref no. | Number of QTL population(s) | Parents of population | Population type | Population size | No. of markers | Map density (cM) | Marker type | Trait(s) | References |
|---------|-----------------------------|------------------------|----------------|----------------|----------------|------------------|------------|---------|------------|
| 39      | 3                           | Kinandang Patong × ARC5955 | F2             | 138            | 1307           | 0.23             | SNP, SSR   | RDR     | 130        |
|         |                             | Kinandang Patong × Pinulupot1 | F2             | 134            | 577            | 0.24             | SNP, SSR   | RDR     |            |
|         |                             | Kinandang Patong × Tupa729 | F2             | 133            | 1259           | 0.22             | SNP, SSR   | RDR     |            |
| 40      | 1                           | IR64 × Drol-1-NIL       | BC             | 4560           | 406            | 0.33             | SSR        | RDR     | 131        |
| 41      | 2                           | Tarom Molaei × Teqing   | BC             | 85             | 718            | 2.49             | SSR        | YLD, GW  | 132        |
|         |                             | Tarom Molaei × IR64     | BC             | 72             | 718            | 2.49             | SSR        | YLD, GW  |            |
| 42      | 1                           | IR77298 × Sahitri        | BC             | 294            | 68             | 3.39             | SSR        | YLD, HD  | 133        |
| 43      | 1                           | IR55419 × TDK1          | BC             | 365            | 418            | 0.68             | SSR        | YLD, HD, PH | 134        |
| 44      | 1                           | Xiaobaijin × Kongyu 131 | RIL            | 220            | 73             | 12.89            | SSR        | YLD, PH  | 135        |
| 45      | 3                           | Kinandang Patong × Momiroman | RIL            | 123            | 3129           | 0.20             | SNP, SSR   | RDR     | 136        |
|         |                             | Kinandang Patong × Yumeaoba | F2             | 128            | 4749           | 0.22             | SNP, SSR   | RDR     |            |
|         |                             | Kinandang Patong × Tachiusagata | F2           | 121            | 2923           | 0.23             | SNP, SSR   | RDR     |            |
| 46      | 1                           | Yuefu × IRAT109         | F2             | 2013           | 5              | 5.48             | SSR        | RT, RL   | 137        |
| 47      | 1                           | Zhenshan 978 × IRAT109 | RIL            | 180            | 3129           | 0.22             | SSR        | RDR     |            |
| 48      | 3                           | IR20 × Nootripathu      | RIL            | 397            | 51             | 16.79            | SSR        | PH, RWC, CT, LR | 138        |
|         |                             | IR20 × Nootripathu      | RIL            | 340            | 51             | 16.79            | SSR        | YLD, HD, GW, PH, TN | 139        |
|         |                             | IR20 × Nootripathu      | RIL            | 330            | 51             | 16.79            | SSR        | YLD, PH  |            |
| 49      | 1                           | Nipponbare × Kasalath   | F2             | 155            | 934            | 0.38             | SSR, RFLP, AFLP | RN         | 138        |
| 50      | 1                           | Kinandang Patong × IR64 | F2             | 121            | 1220           | 0.21             | SSR, SNP   | RDR     | 139        |
| 51      | 1                           | KaliAas × AU5276        | BC             | 276            | 6969           | 0.20             | SNP        | RDW, RL  | 140        |
| 52      | 1                           | IR64 × Dular            | RIL            | 490            | 1892           | 0.24             | SSR        | RL, RDW, RN, RDR | 141        |
| 53      | 1                           | N-22 × Cocodrie         | RIL            | 183            | 2670           | 0.25             | SNP        | RL, RDW  | 142        |
| 54      | 1                           | Cocodrie × Vandana      | F2             | 187            | 136            | 7.75             | SNP        | YLD     | 143        |
| 55      | 2                           | D123 × Shennong265      | BC             | 178            | 40             | 12.24            | SSR        | GW, PH, HD | 144        |
|         |                             | D123 × Shennong265      | BC             | 314            | 29             | 19.04            | SSR        | YLD, GW, PH, TN | 145        |
| 56      | 1                           | IR55419 × Super Basmati | F2             | 418            | 1702           | 0.25             | SSR        | RDW, RL  | 146        |
| 57      | 1                           | M-203 × M-206           | RIL            | 241            | 2474           | 0.23             | SNP        | RL, RDW  | 147        |

Table 1. Summary of QTL studies used in the QTL meta-analysis for YLD, GW, HD, PH, TN, RWC, CT, LR, LD, DRI, RDW, RL, RN, RT, and DT traits in rice under water deficit condition. BC backcross, DH double haploids, RIL recombinant inbred lines, YLD yield, GW grain weight, PH plant height, HD heading date, TN tiller number, RWC relative water content, CT canopy temperature, LR leaf rolling, LD leaf drying, DRI drought response index, RDW root dry weight, RL root length, RN root number, RT root thickness, RDR ratio of deep rooting.
Figure 1. The number and distribution of QTLs and MQTLs. (A) The number of initial QTLs used in the MQTL analysis for YLD, HD, PH, GW, TN, DT, RT, RL, RDR, RDW and RN. (B) The distribution of QTLs and MQTLs on the twelve chromosomes of rice shown in dark blue and purple, respectively. (C) The number of MQTLs for different traits on each chromosome of rice.
GRAS23 some 4, we detected chromosome 1 with MQTL-RN1 for the same root number trait. Moreover, at MQTL-YLD4 interval on chromosome 8 and 12, two MQTLs for HD (MQTL-HD1 and HD3) on chromosomes 3 and 5 and one MQTL PH4, PH7, PH8 and PH9) on chromosomes 1, 2, 4, 7 and 8, two MQTLs for GW (MQTL-GW4 and GW5) on chromosomes 3 and 5, one MQTL GW7 on chromosome 11 and one MQTL GW8 on chromosome 12, two MQTLs for HD (MQTL-HD1 and HD3) on chromosomes 3 and 5 and one MQTL for YLD (MQTL-YLD3) on chromosome 3 (Fig. 3; Additional file 2).

