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Meta-QTL analysis for mining key genes associated with seed oil content in maize

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Abstract

Background Maize seed oil plays a significant role in human nutrition, animal feed, and bioenergy applications. Despite extensive quantitative trait loci (QTL) studies conducted on this trait, the broad confidence intervals of the identified QTLs have made it difficult to precisely pinpoint candidate genes, thereby limiting their practical application in high-oil maize breeding.

Results In this study, we integrated QTL data related to maize seed oil content reported over the past two decades, compiling a total of 339 QTLs from 31 studies. By integrating high-density genetic linkage maps, 72 oil content-related meta-QTLs (MQTLs) were identified. Compared with previous studies on seed oil content QTLs, the average confidence interval of the MQTLs was reduced by 5.89-fold. Through colocalization analysis with genome-wide association study (GWAS) marker-trait associations (MTAs), over 60% of the MQTLs were validated by GWAS-MTAs. Additionally, four known functional genes were identified within the MQTL regions, and 44 candidate genes were further uncovered through homologous gene comparison. These genes are likely involved in critical biological processes such as transcriptional regulation (e.g., *CADTFR7*), fatty acid biosynthesis (e.g., *Zm00001d036137*), and material transport (e.g., *Zm00001d013817*), thereby influencing seed oil content accumulation.

Conclusions Collectively, these findings provide valuable insights into the genetic regulation of maize seed oil content and offer potential molecular targets for the development of high-oil maize varieties.

Keywords Maize, Seed oil content, Meta-QTL, Candidate genes

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Background

Maize (*Zea mays* L.), as a major staple crop, its seed oil content not only determines the nutritional quality of the seeds but also plays a significant role in human nutrition, industrial materials, and livestock feed [1]. However, the average oil content in most regular maize hybrids is only 4–5%, which is insufficient to meet the growing demands in human consumption, animal feed, and bioenergy [2].

In maize seeds, oil is primarily stored in the form of triacylglycerol (TAG) within oil bodies. TAG synthesis occurs through two pathways: the acyl-CoA-dependent Kennedy pathway and the acyl-CoA-independent Kennedy pathway. Diacylglycerol acyltransferase (DGAT) catalyzes the acyl-CoA-dependent pathway [3, 4], while

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phospholipid diacylglycerol acyltransferase (PDAT) catalyzes the acyl-CoA-independent pathway [4]. Both convert diacylglycerol (DAG) to TAG, driving lipid synthesis and storage. Previous studies have shown that the insertion of phenylalanine at position 469 in *DGAT1-2* leads to increased oil and oleic acid content, with its ectopic expression resulting in a 41% increase in oil content and a 107% increase in oleic acid content in maize seeds [3]. Overexpression of the transcription factor *LEAFY COTYLEDON1* (*ZmLEC1*) can increase oil content by 48% but negatively affects seed germination and leaf growth. In contrast, overexpression of its downstream transcription factor *WRINKLED1* (*ZmWRI1*) can increase oil content by 30.6% without adversely affecting plant growth and development [5]. Additionally, *ZmGE2*, a cytochrome P450-encoding gene that regulates the embryo-to-endosperm ratio (EER), has been associated with increased EER and higher oil content due to a 247-bp transposon insertion in its 3′ untranslated region [6]. Although the functions of several key genes have been elucidated, seed oil content is a quantitative trait influenced by multiple genes, necessitating QTL analysis to uncover its genetic basis and enable precise breeding improvements.

Over the past few decades, researchers have extensively studied the genetic mechanisms of oil content in maize seeds through QTL mapping, with many studies identifying numerous QTLs based on different genetic backgrounds and population types. In 2004, Song et al. conducted QTL mapping using a high-oil maize population derived from the By804×B73 cross; their study identified 27 QTLs related to oil content in an $F_2/F_{2:3}$ population, collectively explaining 1.74% to 17.51% of the phenotypic variation [7]. In 2008, Zheng et al. identified 12 oil content-related QTLs in a BC_2 population of 281 individuals derived from the ASKC28IB1×PH09B cross, with each QTL explaining 2.2% to 32.7% of the phenotypic variation [3]. In 2016, Zhao et al. used a population of 212 $F_{2:3}$ families derived from inbred lines LH8012 and 13218008 and identified nine oil content-related QTLs across two environmental conditions, explaining 1.51% to 26.64% of the phenotypic variation [8]. Although numerous QTLs associated with oil content in maize seeds have been identified, only a few QTLs have been fine-mapped to candidate genes, such as the identification of *DGAT1-2* at the qHO6. Differences in experimental populations, environmental conditions, and mapping markers have led to broad confidence intervals for the detected QTLs, making it difficult to further localize candidate genes and thereby limiting the development of high-oil maize varieties.

Meta-QTL analysis is an effective method for integrating QTL data from multiple studies, helping to overcome the variations caused by differences in genetic backgrounds, population types, and environmental conditions, thus generating reliable and stable MQTLs with narrower confidence intervals [9]. This approach has been successfully applied in the study of agronomic traits in various crops. In rice, meta-QTL analysis has been used to identify MQTLs associated with yield-related traits and stress resistance [10, 11]; similarly, in wheat, this method has been applied not only to yield-related traits but also to the successful identification of MQTLs associated with Fusarium head blight resistance and quality traits [12–14]. In cotton, meta-QTL analysis has integrated QTLs related to various agronomic and quality traits, providing important references for breeding [15–17]; likewise, in maize, meta-QTL analysis has been employed to integrate QTLs related to grain dehydration, fungal disease resistance, and stalk lodging resistance, thus offering strong theoretical support for maize genetic improvement [18–20].

Several meta-QTL analyses for seed oil content have been reported in maize [21–23]. Yang et al. [21] integrated 26 oil content-related QTLs and yielded 9 MQTLs, and Kaur et al. [22] identified one oil content-related MQTL. Tang et al. [23] identified 32 oil content-related MQTLs by using 222 initial QTLs reported between 2008 and 2017. Recently, some new maize seed oil content-related QTL studies were performed in the recombinant inbred line (RIL), doubled haploid (DH) and F_2 populations [24–27]. Here, we collected 339 QTLs related to maize seed oil content from 31 papers published from 2004 to 2024, which led to the identification of 72 oil content-related MQTLs. The average confidence interval of the MQTLs was reduced by 5.89-fold compared to the collected QTLs. Through the integration of GWAS-MTAs, over 60% of the MQTLs were validated. Additionally, we identified four known functional genes within the MQTL regions and uncovered 44 candidate genes through homologous gene comparison. We believe that our research provides important theoretical support for further elucidating the genetic basis of maize seed oil content and for achieving targeted breeding of high-oil maize varieties.

