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Integrated GWAS and transcriptome analysis reveals regulatory networks underlying growth in improved grass carp

Yakui Tai [a,1], Ling Liu [a,1], Yiyan Zeng [a], Mengdan Li [a], Mengxue Luo [a], Wuhui Li [a], Hailu Zhou [a], Jinhui Zhang [a], Xiaohuan Han [a], Conghui Yang [a], Ming Wen [a], Li Ren [a,b,c,*], Qinbo Qin [a,b,c,*], Shaojun Liu [a,b,c,*]

[a] State Key Laboratory of Developmental Biology of Freshwater Fish, Engineering Research Center of Polyploid Fish Reproduction and Breeding of the State Education Ministry, College of Life Sciences, Hunan Normal University, Changsha 410081, China
[b] Yuelushan Laboratory, Changsha 410128, China
[c] Hunan Yuelu Mountain Scienece and Technology Co. Ltd. for Aquatic Breeding, Changsha 410081, China

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ABSTRACT

Grass carp, a globally important aquaculture species, is known for its rapid growth. To explore the genetic basis of this trait, we generated a population through gynogenesis and hybridization with a wild population, resulting in diverse growth traits. To identify genetic variants associated with growth, we performed whole-genome resequencing and transcriptome profiling of 28 individuals from this population. Genome-wide association studies (GWAS) revealed 538 SNPs linked to growth traits. Weighted gene co-expression network analysis (WGCNA) identified shared regulatory modules in liver and muscle tissues, highlighting the coordinated regulation of growth across these tissues. Interestingly, we observed that genes within the same module, such as *igf1*, *wnt1*, and *wnt9b* in the liver, and *igf1ra*, *igf1rb*, *fzd1*, and *fzd9b* in the muscle, are expressed in extracellular and cell membrane compartments, respectively. This suggests a potential coordinated regulation of growth traits between liver and muscle tissues. To further dissect the regulatory mechanisms, we conducted expression quantitative trait loci (eQTL) analysis. This analysis identified both *cis*- and *trans*-eQTLs for numerous growth-related genes in both liver and muscle tissues. Our findings provide valuable insights into the genetic architecture of growth in grass carp, shedding light on the potential interplay between digestion and growth in herbivorous fish. These insights have significant implications for the development of strategies to improve growth performance and enhance aquaculture practices.

1. Introduction

Grass carp (*Ctenopharyngodon idella*), a cyprinid species within the order Cypriniformes, is the world's most widely cultivated freshwater fish. Native to major Chinese river systems such as the Yangtze, Pearl, and Heilongjiang basins, it boasts a domestication history exceeding 1700 years in China and has been globally introduced for aquaculture since the 20th century (Krynak et al., 2015). The breakthrough in artificial propagation in 1958 catalyzed its industrial-scale farming. As a cornerstone of China's "Four Major Cultured Cyprinids"—alongside bighead carp (*Hypophthalmichthys nobilis*), silver carp (*Hypophthalmichthys molitrix*), and black carp (*Mylopharyngodon piceus*)—grass carp is integral to traditional polyculture systems. In 2023, it yielded 5.941 million tons, accounting for 17.40 % of China's freshwater aquaculture output, delivering high-quality animal protein and essential micronutrients, thus bolstering economic value and nutritional security (Tang et al., 2025).

Grass carp's prominence in aquaculture stems from its distinctive biological traits. Its herbivorous diet, unlike the omnivorous or carnivorous preferences of most cultured fish, evolves from zooplankton and insects in juveniles to aquatic plants in adults, facilitated by specialized pharyngeal teeth (Dibble, and Kovalenko, K.J.J.o.A.P.M, 2009; Li et al., 2023). This adaptation enhances its efficiency in plant-rich freshwater ecosystems with minimal herbivorous competition. The species also

* Corresponding authors at: State Key Laboratory of Developmental Biology of Freshwater Fish, Engineering Research Center of Polyploid Fish Reproduction and Breeding of the State Education Ministry, College of Life Sciences, Hunan Normal University, Changsha 410081, China.
E-mail addresses: rl@hunnu.edu.cn (L. Ren), qqb@hunnu.edu.cn (Q. Qin), lsj@hunnu.edu.cn (S. Liu).
[1] These authors contributed equally to this work.

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exhibits remarkable environmental resilience, thriving across a temperature range of 0–35 °C (optimal at 20–30 °C) (Liang et al., 2022), and achieves rapid growth, reaching 1–1.5 kg within a year under favorable conditions (Zhao et al., 2018). These attributes—herbivory, resilience, and fast growth—underscore its critical economic and ecological contributions to global aquaculture.