The MQTL analysis considerably narrowed the CI allowing for exploration of a reduced number of candidate genes (CGs) for the investigated traits. The average CI was reduced from 15.57 cM in the initial QTLs to 5.48 cM in the MQTL with 65% of MQTLs having CI < 5 cM (Table 3). In 10 MQTLs, MQTL-GW4, HD4, HD7, PH3, PH5, YLD1, YLD7, DT1, DT3, RL4, RDW1 and RDW7, the CI was reduced to < 1 cM (Table 3). Therefore, MQTL analysis can significantly raise the accuracy of identification of CGs. All the annotated genes located within the CI of each MQTL and the most promising CGs based on their reported function in previous studies are reported in Additional file 3. Some functionally characterized genes such as GRAIN SIZE 2 (GS2), GRAIN WEIGHT 7 (GW7), Early heading date 1 (Ehd1), DWARF 10 (d10) and Grain number, plant height, heading date7 (Ghd7), OsPIN3t, OsSAUR45, and WEG1 were located within MQTL-GW1, GW3, HD6, PH2, PH8, RT1, RL4, RDW5, respectively, and OsAIR1 located at MQTL-RN2 and RDW2, and OsMGT1 located at MQTL-RT2 and RDW1, that are assumed to control the aforementioned traits. Putative novels CGs for each trait are discussed below.

In addition, the positions of MQTLs on the rice genome were compared with the gene density, and densities of SNPs, structural variants (SV), recombination and functional variants, and the reported selective sweep regions33 (Fig. 3). Most of the detected MQTLs were located in sub-telomeric regions where generally the gene, SNP, SV and recombination densities are higher (Figs. 2, 3). This is consistent with previous results in barley, maize and rice15,19,26. The regions with high SV frequency could play an effective role in stress response27. A total of 13 MQTLs (MQTL-YLD3, YLD6, GW2, GW5, HD5, TN2, DT2, RT3, RT4, RL3, RL4, RDW3 and RDW6) were co-located with selective sweep regions reported by Huang et al. These MQTLs are likely effective for selection towards drought adaptation during rice breeding and domestication processes25. Five of these MQTLs including MQTL-YLD3, TN2, GW5, RT4 and RDW6 were also co-located with the position of reported functional variants33.

The investigation of collinear regions within the rice genome resulted in identification of five duplicated regions containing MQTLs for the same traits. MQTL-YLD2 and MQTL-YLD4 on chromosomes 2 and 4, and MQTL-YLD9 on chromosomes 11 and 12 for yield, MQTL-RWD1 and MQTL-RWD2 on chromosomes 1 and 5, MQTL-RWD4 and MQTL-RWD5 on chromosomes 8 and 9, and MQTL-RN1 and MQTL-RN2 on chromosomes 1 and 5 for root-related traits are co-located at rice genome duplicated regions (Fig. 3). Duplicated genomic regions derived from common ancestors might contain paralogous genes with similar functions that can be considered as promising CGs controlling the trait26. Consequently, we carefully surveyed these regions for detecting possible paralogous CGs in the duplicated regions. In MQTL-RN2, we note the OsABIL3 or P22C50 gene which has a key role in root architecture and response to drought stress by affecting ABA signaling: overexpression of this gene was reported to lead to the ABA insensitivity along with stomatal density and root architecture28. The paralogous gene Os01g0618200 encoding P22C07 is also present at the duplicated region on chromosome 1 with MQTL-RN1 for the same root number trait. Moreover, at MQTL-YLD4 interval on chromosome 5, we detected GRAS23 that contributes to drought response in rice29, with paralogues HAM1 and HAM2 colocalizing with the duplicated genome on chromosome 2 with MQTL-YLD2 for the yield under drought stress.