Methods

Collection and processing of initial QTL

For the initial QTLs associated with oil content in maize seed, we collected 339 QTLs from 31 published studies [3, 7, 8, 21, 24–50]. The collected QTL data include QTL names, mapping populations, population sizes and types, mapping methods, chromosomal locations, LOD scores, phenotypic variation explained (PVE), confidence interval, genetic markers, and positions. For initial QTLs lacking LOD scores, the LOD score was set to a default value of 2.5 [51]. A confidence interval refers to a genomic region on a chromosome that contains the true QTL position with a statistical confidence level (95%) [52],

and is a parameter associated with the accuracy of QTL mapping. To generate a more comprehensive set of initial QTLs for meta-QTL analysis, we calculated the corresponding confidence intervals for the QTLs that lacked such values. The confidence interval is mainly associated with the size of the mapping population (N) and the phenotypic variation explained (R^2) of the QTL [52]. In addition, the optimal formulas used for calculation of the confidence interval are varied for different mapping populations. Here, three formulas were used to calculate the confidence interval, including C.I. = $530/(N\times R^2)$ (1), C.I. = $163/(N\times R^2)$ (2), and C.I. = $97.462/(N\times R^2)^{0.835}$ (3). Based on the original types of mapping population used for derivations of these formulas [52–54], formula (1) was used for backcross and F_2 mapping populations, formula (2) was used for recombinant inbred line (RIL) mapping populations, and formula (3) was used for doubled haploid (DH) mapping populations here. Notably, the QTLs with no provided R^2 values were excluded from the meta-QTL analysis.

For studies utilizing SNPs for QTL mapping, where SNP markers could not be directly positioned on the genetic map, the physical locations of SNPs were converted to their corresponding genetic positions on the reference genetic map IBM2 2008 Neighbors [55] (https://www.maizegdb.org/data_center/map) prior to meta-QTL analysis. Furthermore, in cases where articles did not provide a genetic map but only listed flanking markers, these flanking markers were mapped onto the reference genetic map IBM2 2008 Neighbors. The flanking markers were subsequently used to define the confidence interval and determine their updated genetic positions. If only one flanking marker was reported in an article, that marker was mapped to IBM2 2008 Neighbors to represent one side of the confidence interval, while the other side of the confidence interval was estimated using the aforementioned formulas. QTL studies for genetic markers that could not be mapped to the IBM2 2008 Neighbor were excluded from the meta-QTL analysis.

Identification of MQTL and acquisition of interval genes

BioMercator V4.2 was employed to integrate the collected QTL genetic maps with the reference genetic map IBM2 2008 Neighbors, resulting in the construction of a high-density genetic map. The initial QTL studies were then mapped onto the high-density genetic map for further meta-QTL analysis. Based on previous studies [20], the Akaike Information Criterion (AIC) model was applied for MQTL identification, with K selected as the value where the Delta value equals 0 (or the smallest positive value close to 0). In the second phase of the meta-QTL analysis, KMin and KMax were set to K-1 and K, respectively, while other parameters remained at their default settings. Finally, MQTLs containing at least two initial QTLs were retained as the finally MQTL set.

For the MQTLs identified, their genetic positions could not be directly mapped to the physical positions on the IBM2 2008 Neighbors genetic map. Here, we employed the linear interpolation method to calculate the physical positions of the MQTLs, which is more accurate than using the physical positions as compared to the using of physical positions of the genetic markers adjacent to the MQTLs as the physical intervals of the MQTLs directly [56, 57]. Specifically, the genetic position (g) of each MQTL was mapped to the neighborhood of the IBM2 2008 reference genetic map, and two genetic markers closest to this genetic position (g) were selected. The genetic positions of these markers are denoted as g1 and g2, with their corresponding physical positions denoted as p1 and p2, respectively. The physical position of the MQTL is denoted as p, and its calculation formula is as follows [56]:

$$p=p1+(p2-p1)\frac{g-g1}{g2-g1}$$

Subsequently, based on the physical positions of the MQTLs, all genes within the MQTL intervals were retrieved from the B73 genome (AGPv4) [58].

Validation of MQTL with GWAS

To validate the reliability of the MQTLs identified in this study, we collected the physical positions of 155 GWAS-MTAs significantly associated with oil content-related traits from five GWAS studies of maize seed oil content [59–63]. We used the Assembly Converter tool in Ensembl Plants (https://plants.ensembl.org/index.html) to convert their physical positions uniformly to the B73 genome (AGPv4) for comparison with the MQTL physical positions. The physical positions of the 155 GWAS-MTAs were compared with the MQTLs identified in this study. The MQTL was considered as validated by the GWAS study if it is overlapped with the 2.5 Mb upstream and downstream regions of at least one GWAS-MTAs [19]. TBtools was utilized for generating Circos plots [64].

Identification of candidate genes from MQTLs

The expression patterns of genes within the MQTL intervals were analyzed based on the previously reported dynamic transcriptome landscape of seed-related tissues, including nucellus, embryos, endosperms and whole seeds [65, 66]. The genes that were expressed in at least one sample of these seed-related tissues were regarded as candidate genes. Furthermore, a homolog-based method was used to mine high-confidence candidate genes. First, we collected 30 oil content-related genes, including 13

genes associated with the oil content of maize seed [3–6, 59, 67–71], and 17 genes associated with seed oil content of Arabidopsis, oilseed rape, wheat [2, 72–82] (Table S4). Then, the BLASTP analysis was performed. For the expressed genes within the MQTL intervals, the genes that were homologous with at least one of the 30 known oil content-related genes, with the threshold of E-value lower than 1×10^{-2} and alignment score greater than 100, were considered as high-confidence candidate genes.

Results

Characteristics of the QTLs for maize seed oil content

A total of 339 QTLs from 31 studies on maize seed oil content, published over the past 20 years, were selected for meta-QTL analysis (Table S1). These QTLs were derived from 42 mapping populations, including 14 F_2 populations, 13 recombinant inbred line (RIL) populations, 8 doubled haploid (DH) populations, 5 backcross (BC) populations, and 2 testcross (TC) Population, with an average population size of 225, ranging from 41 to 500 (Table S1). The distribution of these QTLs varied greatly among different chromosomes, with the most abundant (52) on chromosome 6 (chr6) and the fewest (16) on chr10 (Fig. 1A).

The initial QTLs exhibited relatively large confidence intervals, with an average confidence interval of 49.28 cM, and the majority (248, 73.16%) having a confidence interval greater than 10 cM (Fig. 1B). The average LOD scores of these QTLs was 4.76, with 58.80% of QTLs had a LOD scores between 3 and 5 (Fig. 1C). Regarding the phenotypic variation explained (PVE), another key feature of these QTLs, the average PVE was 8.87%, with individual values ranging from 0.19% to 58.81%. Among these, 138 QTLs had PVEs between 5% and 10% (Fig. 1D).