Gynogenesis has emerged as a pivotal technique for generating single-sex populations and homozygous offspring (Tan et al., 2024; Zhang et al., 2011). To date, artificial induction of gynogenesis has been successfully applied in numerous commercial fish species, including grass carp, common carp, catfish, tilapia, and salmonids (Manan et al., 2022; Wang et al., 2019; Zhang et al., 2011). Gynogenetic grass carp are produced by fertilizing mature eggs with irradiated sperm and subsequently subjecting them to temperature manipulations, such as cold shock, which effectively inhibits the extrusion of the second polar body and first meiotic division (Wang et al., 2024; Zhang et al., 2011). By utilizing gynogenetic technology, partially homozygous offspring are obtained, carrying two copies of a recessive allele for a specific gene. The selection of these offspring with desirable traits holds immense potential for advancing aquaculture.

Advances in high-throughput whole-genome sequencing have enabled the creation of high-quality grass carp genomes, providing essential tools for molecular-assisted breeding. This research aims to identify genetic variants and regulatory pathways associated with growth traits through GWAS, transcriptomic profiling, and eQTL analysis, offering insights into the interaction between growth and digestion. These findings are expected to enhance breeding efficiency and support the development of grass carp with superior growth performance, boosting aquaculture productivity.

2. Materials and methods

2.1. Sample collection

In this study, we utilized an improved grass carp population as our experimental sample. This population was generated through gynogenesis, a process involving the activation of grass carp eggs with haploid sperm of koi carp under low-temperature conditions (0–4 °C), followed by hybridization with normal male grass carp (Wang et al., 2022). Following hatching, approximately 20,000 healthy grass carp (*Ctenopharyngodon idella*) were reared for six months (May to November) in an outdoor 20-mu pond (approximately 1.33 ha). The pond, located at the Buckwheat Lake Fish Research Institute in Yueyang, Hunan, China (coordinates: 28°57′42“ N, 112°55’42” E), was supplied with natural water sources. No supplemental feed was provided, and the fish relied entirely on the organisms within the water body to fulfill their nutritional requirements for growth. A total of 28 healthy grass carps were collected for this study. Growth-related traits, including body weight, body length, and body height, were measured for each individual. To collect tissues, all individuals were euthanized in a separate tank with 300 mg/L tricaine methanesulfonate (Sigma-Aldrich, St. Louis, MO, USA) for 10 min at 20 °C. Muscle and liver tissues were then carefully harvested using sterilized scissors and tweezers.

2.2. DNA isolation and whole genome sequencing

High-quality genomic DNA was extracted from the muscle tissue of 28 individuals using the QIAGEN® Genomic Kit, following the manufacturer’s instructions. The extracted DNA was assessed for degradation and contamination through gel electrophoresis on 1 % agarose gels. Additionally, DNA purity (260/280 and 260/230 ratios) and concentration were quantified using a NanoDrop™ One UV–Vis spectrophotometer (Thermo Fisher Scientific, USA) and a Qubit® 4.0 Fluorometer (Invitrogen, USA), respectively.

Whole-genome resequencing was conducted on the genomic DNA of all 28 individuals. High-quality DNA samples were used to prepare single-stranded circular libraries. These libraries were then transformed into DNA nanoballs (DNBs), each containing millions of copies of the circular DNA template. The DNBs were loaded onto patterned nanoarrays for combinatorial probe anchor synthesis sequencing. Finally, DNBSEQ-T7 sequencing was performed using a paired-end 150 bp × 2 read length following the manufacturer’s protocol. Adapter sequences and low-quality bases were filtered from the reads using Fastp (v. 0.23.4) (Chen et al., 2018) before assembly.

2.3. SNP calling

For whole-genome sequencing data, clean paired-end reads aligned to the genome file of grass carp (GCF_019924925.1 in NCBI database) using bwa (v. 0.7.18) (Li and Durbin, 2010). Aligned reads were converted to BAM format using SAMtools (v. 1.16) (Li et al., 2009), and duplicate reads were marked with the MarkDuplicates method of Picard (v. 3.1.1) (http://broadinstitute.github.io/picard). Next, HaplotypeCaller, CombineGVCFs, GenotypeGVCFs, SelectVariants, and VariantFiltration in the Genome Analysis Toolkit (GATK, v. 4.1.6.0) (McKenna et al., 2010) pipeline were used to call, filter, and select single nucleotide polymorphisms (SNPs) and small insertions and deletions (InDels). Subsequently, SNPs and InDels were separated using VCFtools (v. 0.1.16) (Danecek et al., 2011). To ensure SNP locus reliability, we applied stringent quality filters, excluding SNPs with any of the following criteria: Quality Depth (QD) < 2.0, Fisher strand bias (FS) > 60.0, Mapping Quality (MQ) < 45.0, Read Position Rank Sum < -8.0, Mapping Quality Rank Sum < -12.5, Minor Allele Frequency (MAF) < 0.05, and Missing Rate > 0.2. The remaining high-quality SNPs were used for subsequent analysis.