### MQTLs and CGs for grain weight

GW is one of the most important components of YLD in rice31 and it critically limits YLD during late season drought stress32,33. A total of five MQTLs were identified for GW (Table 3). MQTL-GW2 on chromosome 5 is the most stable MQTL for GW with the highest number of initial

| Chromosome | PH | RT | RL | YLD | HD | RDR | DT | RDW | TN | RN | GW | Total |
|------------|----|----|----|-----|----|-----|----|-----|----|----|----|-------|
| 1          | 24 | 11 | 4  | 7   | 2  | 3   | 7  | 7   | 7  | 3  | 3   | 83    |
| 2          | 10 | 4  | 2  | 5   | 2  | 9   | 8  | 1   | 3  | 2  | 3   | 49    |
| 3          | 5  | 3  | 4  | 12  | 14 | 5   | 2  | 5   | 4  | 60 |
| 4          | 9  | 12 | 8  | 6   | 1  | 11  | 2  | 1   | 1  | 3  | 2   | 56    |
| 5          | 2  | 2  | 3  | 0   | 2  | 0   | 1  | 3   | 2  | 4  | 21  |
| 6          | 7  | 7  | 1  | 10  | 5  | 3   | 3  | 2   | 7  | 3  | 51  |
| 7          | 4  | 2  | 1  | 1   | 2  | 5   | 3  | 3   | 2  | 2  | 27  |
| 8          | 7  | 6  | 3  | 5   | 5  | 2   | 6  | 4   | 4  | 1  | 3   | 46    |
| 9          | 3  | 12 | 13 | 0   | 6  | 4   | 6  | 4   | 2  | 2  | 0   | 52    |
| 10         | 2  | 3  | 1  | 4   | 3  | 5   | 1  | 0   | 2  | 0  | 21  |
| 11         | 3  | 4  | 3  | 3   | 3  | 3   | 4  | 6   | 2  | 2  | 37  |
| 12         | 5  | 3  | 3  | 5   | 4  | 0   | 1  | 1   | 1  | 2  | 25  |
| Total      | 83 | 69 | 46 | 58  | 49 | 49  | 47 | 34  | 34 | 30 | 28  | 527   |

Table 2. The number of initial QTLs on the 12 chromosomes of rice for YLD, GW, HD, PH, TN, DT, RT, RL, RDR, RDW and RN traits under water deficit condition used for MQTL analysis after integrating into the reference map. YLD yield, GW grain weight, PH plant height, HD heading date, TN tiller number, DT drought tolerance, RDW root dry weight, RL root length, RN root number, RT root thickness, RDR ratio of deep rooting.
| Trait | Chr | MQTL | Flanking markers | Position on the consensus reference map (cM) | Confidence interval (cM) | Genomic position on the rice genome (Mb) | Number of initial QTLs | Number of studies/populations | Phenotypic variance range (%) | Number of genes underlying the MQTL interval |
|-------|-----|------|------------------|---------------------------------------------|--------------------------|-----------------------------------------|----------------------|-------------------------------|--------------------------------|---------------------------------|
| GW    | 2   | MQTL-GW1 | RG102-R418 | 118.97 | 1.84 | 27.48–28.94 | 2 | 2/2 | 5.9–10 | 170 |
|       | 5   | MQTL-GW2 | C619835-RM3419 | 34.86 | 2.54 | 4.33–5.28 | 4 | 4/4 | 8.63–14.2 | 76 |
|       | 7   | MQTL-GW3 | C1467-R100225 | 83.45 | 19.85 | 20.73–25.43 | 2 | 1/2 | 6.95–8.82 | 597 |
|       | 8   | MQTL-GW4 | S3680-RM3689 | 79.81 | 0.96 | 18.25–19.33 | 2 | 2/2 | 4.15–10 | 78 |
|       | 12  | MTQL-GW5 | R108516-RM3736 | 79.84 | 19.14 | 19.87–23.44 | 2 | 2/2 | 8–21.9 | 257 |
| HD    | 3   | MQTL-HD1 | C669805-RM6496 | 43.96 | 3.92 | 8.80–10.14 | 5 | 2/2 | 10.2–22.3 | 194 |
|       | 3   | MQTL-HD2 | S1764-RM6881 | 80.74 | 2.93 | 15.94–16.87 | 3 | 2/2 | 9.3–10.6 | 70 |
|       | 5   | MQTL-HD3 | RM305-RM2357 | 92.66 | 33.1 | 20.94–26.85 | 2 | 2/2 | 8.5–17.15 | 750 |
|       | 9   | MQTL-HD4 | S781-G1047 | 44.29 | 0.3 | 1.21–4.70 | 7 | 2/2 | 9.97–15.8 | 181 |
|       | 10  | MQTL-HD5 | C1467-R100225 | 83.43 | 19.85 | 20.73–25.43 | 2 | 1/2 | 6.95–8.82 | 597 |
|       | 12  | MQTL-HD6 | RM4455-C1369 | 32.9 | 22.85 | 11.66–17.15 | 3 | 2/2 | 3.54–8.06 | 456 |
| PH    | 1   | MQTL-PH1 | RM8066-RM627 | 54.37 | 3.01 | 9.56–10.30 | 3 | 2/2 | 5.22–11.48 | 75 |
|       | 1   | MQTL-PH2 | R530-RM3324 | 129.7 | 3.07 | 30.50–31.71 | 2 | 2/2 | 10–22.7 | 182 |
|       | 1   | MQTL-PH3 | RM6387-RM3285 | 137.42 | 0.12 | 32.54–33.04 | 3 | 2/3 | 9.9–27.5 | 62 |
|       | 2   | MQTL-PH4 | S14115-G1340 | 45.05 | 6.29 | 8.72–10.42 | 2 | 2/2 | 5.2–11.48 | 75 |
|       | 2   | MQTL-PH5 | RM208-RM498 | 140.44 | 0.03 | 35.13–35.39 | 5 | 2/2 | 2.9–13.9 | 46 |
|       | 3   | MQTL-PH6 | S21045-E1419S | 92.38 | 1.27 | 23.13–23.88 | 2 | 2/2 | 4.62–6.06 | 58 |
|       | 7   | MQTL-PH7 | RM3718-R1788 | 49.37 | 3.68 | 7.95–15.20 | 3 | 2/2 | 10–22.7 | 182 |
|       | 8   | MQTL-PH9 | RM7049-E0162S | 92.7 | 4.15 | 20.81–21.76 | 2 | 2/2 | 10–28.2 | 92 |
|       | 12  | MQTL-PH10 | S10904-C53024S | 49.59 | 1.41 | 7.98–10.60 | 4 | 3/3 | 4.94–13.11 | 120 |
| TN    | 5   | MQTL-TN1 | C1268-S10569 | 80 | 5 | 20.15–20.80 | 2 | 2/2 | 4.19–14.7 | 76 |
|       | 6   | MQTL-TN2 | C1032-RM8258 | 14.54 | 2.76 | 3.16–4.73 | 2 | 2/2 | 9.3–10 | 230 |
|       | 1   | MQTL-YLD1 | RM1152-G1372 | 127 | 0.6 | 30.09–30.49 | 3 | 2/2 | 5–14.57 | 70 |
|       | 2   | MQTL-YLD2 | RM5796-L107 | 111.56 | 3.6 | 26.47–27.59 | 2 | 2/2 | 10–43.2 | 142 |
|       | 3   | MQTL-YLD3 | S51158-RM3525 | 131.47 | 9.37 | 28.56–30.38 | 4 | 2/2 | 6.35–15 | 224 |
|       | 4   | MQTL-YLD4 | R2737-RG329 | 100.94 | 7.3 | 29.15–30.85 | 2 | 2/2 | 1.31–15.8 | 229 |
|       | 6   | MQTL-YLD5 | RM5531-R1069S | 54.48 | 7.05 | 7.17–10.46 | 2 | 2/2 | 6.7–12.18 | 183 |
|       | 8   | MQTL-YLD6 | RM2344-RZ143 | 16.62 | 5.96 | 0.07–1.52 | 2 | 2/2 | 3.24–8.5 | 198 |
|       | 10  | MQTL-YLD7 | R1261-C63979S | 16.65 | 0.4 | 8.85–9.92 | 2 | 2/2 | 9.5–11.4 | 53 |
|       | 11  | MQTL-YLD8 | RM6085-S20163 | 28.03 | 12.3 | 3.04–5.37 | 2 | 2/2 | 8.5–15.5 | 219 |
|       | 12  | MQTL-YLD9 | E30009S-R3276S | 46.69 | 6.68 | 6.98–10.43 | 3 | 2/2 | 13.89–30 | 178 |
|       | 12  | MQTL-YLD10 | S10043S-S826 | 58.47 | 3.9 | 15.32–17.56 | 2 | 2/2 | 9.27–22.3 | 66 |