Identification of MQTLs related to oil content

We integrated 29 individual genetic maps associated with QTL mapping for seed oil content, collected from 31 previous studies, onto a published reference genetic map IBM2 2008 Neighbors [55], and thus constructed a high-density consensus genetic map for the following meta-QTL analysis. The map contained 19,782 genetic markers, with a total length of 11,710.57 cM and an

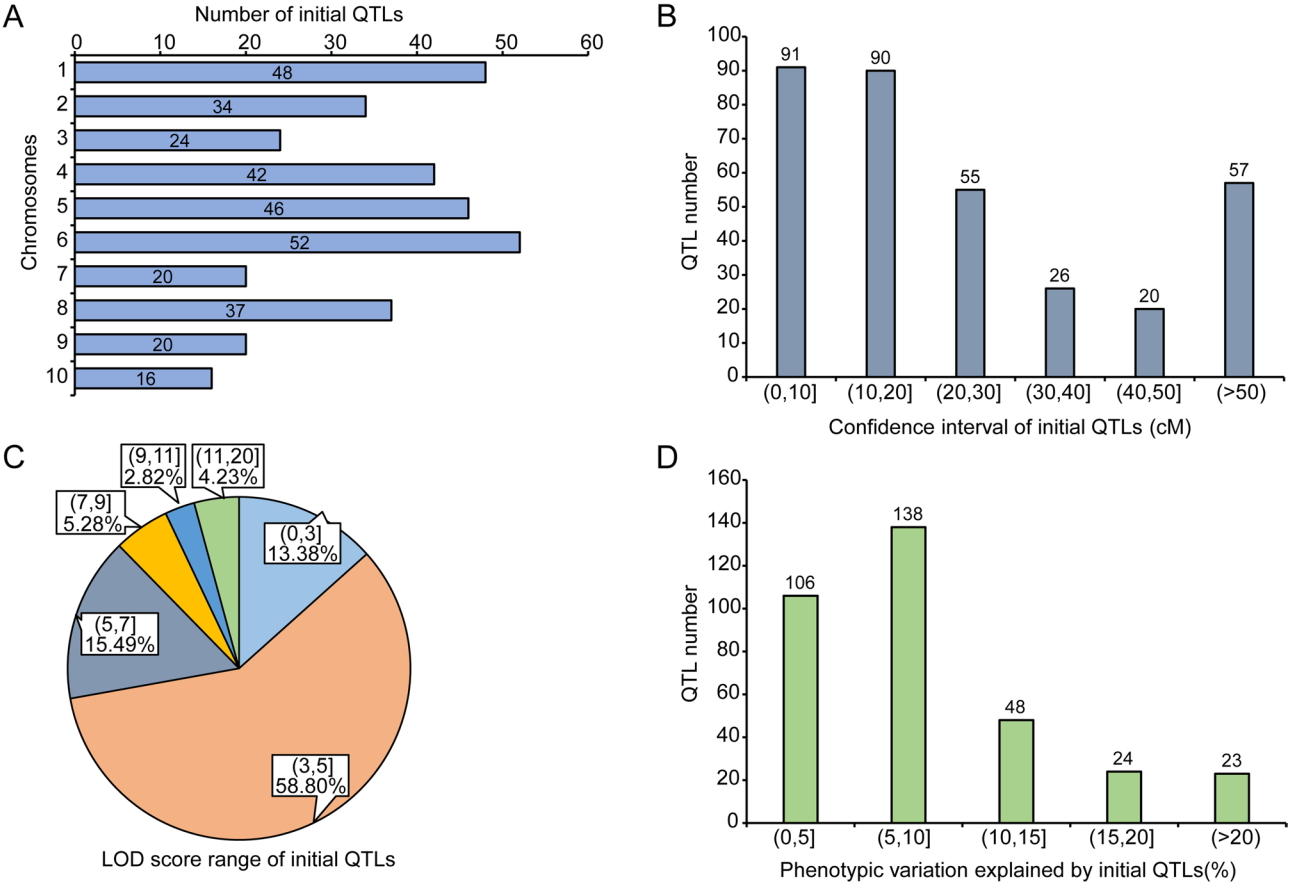


Fig. 1 Characterization of initial QTLs associated with maize seed oil content collected in this study. **A** Distribution of initial QTLs across chromosomes. **B** Proportion distribution of QTLs across different confidence interval ranges. **C** Percentage distribution of QTLs across different LOD score ranges. **D** Distribution of phenotypic variation explained (PVE) values for the collected QTLs

average marker density of 1.69 markers per cM (Fig. 2, Table S2). The genetic lengths of individual chromosomes ranged from 618.19 cM to 1,675.62 cM (Fig. 2, Table S2). Similar as that reported previously [12, 13, 57], the genetic markers were unevenly distributed on chromosomes.

For 339 initial oil content-related QTLs, 269 of which were successfully projected onto the high-density genetic map, forming the final MQTL set. A total of 72 MQTLs were identified (Fig. 3), which each integrated with at least 2 initial QTLs, with an average of 9 QTLs per MQTL (Fig. 4A). Notably, there were 4 MQTLs contained more than 20 QTLs, including mOC4-5 (20), mOC6-5 (24), mOC6-6 (26), and mOC6-7 (25) (Table S3). Except for chr1 without any MQTL identified, each of the remained chromosomes contained more than 6 MQTLs, with the maximum number of MQTL (10) observed on chr5 (Figs. 3 and 4B).

The PVE values of the MQTLs ranged from 2.49% to 17.98%, with an average of 8.29%, reflecting a moderate impact on phenotypic variation. About one quarter (26.39%) of MQTLs exhibited an PVE value larger than 10% (Fig. 4C). Particularly, there were seven MQTLs with PVE exceeding 15%, including mOC8-2 (15.07%), mOC8-3 (15.33%), mOC2-1 (16.27%), mOC2-7 (16.45%), mOC8-8 (16.91%), mOC2-3 (17.83%), and mOC8-1 (17.98%) (Table S3). The average confidence interval of the MQTLs was 19.87 cM, about 5.89-fold less than that of the initial QTLs, which facilitates the identification of candidate genes. The extent of confidence interval reduction varied for different chromosomes, with the largest reduction (12.49-fold) for chr6 and the smallest reduction (2.80-fold) for chr10 (Fig. 4D, Table S3). As for physical intervals, the majority of MQTLs (62.5%) were smaller than 5 Mb, including 11 MQTLs with intervals less than 1 Mb (Fig. 4E, Table S3). An extreme case is mOC6-3, which is an MQTL integrated with 13 initial QTLs and had a physical interval of only 20 kb (Table S3). Notably, no genes were identified in mOC6-3 (Table S3), which suggests that regulatory elements or candidate genes associated with seed oil content may be located in the vicinity of this region.