2.4. Genome-wide association study

Prior to conducting GWAS, population structure was assessed to evaluate potential genetic relatedness within the grass carp population. PLINK (v. 1.90b6.10) (Purcell et al., 2007) was employed to perform principal component analysis (PCA), and the resulting population structure was visualized using a scatter plot generated by the ggplot2 package (Ito and Murphy, 2013). The first two principal components (PC1 and PC2) were utilized as the primary axes for this visualization. A genome-wide association study (GWAS) was conducted to identify genes associated with three growth traits (body weight, length, and height) in the grass carp population. To mitigate population stratification, principal component (PC) and kinship matrix analyses were performed. The first three PCs were incorporated into the GWAS model as covariates. GWAS was conducted using PLINK (v. 1.90b6.10). A significance threshold of $-\log_{10}(P) = 6$ was determined based on the effective number of independent SNPs. Manhattan and quantile-quantile (QQ) plots were generated to visualize association signals and assess data quality. To elucidate the biological functions of identified genes, GO term enrichment analysis was performed. Enriched GO terms (p-value ≤ 0.001) were identified, providing insights into the biological pathways underlying growth trait variation.

2.5. RNA isolation and library preparation

Total RNA was extracted from the liver and muscle tissues of 28 grass carp individuals using the TRIzol method (Rio et al., 2010), respectively. RNA quality and quantity were assessed using NanoDrop technology and a Bioanalyzer system, respectively. DNase I treatment was performed to remove genomic DNA contamination. The purified RNA was then quantified using a 2100 Bioanalyzer system (Agilent, Santa Clara, CA, USA). The purified RNA was then used to construct sequencing libraries using the MGI Library Prep Kits. DNBSEQ-T7 technology was employed for transcriptome sequencing. The library preparation process involved single-stranded circular library preparation, combinatorial probe anchor sequencing, high-resolution imaging, digital processing, and

sequencing (Patterson et al., 2019). Low-quality bases and adapter sequences were filtered from the raw reads using Fastp (v. 0.23.4) (Chen et al., 2018).

2.6. Gene expression analysis

Clean reads from 56 samples were mapped to the genome file of grass carp using bowtie2 (v. 2.3.5.1) (Langmead et al., 2009) with default parameters, respectively. Mapped reads were processed with SAMtools (v. 1.10) to obtain uniquely mapped reads, which were then quantified using htseq-count (v. 0.12.4) (Srinivasan et al., 2020). Genes with less than five mapped reads in any sample were excluded. Following this filtering step, gene expression values for mRNA-seq were normalized and calculated as transcripts per million (TPM) for subsequent analyses.

2.7. Weighted gene correlation network analysis (WGCNA) and functional annotation

A weighted gene co-expression network analysis (WGCNA) was performed using the WGCNA R package (v. 1.71) (Langfelder and Horvath, 2008) on the standardized gene expression matrix. A soft-thresholding power of 2 was selected, and the network was constructed in a blockwise manner using the blockwiseModules function. The resulting adjacency matrix was transformed into a topological overlap matrix (TOM), and hierarchical clustering based on the TOM was used to identify gene modules with similar expression profiles. A minimum module size of 30 genes was set. To identify gene modules associated with the three phenotypes, the correlation between each module and the phenotypes was calculated. Modules with significant correlations (p-value $\leq$0.01) were selected. Furthermore, hub genes within each module were identified based on their module membership ($|MM| > 0.8$, p-value $\leq$0.01) and gene significance ($|GS| > 0.6$, p-value $\leq$0.01). Functional enrichments were conducted and annotated with GO and KEGG databases.

2.8. eQTL analysis

We conducted expression quantitative trait loci (eQTL) analysis using the R package Matrix eQTL (v. 2.3) (Shabalin, 2012) to examine associations between single nucleotide polymorphisms (SNPs) and gene expression. *Cis*-eQTLs were defined as SNPs located within 1 Mb upstream of the transcription start site (TSS) and 1 Mb downstream of the gene end (Liu et al., 2020). *Trans*-eQTLs were identified as SNPs situated more than 5 Mb from the gene (Vosa et al., 2021). In liver tissue, we applied a significance threshold of FDR $\leq$ 0.01, corresponding to p-value $\leq$3.87exp(−6) for *cis*-eQTLs and p-value $\leq$5.69exp(−8) for *trans*-eQTLs. Similarly, in muscle tissue, we used an FDR $\leq$ 0.01, equating to p-value $\leq$2.86exp(−6) for *cis*-eQTLs and p-value $\leq$6.64exp(−8) for *trans*-eQTLs.

3. Results

3.1. Sample and growth traits

To explore the diversity of growth traits, we crossed gynogenetic female grass carp with wild-type male grass carp, generating a new population with a wide range of growth phenotypic variation (Fig. 1). To understand the genetic mechanisms underlying the growth phenotypes of the improved grass carp, we randomly selected 28 healthy improved grass carp (*Ctenopharyngodon idella*) from a 6-month-old population for phenotypic characterization. Three growth-related traits, body weight (BW), body length (BL), and body height (BH), were measured and recorded as phenotypic data (Table S1). The average values of BW, BL, and BH were 130.7 ± 137.5 g, 18.6 ± 5.3 cm, and 4.3 ± 1.1 cm, respectively (Table S2). Pearson correlation analysis revealed significant positive correlations among all pairs of the three growth-related traits (BW, BL, and BH), with correlation coefficients ranging from 0.920 to 0.964 (Table S3).