**Continued**
| Trait | Chr | MQTL | Flanking markers | Position on the consensus reference map (cM) | Confidence interval (cM) | Genomic position on the rice genome (Mb) | Number of initial QTLs | Number of studies/populations | Phenotypic variance range (%) | Number of genes underlying the MQTL interval |
|-------|-----|------|-----------------|-------------------------------------------|------------------------|------------------------------------------|-----------------------|-------------------------------|-------------------------------|----------------------------------|
| RL    | 4   | MQTL-RL1 | RM6992-RM6909   | 105.97                                   | 6.41                   | 30.76–32.06                             | 2                    | 2/2                           | 8.45–11.86                     | 194                              |
|       | 9   | MQTL-RL2 | C2985-C397      | 81.42                                    | 3.07                   | 11.79–12.28                             | 6                    | 3/3                           | 9.11–11                       | 47                               |
|       | 9   | MQTL-RL3 | S46775-RM6839   | 92.16                                    | 3.33                   | 13.62–14.56                             | 4                    | 4/4                           | 8.2–32.5                       | 91                               |
|       | 9   | MQTL-RL4 | C123575-RM6643  | 132.34                                   | 0.58                   | 21.52–21.70                             | 2                    | 2/2                           | 12.9–13.4                     | 35                               |
| RDR   | 2   | MQTL-RDR1 | R418-RM6244     | 124.07                                   | 2.14                   | 28.94–29.62                             | 4                    | 2/3                           | 9.3–19.9                      | 88                               |
|       | 4   | MQTL-RDR2 | RM5320-R7237    | 91.65                                    | 8.52                   | 28.01–29.15                             | 4                    | 3/3                           | 10.56–66.12                   | 133                              |
|       | 9   | MQTL-RDR3 | RM5526-RM7038   | 78.11                                    | 4.22                   | 7.31–11.80                              | 2                    | 2/2                           | 7.99–10.2                    | 220                              |
| RDW   | 1   | MQTL-RDW1 | E50125S-RM6593  | 148.37                                   | 0.95                   | 37.23–38.02                             | 3                    | 3/3                           | 7.6–26.8                      | 134                              |
|       | 5   | MQTL-RDW2 | E4175S-RM3631   | 104.43                                   | 3.42                   | 24.11–25.83                             | 2                    | 2/2                           | 10–12.2                      | 214                              |
|       | 8   | MQTL-RDW3 | RM8266-RM8256   | 53.06                                    | 12.21                  | 3.98–7.78                               | 2                    | 2/2                           | 3.3–7.9                      | 294                              |
|       | 8   | MQTL-RDW4 | S11102-RM4043   | 103.72                                   | 1.56                   | 22.87–23.57                             | 2                    | 2/2                           | 4.4–16.1                      | 72                               |
|       | 9   | MQTL-RDW5 | RM3909-C11503S  | 120.57                                   | 1.19                   | 19.53–19.88                             | 2                    | 2/2                           | 4.31–13.1                    | 51                               |
|       | 11  | MQTL-RDW6 | S2137-C6188S    | 57.03                                    | 8.53                   | 8.29–10.13                              | 2                    | 2/2                           | 6.14–14                      | 94                               |
|       | 11  | MQTL-RDW7 | RM7240-RM6688   | 119.95                                   | 0.25                   | 27.02–27.54                             | 4                    | 3/3                           | 2.2–11.1                      | 46                               |
| RN    | 1   | MQTL-RN1  | RM2772-C808     | 104.4                                   | 3.38                   | 24.08–25.63                             | 2                    | 2/2                           | 12–22.8                       | 182                              |
|       | 5   | MQTL-RN2  | RM5401-RM2457   | 100.8                                    | 16.25                  | 22.28–26.87                             | 2                    | 2/2                           | 5.1–10                        | 602                              |
|       | 9   | MQTL-RN3  | RM3808-C482     | 124.14                                   | 2.2                    | 20.54–21.05                             | 2                    | 2/2                           | 8.6–11.6                      | 75                               |