Validation of MQTLs with GWAS-MTAs and known genes related to seed oil content

To determine the reliability of the MQTL analysis, the physical positions of MTAs from published GWAS studies for seed oil content were compared with those of MQTLs. A total of 155 GWAS-MTAs were collected from five GWAS studies [59–63], comprising those from natural populations, general inbred line populations, tropical maize populations, and mixed populations of general inbred lines and high-oil lines. Only GWAS-MTAs with a 5 Mb region overlapping with MQTL were considered to be co-located with MQTL. Forty-four (61%) of 72 MQTLs were supported by at least one GWAS-MTA, including 20 MQTLs validated by at least two GWAS-MTAs (from five GWAS studies) (Fig. 5). It is worth to note that the four MQTLs integrating more than 20 initial QTLs were all validated by at least five GWAS-MTAs, including mOC6-7 (10), mOC6-6 (9), mOC6-5 (9), and mOC4-5 (5) (Fig. 5). Additionally, the

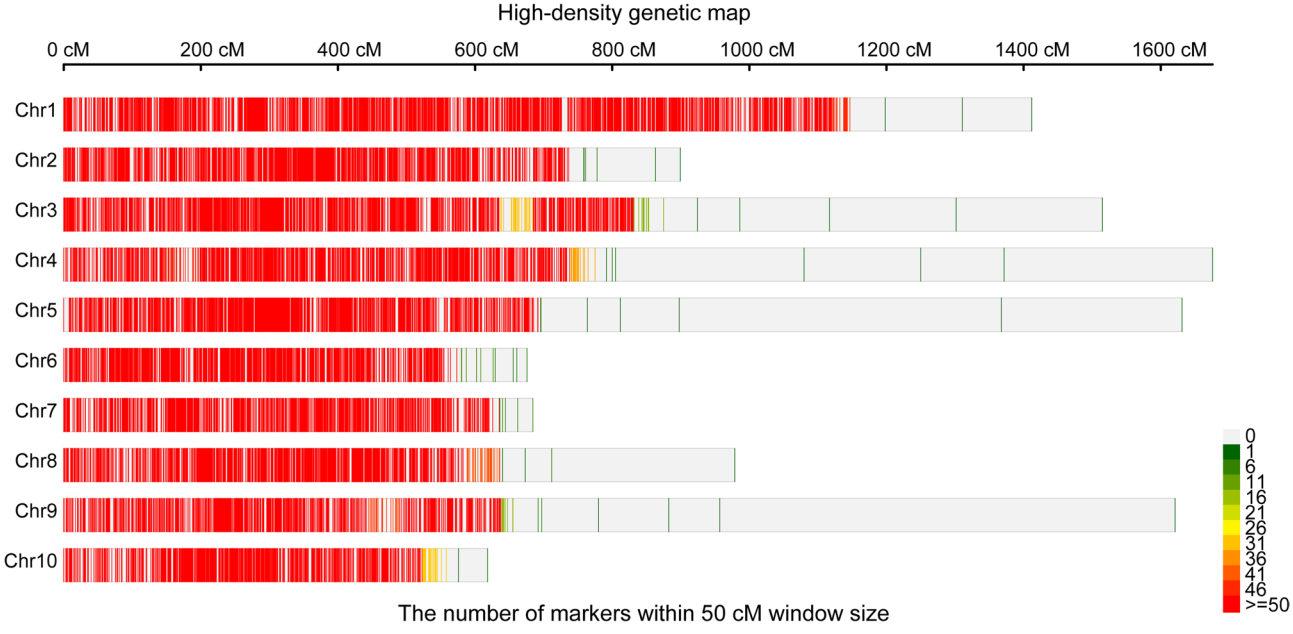


Fig. 2 The high-density genetic map used for meta-QTL analysis, with red representing regions of dense marker distribution and areas near green or white indicating regions with sparse marker distribution

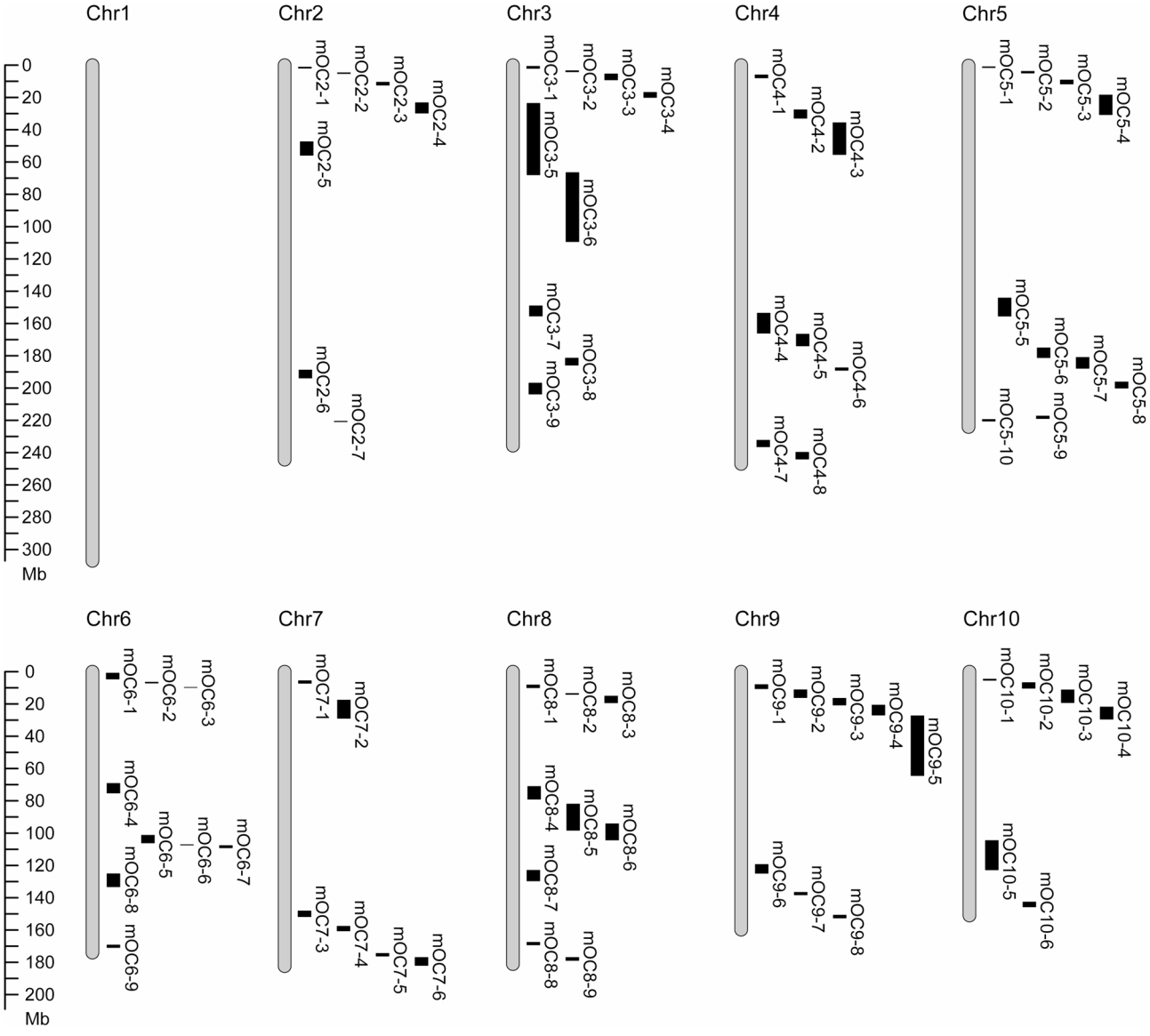


Fig. 3 Distribution of the 72 MQTLs identified by meta-QTL analysis on the B73 (AGPv4) genome. The scale on the left side of the figure represents the physical map of the B73 genome

eight GWAS-MTAs (M6c102823048, M6c103139944, M6c103867816, M6c104455181, M6c104760351, M6c104859429, M6c104966089, PZE_106054189) identified in two GWAS studies [59, 63] were found to co-localize with three MQTLs (mOC6-5, mOC6-6, and mOC6-7) (Fig. 5), suggesting that that these GWAS-MTAs and the three MQTLs may represent hotspot regions for investigating seed oil content.