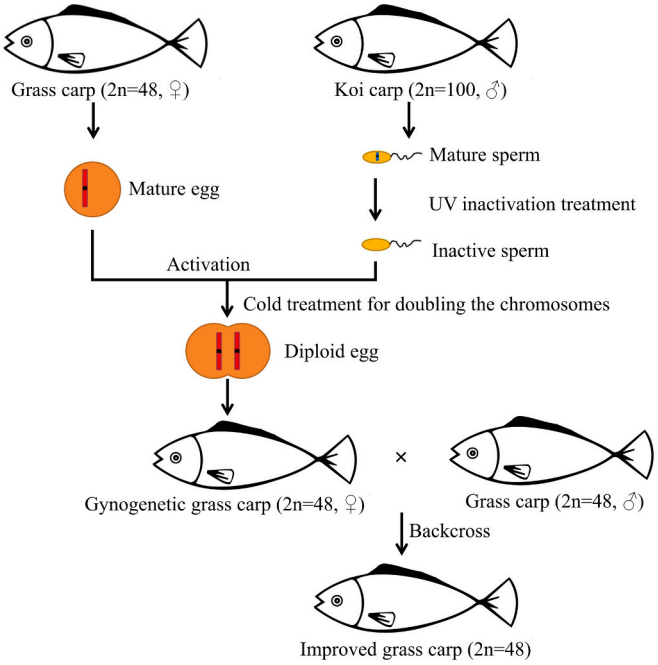

Fig. 1. Production processes of improved grass carp.

3.2. SNPs detection

For 28 individuals of the improved grass carp, 389.33 Gb clean data were obtained from whole-genome resequencing. The average sequencing depth of each sample was 15.40×, with the mapping rates ranging from 97.62 % to 98.32 % for all samples, and the genomic coverage varied from 86.99 % to 96.21 % (Table S4). After applying the stringent filtering criteria, a total of 399,876 high-quality SNPs were retained for subsequent analysis. The chromosome with the highest number of SNPs is chromosome 3, with a total of 26,025. Chromosome 23 has the fewest SNPs, totaling 11,434. There are 40,739 SNPs located in exonic regions, 190,671 in intronic regions, and 114,576 in intergenic regions. Exonic SNPs are predominantly located on chromosomes 1, 7, and 10, whereas intronic SNPs are mainly distributed on chromosomes 3, 7, and 10. In addition, SNPs located in intergenic regions are also significantly enriched on chromosomes 1, 3, and 7. The number of SNPs within the 100 Kb window size after filtering for each chromosome is shown in Fig. 2A.

3.3. Identification of growth-regulated SNPs and genes using GWAS

The PCA plot indicates the presence of some degree of population stratification within the grass carp population (Fig. S1). To identify genomic regions associated with growth traits in the improved grass carp, a GWAS analysis was conducted in the 399,876 SNPs. This analysis identified 649 significant SNPs ($-\log_{10}(p) \geq 6$) linked to three growth-related traits (Fig. 2B and Table S5). Of these, 406 SNPs were associated with body weight (BW), 229 with body length (BL), and 14 with body height (BH). For BW, 228 SNPs were located in coding regions, while 178 were in regulatory regions. For BL, 149 SNPs were within coding regions and 80 in regulatory regions. For BH, 13 SNPs were found in coding regions and one in a regulatory region. Notably, 8 SNPs showed significant associations with all three traits. Additionally, 8 SNPs were shared between BW and BH, and 12 were shared between BH and BL. A further 99 SNPs were jointly associated with BW and BL (Fig. 2C). A comparative analysis of growth-related SNPs identified in two published GWAS studies (Hao et al., 2023; Zhang et al., 2024) revealed that the SNPs associated with BW, BL, and BH in our study were distinct from those reported previously (Table S5 and Table S6).