Table 3. Summary of the detected MQTLs for YLD, GW, HD, TN, DT, RT, RL, RDR, RDW and RN traits in rice under water deficit condition. YLD yield, GW grain weight, HD heading date, TN Tiller number, DT drought tolerance, RDW root dry weight, RL root length, RN root number, RT root thickness, RDR ratio of deep rooting, Chr chromosome.

MQTLs from four independent studies. Among the identified MQTLs for GW, MQTL-GW4 and GW5 on chromosomes 8 and 12 were located at the same region of GW MQTLs under well-water conditions. Therefore, the same genes might control GW under both conditions. MQTL-GW5 and GW2 were co-located with selective sweep regions and functional variants were reported on the former. These MQTLs could be effective for selection towards drought adaptation. The same source of favorable allele from ‘Taram Molaei’ parent derived from two independent populations was detected in QTLs located at MQTL-GW3 (Additional file 4).

Some well-known genes controlling GW such as GS2 and GW95 were located within MQTL-GW1 and MQTL-GW3, respectively, suggesting that these genes may play the same role under water deficit conditions. The list of functionally characterized and novel CGs within each MQTL interval are reported (Additional file 3). For instance, the genomic region spanning MQTL-GW3 contains the CYP78A13 and DEP2 genes that are reported to control grain size and YLD in rice. MQTL-GW4 on chromosome 8 and MQTL-GW5 on chromosome 12 contain Os08g0390000 encoding brassinosteroid receptor kinase (BRI1) and the OsVIL2 genes, respectively, which regulate grain size in rice.

**MQTLs and CGs for heading date.** It is well known that HD is highly correlated with YLD and drought adaptation. We detected seven MQTLs for HD under water deficit conditions including two MQTLs on chromosomes 3 and 9 and one MQTL each on chromosomes 5, 10 and 12 (Table 3). MQTL-HD1 on chromosome 3 had the highest number of supporting QTLs with five QTLs from two independent studies (Table 3).

Among annotated genes within MQTL-HD1, MQTL-HD3 and MQTL-HD6 intervals, OsCCT11, HBF1 and Ehd1, respectively, were identified as potential candidates for HD under water deficit conditions. OsCCT11 is considered as a positive regulator of heading date since RNAi-mediated downregulation of this gene delays HD, while HBF1 is considered as a negative regulator of HD since mutation promotes flowering. Among genes within the MQTL-HD3 interval, basic region/leucine zipper motif (bZIP), FT-like and circadian clock genes are promising candidates. Another CG at this MQTL is OsHAP1L1, known to prevent flowering under long-day conditions. OsTrx1 and OsCCT31 are potential candidates for MQTL-HD4. In MQTL-HD6, the BRD2 gene and the Ehd2 and Ehd1 genes are reported to modify flowering time in rice.

**MQTLs and CGs for plant height.** Since the Green Revolution, PH has been considered as a major target for YLD improvement and it also contributes to drought tolerance. Among the studied traits, PH and YLD had the highest number of MQTLs; we identified 10 MQTLs for PH including three MQTLs on chromosome 1, two MQTLs on chromosome 2 and one MQTL each on chromosomes 3, 4, 7, 8 and 12. The MQTL-PH7 on
chromosome 4 had the largest number of initial QTLs with six QTLs from four independent studies followed by MQTL-PH10 on chromosome 12 with three QTLs reported from three independent studies. These MQTLs are the most stable QTLs for PH under water deficit conditions.