Four known functional genes related to seed oil content were also co-localized with the MQTLs. *Fad2*, which is located in mOC4-4, encodes a delta-12 desaturase that functions in the endoplasmic reticulum. According to previous studies, *fad2* catalyzes the conversion of oleic acid (18:1) to linoleic acid (18:2) by introducing a double bond at the delta-12 position, and its enzymatic activity directly regulates fatty acid biosynthesis in seed oil (Fig. 5) [68]. *ZmDGAT1-2* and *ZmPDAT* (*pza01735*), which encode an acyl-CoA: diacylglycerol acyltransferase and a phospholipid: diacylglycerol acyltransferase, respectively, play crucial roles in catalyzing the final acylation step in TAG synthesis [3, 4], were found in mOC6-7 and mOC2-6, respectively (Fig. 5). Notably, overexpression of *ZmDGAT1-2* in maize has been shown to increase oil content by up to 41% and oleic acid content by up to 107% [3]. Additionally, the acyl-ACP thioesterase-encoding gene *ZmFATB*, located in mOC9-3 (Fig. 5), plays a crucial role in maize seed fatty acid synthesis. Specifically, an 11-bp insertion in the last exon of *ZmFATB* can reduce palmitic acid content by up to 4.57 mg/g, thereby

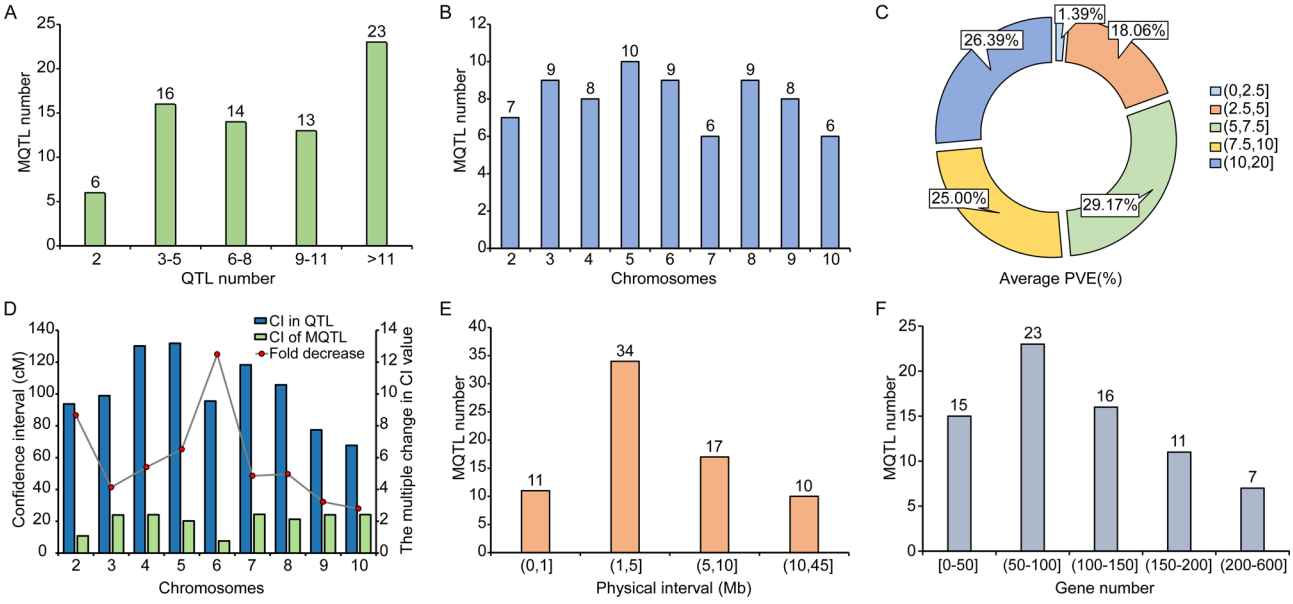


Fig. 4 Overview of the basic characteristics of the identified MQTLs. **A** Chromosomal distribution of MQTL numbers. **B** Number of initial QTLs integrated into MQTL. **C** Proportional distribution of the average phenotypic variation explained (PVE) by the MQTLs. **D** Reduction in confidence interval of the MQTLs; blue and green bars represent the extent of confidence interval reduction on each chromosome, while the line graph indicates the corresponding fold decrease. **E** Distribution of the physical sizes of MQTL intervals. **F** Gene count distribution within the MQTL regions

optimizing the ratio of saturated to unsaturated fatty acids without altering the seed oil content [70, 71].

Identification of candidate genes in the MQTL regions

A total of 8,248 genes were identified within the 72 MQTL intervals, averaging 116 genes per MQTL (Fig. 4F, Table S3). Most MQTLs contained dozens to hundreds of genes, but 5 MQTLs had fewer than 20 genes, including mOC2-7, mOC6-2, mOC6-3, mOC6-6, and mOC8-2 (Table S3). For instance, mOC6-6, which integrated 26 initial QTLs with an average PVE of 9.87%, contained only 8 genes (Table S3), five of which were expressed in the seed [66]. A TETRASPANIN family gene (*Zm00001d036956*) in mOC6-6 was highly expressed in the embryo during the grain-filling stage, a period when lipid metabolism-related genes typically show high expression levels [70]. Similarly, mOC8-2, with 19 genes (the most among MQTLs with fewer than 20 genes), integrated 12 initial QTLs with an average PVE of 15.07% (Table S3), and 13 of its genes were expressed in the seed, among which *Zm00001d008592* (encoding phosphatidic acid phosphatase) and *Zm00001d008585* (encoding protein kinase) were highly expressed in embryo during the grain-filling stage (Fig. 6A) [66].

To further explore genes associated with seed oil content, we focused on 5072 candidate genes expressed in seeds [66]. Subsequently, a homology-based gene mining strategy was employed to identify genes more likely to influence maize seed oil content. In this process, we collected 30 functional genes related to seed oil content that had been previously reported in maize and other species (Table S4) [2–6, 59, 67–82]. Previous studies have demonstrated that these genes have been shown to influence maize seed oil biosynthesis through mechanisms such as transcriptional regulation, carbohydrate transport, fatty acid synthesis and transport, biosynthesis of TAG, stabilization of oil bodies, and modulation of the embryo size. Based on BLASTp alignment against 5072 genes expressed in seed, we identified 44 homologous genes in 31 MQTLs (Table 1).