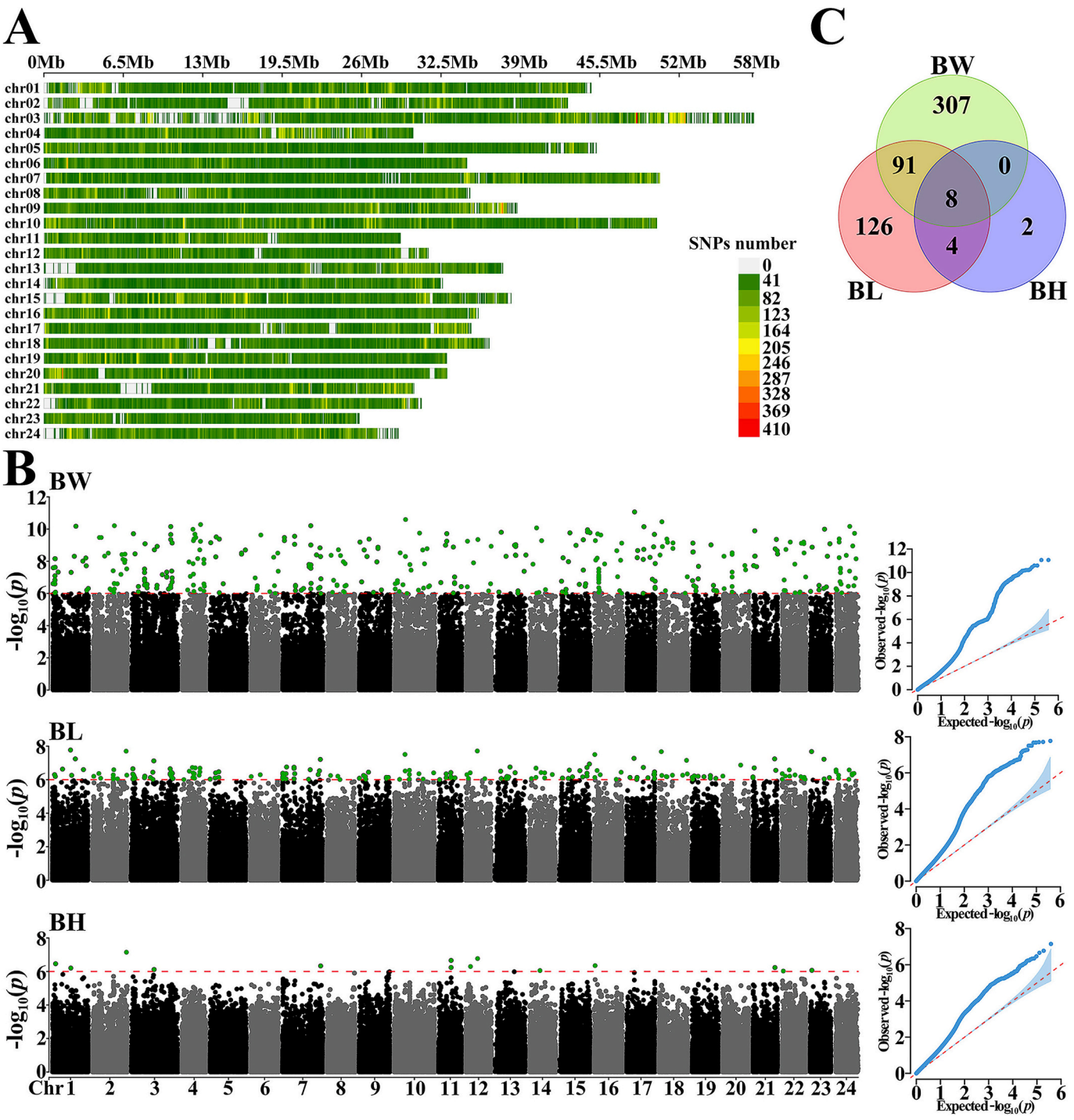

Fig. 2. Results of correlation analysis from the genome-wide association study (GWAS).
A. Density and distribution of the filtered SNPs for each chromosome in improved grass carp within 100 Kb window.
B. GWAS analysis of growth-related traits in improved grass carp. Manhattan and Quantile-Quantile (Q-Q) plots for body weight (BW), body length (BL), and body height (BH). The red dotted line indicates the significance threshold (6.0), and the significance SNPs are marked in green.
C. SNP distribution among BW and BL and BH. "BW" represents SNPs significantly associated with body weight; "BL" represents SNPs significantly associated with body length; "BH" represents SNPs significantly associated with body height. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Growth-regulated genes predicted based on WGCNA

Using transcriptomic data from the liver and muscle of the same individual, we conducted weighted gene co-expression network analysis (WGCNA) on both tissues simultaneously. This integrated approach enabled the identification of potential regulatory genes associated with growth-related phenotypic changes in both the liver and muscle. By combining gene expression datasets from the two tissues, we performed WGCNA and linked the resulting gene modules to growth phenotypes.

We obtained 231.11Gb of clean data from the liver and 266.15 Gb of clean data from the muscle of 28 individuals (Table S7 and Table S8). After mapping to the reference genome, 2,835,796,754 mapped reads

were obtained across the 56 samples, with an average mapping ratio of 88.68 %. Following gene expression quantification, we conducted WGCNA analyses using the merged gene expression data from liver and muscle tissues. After filtering with a significance threshold (p-value $\leq$0.01), eight modules were identified as associated with the three growth phenotypes, encompassing 10,650 genes from the liver and 9065 genes from the muscle. Body weight was associated with the modules MEbrown, MEroyalblue, MEgreen, and MEplum2. Body length was linked to MEbrown, MEroyalblue, MEdarkorange, and MEplum2, while body height was connected to MEturquoise, MEbrown, MEwhite, MEtan, MEroyalblue, MEdarkorange, MEgreen, and MEplum2 (Fig. 3A). For instance, the MEroyalblue module contained 109 genes expressed in the liver and 142 in the muscle, whereas the MEbrown module included 229 liver-expressed genes and 2217 muscle-expressed genes (Table S9).