The $d10$ and $Ghd7$ genes are reported to regulate plant height in rice, and they are positioned within MQTL-PH2 and MQTL-PH8 genomic regions, respectively. MQTL-PH4 contains $EP3/LP$ gene, whose mutant shows increased panicle size and PH in rice. Conversely, mutations in $OsKS2$ and $NAL1$ at MQTL-PH7 and $OsSEC3A$ at MQTL-PH6 decrease PH in rice. In MQTL-PH10, we detected $Os12g0271600$ that encodes BRI1 and the mutant alleles could act as a dwarfism gene.

MQTLs and CGs for yield. The maintenance of YLD under drought condition is the ultimate goal in cereal breeding. We identified 10 MQTLs for YLD consisting of two MQTLs on chromosome 12 and one MQTL each on chromosomes 1, 2, 3, 4, 6, 8, 10 and 11 (Table 3). Among them MQTL-YLD3 on chromosome 3 overlapped with a YLD MQTL identified under well-water conditions. Therefore, the same genes might control YLD under both mentioned conditions at this position.

We detected some genes which affect the photosynthetic rate including $Roc5$ at MQTL-YLD2, $UCL8$ at MQTL-YLD3 and $OsPTR6$ at MQTL-YLD4 that might indirectly contribute to the final YLD. $OsALMT7$ is located at the MQTL-YLD2 interval with pleiotropic effects on YLD and panicle size. $TAC3$ might indirectly regulate YLD through changing HD and tiller angle in rice at MQTL-YLD3. The most likely CGs at

**Figure 2.** Heatmap of MQTLs for YLD, HD, PH, GW, TN, DT, RT, RL, RDR, RDW and RN presented on the rice genome in Mb. The gene density of each chromosome is indicated on the right chromosome.
MQTL-YLD5 are Os06g0274500 which encodes SERK-like gene and BRI1-associated receptor kinase 1 (BAK1) that affects grain size and number in rice64. The OsNAC5 gene on MQTL-YLD8 is known to have a positive effect on YLD under drought condition65.

MQTLs and CGs for number of tillers. The number of fertile tillers is a major contributor to YLD and its alteration during drought stress can result in drought adaptation6,68. Tillering is a complex process and highly affected by environmental conditions66. We detected only two MQTLs on chromosomes 5 and 6 which were associated with TN (Table 3). In MQTL-TN2, we identified OsAID1 as a gene associated to TN regulation in rice69.

MQTLs and CGs for drought tolerance. Plant water content is highly affected by water deficit conditions and in turn can contribute to drought tolerance. Plant water content can be measured by different criteria.
Table 4. Ortho-MQTLs in rice and maize based on the synteny analyses.

| Ortho-MQTL | Rice MQTL | Rice chr. no. (genomic position in Mb) | Maize original MQTL name | Maize chr. no. (genomic position in Mb) | Maize MQTL reference |
|------------|-----------|----------------------------------------|--------------------------|----------------------------------------|----------------------|
| Ortho-MQTL-PH7 | MQTL-PH7 | 4 (30.86–31.61) | mQTL_PEH_10 | 10 (142.39–143.64) | 85 |
| Ortho-MQTL-YLD2 | MQTL-YLD2 | 2 (26.47–27.59) | MQTL_GY_5 | 5 (196.85–199.69) | 84 |
| Ortho-MQTL-YLD2 | MQTL-YLD2 | 2 (26.47–27.59) | MQTL_GY_5 | 5 (196.85–199.69) | 84 |
| Ortho-MQTL-YLD3 | MQTL-YLD3 | 3 (29.58–30.36) | mQTL_GY_1b | 1 (276.04–279.33) | 84 |
| Ortho-MQTL-YLD4 | MQTL-YLD4 | 4 (29.15–30.82) | mQTL_GY_10b | 10 (135.81–142.38) | 84 |
| Ortho-MQTL-YLD6 | MQTL-YLD6 | 8 (0.26–0.71) | MQTL6.1 | 6 (1.58–3.65) | 10 |

including RWC, CT, LR, LD and DRI. We identified four MQTLs for DT on chromosomes 1, 4, 8 and 11. MQTL-DT1 on chromosome 1 is the most stable MQTL related to rice water content under water deficit conditions with the highest number of initial QTLs (4) from three independent studies. Within the MQTL-DT1 and MQTL-DT4 intervals, we detected several CGs including OsBZ8 and OsPGDH2 that contribute to abiotic stresses tolerance, respectively.

MQTLs and CGs for root architecture. Root architecture develops through dynamic processes that effectively contribute to water deficit adaptation allowing water and nutrient uptake from deep soil25,26. We studied five major traits related to root architecture including RDW, RL, RN, RT and RDR under water deficit conditions and identified 23 MQTLs including seven MQTLs for RDW, four MQTLs for RL, three MQTLs for RN, six MQTLs for RT and three MQTLs for RDR (Table 3). MQTL-R2 had the highest number of initial QTLs (six QTLs from three independent studies) and it was considered as the most stable QTL for root architecture (Table 3). Interestingly, MQTL-YLD4 for YLD under water deficit conditions on chromosome 4 overlapped with MQTL-RDR2 and RL1 (Fig. 2).