For instance, the mOC4-5 integrates up to 20 initial QTLs (from 14 distinct population types) and co-localizes with 5 GWAS-MTAs (Table S3, Fig. 5), with a confidence interval of 9.5 cM and an average PVE of 5.81%. This region encompasses a total of 170 genes, of which 87 are expressed in the seed (Table S3) [66]. Within this interval, we identified the gene *CADTFR7*, which belongs to the NF-Y transcription factor family and shares 74.27% protein sequence identity with the well-characterized transcription factor *ZmLEC1* (Table 1, Table S5), making it the most homologous protein to ZmLEC1 in the maize genome. *ZmLEC1* has been demonstrated to enhance carbon flux in fatty acid biosynthesis by regulating downstream gene expression, thereby increasing maize seed oil content by 48% [5]. Therefore, *CADTFR7* is likely to exhibit a similar expression pattern and functional role. Expression profiling revealed that *CADTFR7* is predominantly expressed during early embryo development (em10-em12) and has negligible expression in the endosperm and seeds (Fig. 6B, Table S5). Its expression

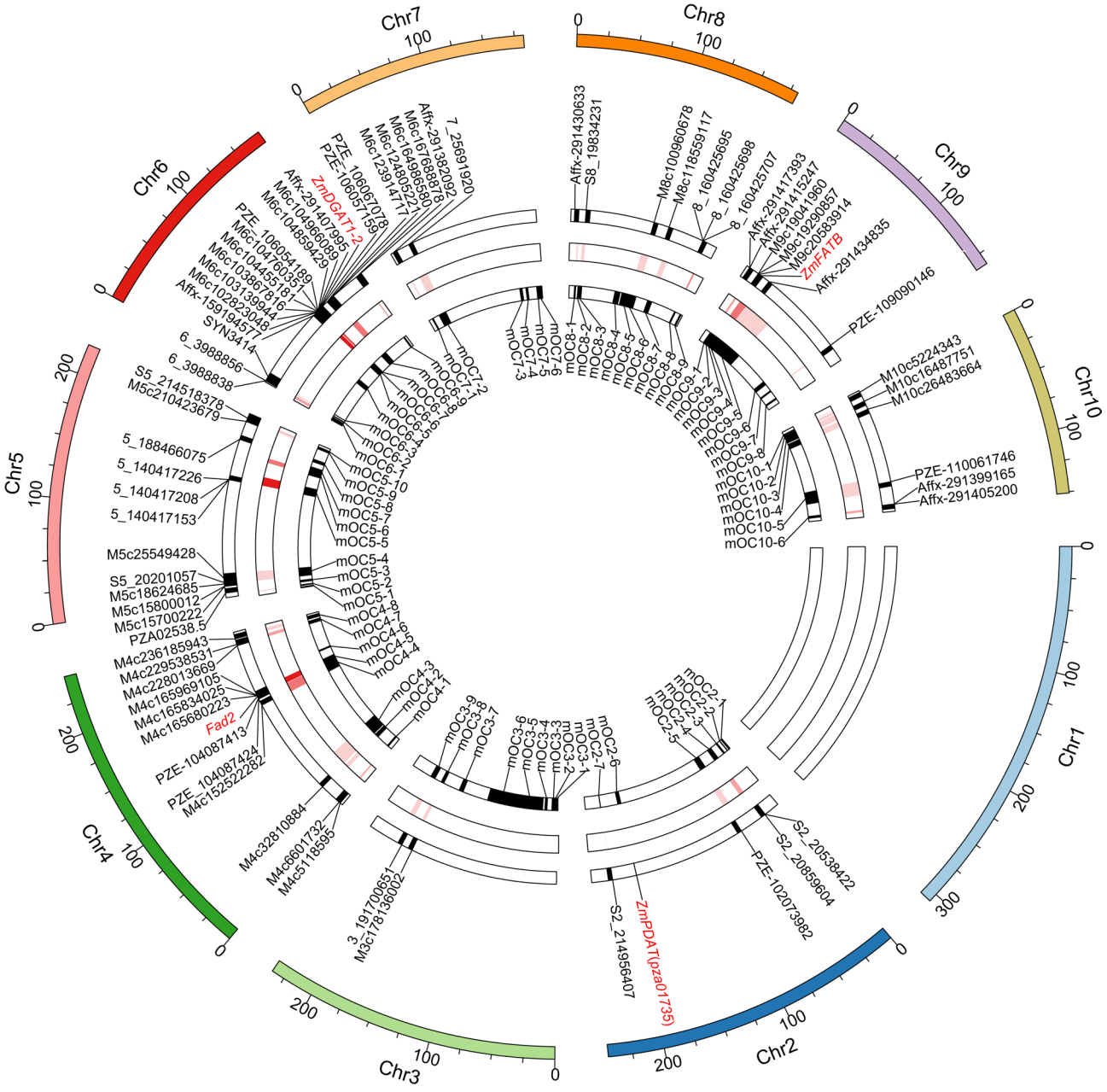


Fig. 5 Validation of MQTLs using GWAS-MTAs and distribution of known functional genes within MQTLs. Distribution of GWAS-MTAs, known functional genes, and MQTLs across chromosomes. The innermost circle represents the distribution of MQTLs; the second circle indicates the number of GWAS-MTAs from five oil content-related GWAS studies that are co-localized within MQTLs, with darker shades of red representing a higher number of GWAS-MTAs co-localized within an MQTL, and the width of the red segments corresponding to the physical interval of the MQTLs. The third circle, in black font, shows GWAS-MTAs co-localized with MQTLs, while red fonts (genes identified within MQTLs) denote known functional genes; the outermost circle represents the ten chromosomes of maize

pattern is highly similar to that of *ZmLEC1* (Pearson correlation coefficient, $r \geq 0.9$) (Fig. 6A), which further supports its reliability as a candidate gene.

Another notable case is the mOC6-4, which has a confidence interval of only 2.42 cM and integrates 18 initial QTLs from 11 populations, with an average PVE of 7.48% (Table S3). This interval contains 66 genes, of which 35 are expressed in the seed (Table S3) [66]. Among these, we identified the gene *Zm00001d036137*, which encodes an acyl-ACP thioesterase and shares 88.89% sequence similarity with the ZmFATB protein (Table 1, Table S5), making it the most highly similar protein in the maize genome. The FATB gene in plants has been demonstrated to influence seed oil content by releasing free fatty acids [83]. In maize, an 11-bp insertion in the last exon of *ZmFATB* can optimize the ratio of saturated to