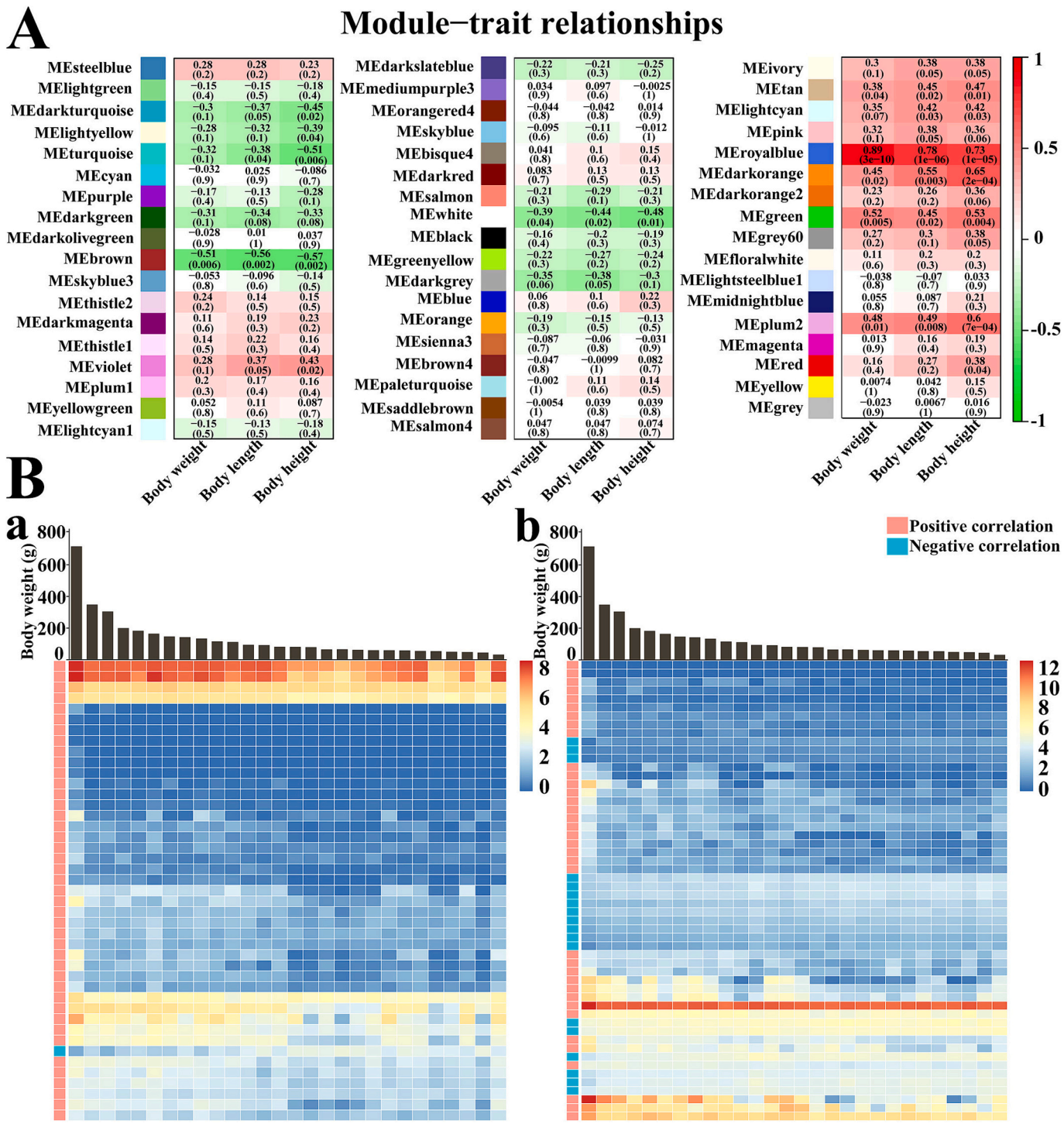

Fig. 3. Correlation analysis results from the weighted gene co-expression network analysis (WGCNA).
A. Heatmap of the correlation between modules and three growth traits.
B. Expression levels of the 97 growth-regulated genes and body weight in 28 improved grass carp. a. Expression levels of 43 genes originating from the liver, which are associated with growth phenotype. b. Expression levels of 54 genes originating from the muscle, which are associated with growth phenotype. "Positive correlation" represents the genes are positively correlated with body weight; "Negative correlation" represents the genes are negatively correlated with body weight.

43 hub genes in liver and 54 in muscle were identified as shared key regulators of the three growth traits (Fig. 3B and Table S10).