Overlapping MQTLs for different root architecture traits included MQTL-RDW1 and MQTL-RT2 on chromosome 1, MQTL-RDW2 and MQTL-RN2 on chromosome 5 and MQTL-RN1 and MQTL-RT1 on chromosome 1, suggesting the possible existence of genes with pleiotropic effects on these traits. For example, the genomic region spanning MQTL-RN2 and MQTL-RDW2 harbors OsAIR1, a gene affecting root architecture and contributing to drought tolerance26. In the overlap region between MQTL-RT2 and MQTL-RDW1, noteworthy is OsMGFI which was shown to affect root architecture during salinity stress27. MQTL-RT1 contains OsPIN328 and OsFBKI29 genes that are reported to control root architecture under water deficit conditions. The SMOS1 gene within MQTL-RT4 determines root meristem size30, and the cZOGT31 gene within MQTL-RDR2 regulates root architecture. Additionally, AMTRI (MQTL-RN2) affects root architecture under drought stress32.

The same source of favorable allele from ‘IRAT109’ parent derived from two independent populations was identified in QTLs located at MQTL-RL3 (Additional file 4). The FC1 gene43 on MQTL-RL1 controls root growth and might contribute to drought tolerance under water deficit conditions. Within MQTL-RL4, we detected a cluster of small auxin-up RNA (SAUR) genes. Over-expression of OsSAUR45 regulates root length and other related root traits46.

For RDW, we detected two co-located MQTLs including MQTL-RDW1 and RDW2 co-locating with OsMGFI and OsAIR1 genes, respectively. Additionally, WEG1 at MQTL-RDW5 is a novel gene that regulates root related traits46 and may keep the same role under water deficit conditions.

Ortho-MQTL mining. To investigate ortho-MQTLs for yield and yield-related traits under water deficit conditions between rice and maize as the two most important cereals with generally high water demand, the syntenic regions of all detected rice MQTLs in this study were compared with published maize MQTLs17,18,67. Comparative genomic analyses provide a valuable approach to transfer information across species and identify conserved genes19. Through synteny analysis between rice and maize, we uncovered 5 ortho-MQTLs including 4 ortho-MQTLs for YLD on chromosomes 2, 3, 4 and 8 and 1 ortho-MQTL for PH on chromosome 4 (Table 4; Fig. 3). The genes located at these syntenic regions were further investigated (Additional file 5; Fig. 4).

MQTL-PH7 and MQTL-YLD4 on chromosome 4 of rice were co-linear with mQTL_PEH_10 and mQTL_GY_10b on chromosome 10 in maize, respectively (Table 4). Three rice MQTLs including MQTL-YLD2, YLD3 and YLD6 on chromosomes 2, 3 and 8, respectively, were situated in syntenic regions of maize yield MQTLs on chromosome 5, 1 and 6, respectively (Table 4; Fig. 3).

The orthologous genes located at these ortho-MQTLs in both rice and maize are shown in the Additional file 5 and Fig. 4. The rice genomic region subtending MQTL-PH7 harbors the NALI1 gene as a regulator of PH55. We identified the ortholog of this gene (Zm00001d026296) in the maize ortho-MQTL. In the syntenic region of rice MQTL-YLD2 on chromosome 5 of maize, there were two MQTLs (mQTL_GY_529, MQTL5.725) containing the orthologs of OsALMT7 and SID1 genes (Zm00001d017571 and Zm00001d017560), known to affect YLD in rice28. The orthologous gene of TAC3 in maize (Zm00001d033857) in the syntenic region of MQTL-YLD3 in maize (mQTL_GY_1b) regulates height that might affect YLD under water deficit conditions63. In the syntenic region of rice MQTL-YLD6, there was a MQTL (MQTL6.117) on chromosome 6 of maize. This rice MQTL contains Ehd3 gene regulating flowering and consequently YLD68 and its orthologous (Zm00001d035008) was detected in its ortho-MQTL in maize, likely to have similar functions. This approach provided better understanding of genes controlling investigated traits under water deficit conditions with similar evolutionary history and
Figure 4. Comparative maps of ortho-MQTLs between rice and maize. (A) ortho-MQTL-PH7, (B) ortho-MQTL-YLD2, (C) ortho-MQTL-YLD3, (D) ortho-MQTL-YLD4 and (E) ortho-MQTL-YLD6. The chromosome number, genomic position in Mb and the original name of MQTLs are indicated. The orthologous genes in rice and maize are indicated in green color with the corresponding rice gene name.
conserved function between these cereals. These results can benefits breeders by tracing CGs and using marker-assisted selection in breeding programs of cereals under water deficit conditions.

Conclusions

Through MQTL analysis this study provides an overview of genomic regions controlling YLD, yield-related traits, root architecture and plant water content including GW, HD, PH, TN, RDW, RL, RT, RN, RDR and DT under water deficit conditions in rice. This approach is useful in overcoming some limitations of single QTL mapping studies on different genetic backgrounds and environments and greatly facilitates the identification of CGs and robust flanking markers for MAS in breeding programs. The results offer a framework for future genetic studies of yield under drought conditions, e.g. through fine mapping, positional cloning, producing chromosome substitution lines, as well as validation of CGs by genome editing using Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR) and similar approaches. This study also demonstrates the value of ortho-MQTL mining among evolutionarily close crop species for identification of genomic regions and CGs controlling complex quantitative traits.