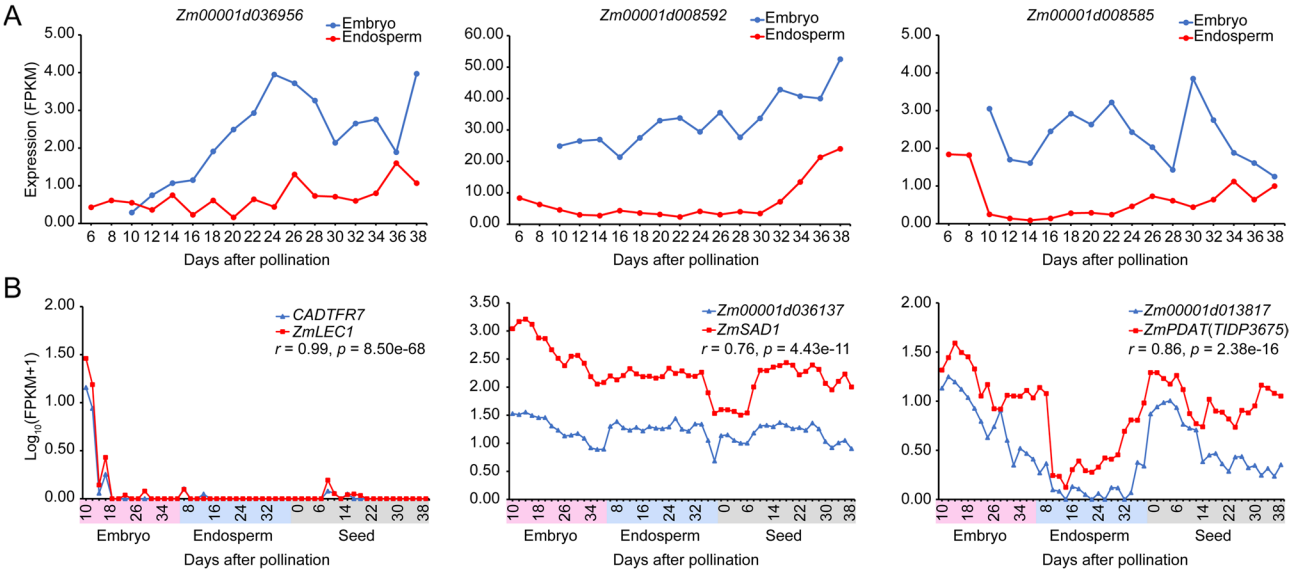


Fig. 6 Examples of candidate genes identified through expression pattern analysis and homologous gene comparison. **A** Based on the high expression characteristics of lipid-related genes in the embryo during the grain-filling stage, the expression patterns of the identified genes *Zm00001d036956* (mOC6-6), *Zm00001d008592* (mOC8-2), and *Zm00001d008585* (mOC8-2) during embryo and endosperm development were analyzed. **B** Expression pattern analysis of the identified genes (*CADTFR7*, *Zm00001d036137*, *Zm00001d013817*) based on homology alignment with known functional genes related to seed oil content

unsaturated fatty acids without altering seed oil content [70]. Furthermore, we found that *Zm00001d036137* exhibits a similar expression pattern to *ZmSAD1* during seed development (Pearson correlation coefficient, $r \geq 0.75$) (Fig. 6B). Given that *ZmSAD1* is responsible for converting stearic acid (C18:0) to oleic acid (C18:1) in maize [84], this suggests that *Zm00001d036137* may function in concert with *ZmSAD1* in the de novo synthesis of fatty acids.

Additionally, several MQTLs harbor multiple candidate genes, such as mOC5-4 (Table S5). This region integrates 16 initial QTLs from nine different population types and co-localizes with five GWAS-MTAs, with an average PVE of 9.63% (Table S3, Fig. 5). It contains 256 genes, 161 of which are expressed in the seed (Table S3) [66]. In mOC5-4, we identified four candidate genes, including a homolog of *BnFAX6*, *Zm00001d013817*, and three homologs of *ZmGE2* (*Zm00001d013830*, *Zm00001d013862*, and *Zm00001d013759*) (Table S5). *Zm00001d013817* is the candidate gene with the highest identity within the mOC5-4 region based on homology alignment (Table S5). Its identity with the BnFAX6 protein is 61.74% (Table S5), making it the most homologous protein to BnFAX6 in the maize genome. In oilseed rape, overexpression of *BnFAX6* has been shown to significantly enhance the expression of genes related to glycolysis and lipid biosynthesis, thereby increasing oil content in seeds and leaves [78], suggesting that *Zm00001d013817* may exhibit similar functions. Furthermore, the expression level of *Zm00001d013817* in the embryo is higher than in the endosperm and seed, and this expression pattern closely resembles that of the oil biosynthesis gene *ZmPDAT* (*TIDP3675*), with a high Pearson correlation coefficient ($r \geq 0.85$) (Fig. 6B).

Discussion

Compared with previous individual and scattered QTL studies, meta-QTL analysis integrates QTL data from multiple sources, significantly enhancing mapping accuracy and reducing confidence interval ranges, thereby bolstering the applicability of QTLs in molecular breeding. Compared with previous oil content-related meta-QTL analyses in maize [21–23], more MQTLs were identified here, which might be due to the use of more initial QTLs. The 72 identified MQTLs were most numerous on chromosome 6, which differs from the results of the previous oil content MQTL studies but is consistent with the highest density of initial QTLs on this chromosome [21–23], suggesting the presence of a hotspot region for oil content regulation on chr6.

Notably, the smallest MQTL confidence interval identified in this study was only 0.12 cM, with a physical interval of just 20 kb, narrower than the smallest confidence intervals identified in previous oil content MQTL studies (2.34 cM,14.27 cM and 1.52 cM, respectively) [21–23]. This demonstrates that increasing the number of initial QTLs can effectively reduce the width of confidence intervals, facilitating the identification of candidate genes. However, no candidate genes were found within this interval. Given that QTL intervals are statistical

Table 1 Information on the 44 representative candidate genes identified based on homology alignment

MQTL ID	Gene ID	Locus Symbol[a]	Gene Function Description
mOC2-1	Zm00001d001838	abi3	VP1, dormancy regulatory protein
mOC2-4	Zm00001d002864	LOC100282697	Sugar (and other) transporter
mOC2-6	Zm00001d005821	LOC100273153	cytochrome P450
mOC2-6	Zm00001d005822	cyp12	cytochrome P450 CYP92
mOC2-6	Zm00001d005823	Zm00001d005823	cytochrome P450
mOC2-6	Zm00001d005831	pza01735	diacylglycerol O-acyltransferase
mOC2-6	Zm00001d005902	pco137522	Sec23/Sec24 zinc finger
mOC3-1	Zm00001d039310	cyp38	cytochrome P450
mOC3-5	Zm00001d040611	lg3	LG3, Homeobox-leucine zipper family protein
mOC3-6	Zm00001d041192	sut2	sucrose transporter
mOC3-8	Zm00001d042870		Lecithin: cholesterol acyltransferase
mOC3-8	Zm00001d042968	ca3p1	NF-YB, CCAAT-box binding protein subunit B
mOC4-3	Zm00001d049595		cytochrome P450
mOC4-4	Zm00001d051554	abh2	(+)-abscisic acid 8′ hydroxylase
mOC4-4	Zm00001d051636	fad1	omega-3 fatty acid desaturase
mOC4-5	Zm00001d051697	cadtfr7	NF-YB, CCAAT-box binding protein subunit B
mOC4-8	Zm00001d053749	knox7	KNOX7, Homeobox-leucine zipper family protein
mOC5-3	Zm00001d013428	pgm2	phosphoglucomutase (glucose-cofactor)
mOC5-4	Zm00001d013759	LOC103626064	cytochrome P450
mOC5-4	Zm00001d013817	GRMZM2G090669	Transmembrane proteins 14 C
mOC5-4	Zm00001d013830	LOC100382116	cytochrome P450
mOC5-4	Zm00001d013862	fah2	Ferulate 5-hydroxylase
mOC5-5	Zm00001d016274	tst2	tonoplast sugar transporter
mOC5-6	Zm00001d016938	sut5	sucrose transporter
mOC5-7	Zm00001d017077	pr1	flavonoid 3′ hydroxylase
mOC6-1	Zm00001d035013	LOC109940614	cytochrome P450
mOC6-4	Zm00001d036137	cl525_1(477)	Acyl-ATP thioesterase
mOC6-7	Zm00001d036982	ln1	diacylglycerol O-acyltransferase
mOC6-9	Zm00001d039131	agp2	ADP glucose pyrophosphorylase
mOC7-1	Zm00001d018803	Zm00001eb300060	Sugar (and other) transporter
mOC7-1	Zm00001d018839	cyp19	cytochrome P450
mOC7-2	Zm00001d019230	sid1	apetala2 transcription factor-like
mOC7-2	Zm00001d019266	agpll2	ADP glucose pyrophosphorylase
mOC7-6	Zm00001d022591		Lecithin: cholesterol acyltransferase
mOC8-4	Zm00001d009600	npi260b	Sugar (and other) transporter
mOC8-4	Zm00001d009669	stp1	sugar transport protein
mOC8-5	Zm00001d009858	cyp47	cytochrome P450, cinnamic acid 4-hydroxylase
mOC9-3	Zm00001d045295	lacs5	long-chain acyl-coA synthase
mOC9-3	Zm00001d045387	fat2	fatty acyl-ACP thioesterase
mOC9-5	Zm00001d045772	cadtfr12	NF-YB, CCAAT-box binding protein subunit B
mOC9-8	Zm00001d048178	IDP2462	Sugar (and other) transporter
mOC10-2	Zm00001d023538	lacs11	long-chain acyl-coA synthase
mOC10-3	Zm00001d023625	thy1	tryptophan 5-hydroxylase
mOC10-5	Zm00001d025170	sacd11	stearoyl-acyl-carrier-protein desaturase