3.5. Cooperative regulation of growth phenotype by genes in liver and muscle

To understand the genetic mechanisms underlying digestion, metabolism, and growth in the improved grass carp, we aimed to identify genes that are co-regulated in the liver and muscle and potentially influence growth phenotypes. To explore this mechanism, we conducted further analysis of genes within the eight modules identified in the previous study. KEGG enrichment analysis of the genes within these eight modules identified growth-related pathways, including the carbon metabolism, mTOR signaling pathway, and regulation of the actin cytoskeleton (Fig. 4). Based on KEGG pathway analysis, we focused on three metabolic pathways closely related to growth phenotypes: the mTOR, insulin, and TGF-beta signaling pathways. We examined the distribution of liver-expressed and muscle-expressed genes within these three pathways under the same module framework (Table S11).

Subsequently, by specifically analyzing extracellular liver-expressed genes and intracellular muscle-expressed genes, we identified three liver-expressed genes (*igf1*, *wnt1*, and *wnt9b*) and four muscle-expressed genes (*igf1ra*, *igf1rb*, *fzd1*, and *fzd9b*) in the mTOR pathway. Interestingly, *igf1*, a key component of the GH/IGF-1 axis, has been extensively reported to be transcribed in the liver and transported via the bloodstream to other tissues or organs. There, it binds to transmembrane proteins such as *igf1ra* and *igf1rb* in muscle, playing a crucial role in regulating individual growth (Weil et al., 2011). Our findings further suggest that liver-derived products of *wnt1* and *wnt9b* may interact with *fzd1* and *fzd9b* on the muscle cell membrane, indicating a coordinated regulatory effect on growth phenotypes (Fig. 5).

3.6. eQTL analysis in liver and muscle

Through eQTL analysis, we aim to better understand how specific SNPs regulate gene expression via *cis*- and *trans*-regulatory mechanisms and how these regulatory effects contribute to the growth phenotype of the improved grass carp.

In the liver, eQTL analysis identified 4111 *cis*-eQTL events, with 3766 SNPs exhibiting *cis*-regulatory effects on 913 genes (*cis*-genes). Additionally, 402,068 *trans*-eQTL events were uncovered, where 44,828 SNPs showed *trans*-regulatory effects on 1983 genes (*trans*-genes). In the muscle, 3078 *cis*-eQTL events were identified, with 2775 SNPs

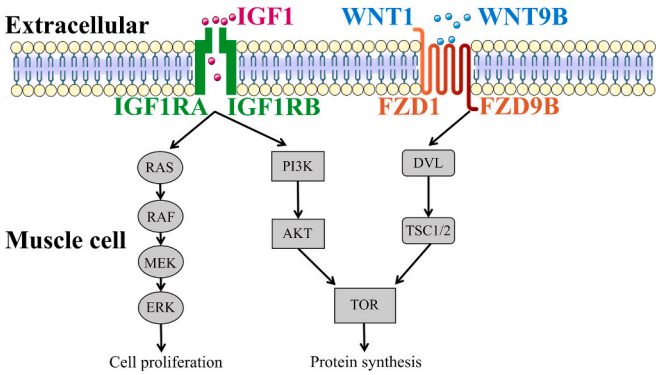

Fig. 5. Schematic diagram of the mTOR pathway showing how extracellular signals bind to muscle cell surface receptors to regulate protein synthesis and cell proliferation. IGF1 binds to IGF1RA and IGF1RB, regulating protein synthesis and cell proliferation through the PI3K/AKT pathway and MAPK signaling pathway. WNT1 and WNT9B binds to FZD1 and FZD9B, regulating protein synthesis through the DVL/TSC1/2 pathway.