Materials and methods

QTL studies used for MQTL analysis. An exhaustive bibliographic review was carried out on rice QTLs related to yield and yield-related traits under water deficit conditions published from 2001 to 2019. All QTL studies except those lacking proper genetic map information or QTL-related information were used in the MQTL analysis. Consequently, a total of 563 QTLs for YLD, PH, TN, HD, GW, RDW, RL, RT, RN, RDR and traits related to water content of plant under water deficit conditions including DRI, RWC, CT, LR and LD from 67 biparental rice populations extracted from 57 studies, including all the five major subpopulations of rice—Indica, tropical japonica, temperate japonica, aus, aromatic and also one wild species O. rufipogon IRGC 105491 and landraces, were implemented for the MQTL analysis (Table 1). The size of mapping populations varied from 72 to 4860 progenies of various types including 7 DH, 17 F2, 15 BC and 28 RIL populations phenotyped in different locations and years (Table 1). Moreover, 56 QTLs related to water content of plant under water deficit conditions including DRI, RWC, CT, LR, LD were subjected to MQTL analysis and resulting MQTLs were reported as drought tolerance (DT). Detailed information on the used QTLs including parents, population type and size, number of markers, map density and evaluated traits are reported in Table 1.

Projection of QTLs on the reference map. A rice reference map of Wu et al. which is the most comprehensive available genetic map integrated from six identified and saturated maps in rice was chosen based on its high marker density and inclusion of different marker types including SSR, RFLP and AFLP markers. It consists of 6969 markers with an average distance of 0.25 cM between markers, and the average chromosome length is 147.65 cM for a total length of 1771.8 cM92. In order to incorporate SNP markers of those initial QTLs with SNP markers (Table 1) into the reference map, we applied our previous approach9 in which the genomic position of SNP markers on the rice genome were determined and in consequence the closest markers based on the physical position were used to project them on the reference map.

QTL position, CI, proportion of phenotypic variance (R²), log of odds ratio (LOD score), additive effects and favorable alleles were compiled for each QTL in the 67 populations (Additional file 4). In order to incorporate SNP markers of those initial QTLs with SNP markers (Table 1) into the reference map, we applied our previous approach19 in which the genomic position of SNP markers on the rice genome were determined and in consequence the closest markers based on the physical position were used to project them on the reference map.

Meta-QTL analysis and ortho-MQTL mining. The MQTL analysis was conducted on integrated and re-positioned QTLs on the reference map using BioMercator V4.211,12,92. The best model of MQTLs was chosen according to the prevalent value among Akaika Information Criterion (AIC), corrected Akaika Information Criterion (AICc and AIC3), Bayesian Information Criterion (BIC) and Average Weight of Evidence (AWE) criteria. Therefore, the consensus QTL from the best model was reported as a “real” QTL/MQTL12,92. Considering the diverse yield-related traits, including DT, high parental yield, high harvest index, high number of grains per spike and grain yield per plant across the populations, the MQTLs identified were analyzed together as DT trait. MQTL analysis was carried out using BioMercator V4.211,92.

The distribution of MQTLs on the rice genome (IRGSP-1.0) compared to the position of centromeric and telomeric regions and the gene density along each chromosome were surveyed and shown by heatmap using phoheatmap and R93. Centromere position, gene density, SNP and structural variations (SV) and recombination rate density of each chromosome, as well as rice genome duplications were retrieved from EnsemblPlants (https://plantsensembl.org/index.html) database. Additionally, the position of identified MQTLs were compared with selective sweep regions and functional variants in coding regions with strong alteration in allele frequency between cultivated and wild rice reported by Huang et al.25. The distribution of aforementioned factors, number of MQTL under water deficit conditions and number of MQTLs under well-water conditions19 over the rice genome were shown by using Circos96.

To detect ortho-MQTLs between rice and maize, syntenic regions between the two species were identified by using EnsemblPlants database97. MQTLs identified for yield and yield-related traits under drought conditions in maize17,86,87 were compared with MQTLs detected for similar traits in our study.

Identification of candidate genes. CGs related to YLD, PH, TN, HD, GW, RDW, RL, RT, RN, RDR and DT traits located in the CI of each detected MQTL were investigated on the rice genome (IRGSP-1.0) using EnsemblPlants and Gramene (http://archive.gramene.org/qtl/). In case of flanking markers without genomic
positions, the closest markers were applied for detecting the genomic coordinates of MQTL. Gene annotations within MQTL genomic regions were carefully explored by EnsemblPlants (https://plants.ensembl.org/index.html) and FunRiceGenes (https://funricegenes.github.io/) databases.

Data availability
The relevant data and additional information are available in the supplementary files and also from the corresponding author on reasonable request.

Received: 16 September 2020; Accepted: 11 March 2021
Published online: 25 March 2021

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Acknowledgements
This work has been supported by the Shiraz University, Iran.

Author contributions
B.K. performed the initial analyses and wrote the draft of manuscript, E.T. conceived and designed the project and complemented the analyses and writing of the manuscript, V.S. enriched the analyses and provided critical advices on the project and the manuscript, L.R. provided critical advices on the manuscript. All authors have read and approved the final manuscript.

Funding
This work has been supported by the Center for International Scientific Studies and collaboration (CISSC), Ministry of Science, Research and Technology, Iran and Shiraz University, Iran.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-021-86259-2.

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