aLocus symbols were obtained from MaizeGDB

estimates, the causal genetic elements could be either protein-coding genes or regulatory elements that might be located in the adjacent regions of this interval.

Furthermore, we validated the identified MQTLs using previous GWAS studies [59–63], and over 60% (44 out of 72) of the MQTLs were validated. Notably, the accurate threshold for colocalization analysis of MQTLs and GWAS, which is associated with linkage disequilibrium (LD) decay distance in maize [12, 85], is difficult to determine because the LD decay distance in maize varies with different population types and sizes, as well as different genome regions [86]. Here, the 5 Mb threshold was used by us, same as the threshold used by a previous study [85]. Several false positives of colocalization might be

introduced under the threshold. According to previous study, future studies with the expansion of the population size of GWAS, development of more precise molecular markers, as well as the integration of multi-omics analyses might can improve of the resolution of GWAS [87], and thus is favor for colocalization analysis of MQTLs and GWAS.

Through the identification of MQTLs in this study, we uncovered four oil-content-related genes with known functions [3, 4, 68, 70, 71], thereby validating the efficacy of our MQTL analysis in identifying candidate genes. Further homology comparison identified 44 candidate genes, such as *CADTFR7*, *Zm00001d036137*, and *Zm00001d013817*, which are homologs of *ZmLEC1*, *ZmFATB*, and *BnFAX6*, respectively [5, 70, 78]. These genes are likely to influence oil content in maize seeds through mechanisms such as transcriptional regulation, material transport, and fatty acid synthesis. In addition to these known genes, our study also identified several novel candidate genes that have not been previously reported to be associated with oil content in seeds. For instance, based on the expression pattern analysis of oil content-related genes in maize seeds, we found that *Zm00001d036956* (a TETRASPANIN family gene) in mOC6-6 and *Zm00001d008592* (encoding phosphatidic acid phosphatase) and *Zm00001d008585* (encoding protein kinase) in mOC8-2 exhibited high expression levels in embryo during the grain-filling stage [70]. These newly identified targets provide new avenues for understanding the genetic regulation of oil accumulation in maize. Despite the valuable insights into potential genes affecting maize seed oil content provided by approaches based on expression pattern analysis and homology comparison, these identified genes represent only the tip of the iceberg. Identifying other genes with unknown functions may require more comprehensive methods that integrate MQTLs, multi-omics data, and GWAS studies to further elucidate the genetic basis of oil accumulation in maize seeds [88]. Considering that maize seed oil content is likely regulated by multiple genes with small effects, subsequent validation of multiple genes using mutant creation, overexpression lines, and CRISPR gene editing technologies is still required.

Moreover, although MQTL analysis has significant advantages in integrating multiple population types, environments, and marker differences, the variation in genetic markers across different studies may still lead to the omission of some important initial QTLs during the integration process, thereby affecting the subsequent identification of candidate genes. To address this limitation, the following strategies are proposed: First, expand data collection from more studies, populations, and environmental conditions to enhance data diversity and accuracy. Second, optimize the integration methods by employing advanced statistical models and incorporating data from multiple environments and populations to improve the precision and stability of meta-QTL analysis. Additionally, integrating multi-omics data (such as transcriptomics, metabolomics, and epigenomics) can further narrow down the range of candidate genes and reveal potential regulatory mechanisms. By implementing these comprehensive measures, the integration capacity of meta-QTL analysis can be enhanced, thereby more fully utilizing the collected QTL information and providing stronger support for molecular breeding and gene function research.

Conclusions

In this study, 72 MQTLs were identified from 339 oil content-related QTLs across 31 published studies, with the average confidence interval reduced by 5.89-fold. Over 60% of the MQTLs were validated through co-localization with GWAS-MTAs. Four known functional genes (*ZmDGAT1-2*, *ZmPDAT*, *fad2*, *ZmFATB*) related to lipid metabolism were identified within the MQTL intervals. A homology-based gene mining strategy revealed 44 homologous genes. These homologous genes may influence maize seed oil synthesis through mechanisms such as transcriptional regulation, material transport, and fatty acid biosynthesis. These results provide valuable insights into the genetic basis of oil accumulation in maize seeds and highlight potential targets for future breeding efforts. Future research should focus on the functional validation of these candidate genes, employing strategies such as multi-gene editing to accelerate the development of improved germplasm.

Abbreviations

BC	Backcross
DAG	Diacylglycerol
DGAT	Diacylglycerol acyltransferase
DH	Doubled haploid
EER	Embryo-to-endosperm ratio
GWAS	Genome-wide association study
LOD	Likelihood of odd
MQTL	Meta-QTL
MTAs	Marker-trait associations
PDAT	Phospholipid diacylglycerol acyltransferase
PVE	Phenotypic variation explained
QTL	Quantitative trait loci
RIL	Recombinant inbred line
TAG	Triacylglycerol
TC	Testcross

Supplementary Information

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Supplementary Material 1.

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Authors' contributions
J.C. and Q.L. conceived and designed the project. Z.Z., K.L., and W.W. carried out the experiments and analyzed the data. Z.Z., K.L., and J.C. drafted the manuscript. F.Y., N.Z. and J.L. conceived the study and contributed to its design. Q.L. and J.C. revised the manuscript. All authors have read and approved the final manuscript.

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Data availability
The datasets generated and analyzed during the current study are available in this article and its supplementary information files.

Declarations

Ethics approval and consent to participate
Not applicable.

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The authors declare no competing interests.

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