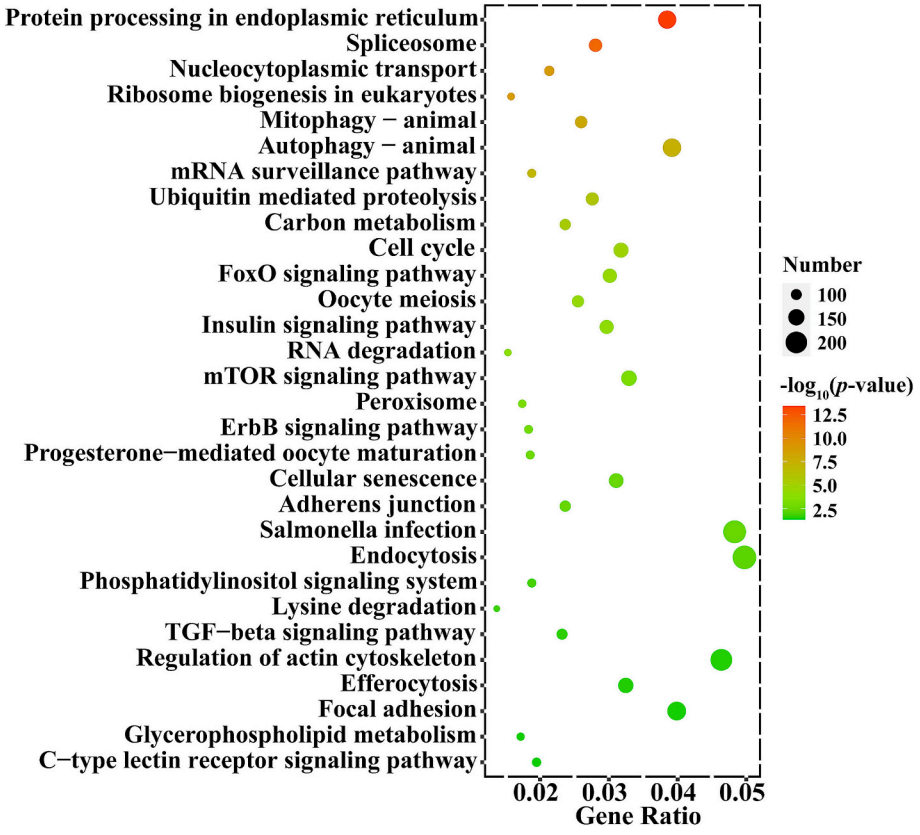

Fig. 4. Top 30 enriched KEGG pathways from the analysis of genes in eight significant WGCNA modules.

regulating 845 genes (*cis*-genes). Furthermore, 317,815 *trans*-eQTL events were observed, where 39,256 SNPs were linked to the regulation of 3100 genes (*trans*-genes) (Table S12).

By integrating the results from eQTL and WGCNA analyses, we identified 17 growth-related genes in the liver regulated by *cis*-acting mechanisms and 20 by *trans*-acting mechanisms. Similarly, in muscle tissue, 28 growth-related genes were regulated through *cis*-regulation and 30 through *trans*-regulation. These findings provide valuable insights into the role of inter-tissue coordination in regulating growth phenotypes, which contribute to the growth traits in the improved grass carp. However, further experimental validation is needed to confirm these results.

4. Discussion

This study investigated the genetic basis of growth in a unique grass carp population derived from backcrossing gynogenetic individuals with wild-type grass carp (Wang et al., 2022). Gynogenesis, a form of artificial reproduction, produces highly homozygous offspring, facilitating the identification of recessive deleterious genes and accelerating selective breeding (Manan et al., 2022; Zhang et al., 2011). This backcrossed population represents a valuable resource for dissecting the genetic architecture of growth in grass carp.

Using whole-genome resequencing and joint muscle and liver transcriptome analysis, we identified 538 additional growth-associated SNPs through GWAS, complementing previous findings in other grass carp populations (Hao et al., 2023; Zhang et al., 2024) and contributing to a more comprehensive understanding of growth traits. Our multi-tissue transcriptome analysis revealed co-regulated genes in liver and muscle, including members of the IGF family, which are known to play crucial roles in growth regulation in various species (Duan et al., 2010; Xu et al., 2019). Furthermore, WGCNA identified additional co-expressed gene modules in both tissues that are significantly correlated with growth phenotypes. These findings pinpoint candidate genes for future functional validation and offer promising targets for marker-assisted selection.

Grass carp is a major aquaculture species in China, and its herbivorous diet is intrinsically linked to its growth performance (Wang et al., 2015). While previous studies have investigated various aspects of growth, including feeding, digestion, and metabolism (Moraes and de Almeida, 2020), a systems-level understanding of their interconnectedness is still lacking. Our study, focusing on the liver and muscle, provides initial insights into potential co-regulatory mechanisms underlying growth. Future research integrating multi-omics approaches and functional studies will be essential to fully elucidate the complex molecular networks controlling growth in grass carp and ultimately inform the development of more effective breeding strategies (Wörheide et al., 2021).

Animal ethics declarations

All procedures performed on animal were approved by the academic committee in Hunan Normal University, Hunan, China.

CRediT authorship contribution statement

Yakui Tai: Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation. **Ling Liu:** Validation, Methodology. **Yiyan Zeng:** Validation, Methodology. **Mengdan Li:** Validation, Methodology. **Mengxue Luo:** Validation, Methodology. **Wuhui Li:** Validation, Methodology. **Hailu Zhou:** Validation. **Jinhui Zhang:** Validation. **Xiaohuan Han:** Validation. **Conghui Yang:** Validation. **Ming Wen:** Validation. **Li Ren:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization. **Qinbo Qin:** Supervision, Project administration, Funding acquisition, Conceptualization. **Shaojun Liu:** Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2025.742393.

Data availability

Whole genome resequencing data have been submitted to the National Genomics Data Center (NGDC) under the BioProject PRJCA029697 (https://ngdc.cncb.ac.cn/bioproject/browse/PRJCA029697) with accession number CRA018699. The mRNA-seq data have been submitted to NGDC under the BioProject PRJCA029697 (https://ngdc.cncb.ac.cn/bioproject/browse/PRJCA029697) with acce ssion number CRA018700.

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