Whole-Genome Sequence Analysis of Four Culm-Variant Forms of Phyllostachys edulis (Postprint)

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Abstract

Moso bamboo is an important economic bamboo species in China that has generated rich variations during long-term cultivation and adaptation. To reveal the whole-genome mutation types of bamboo culm variation forms in Moso bamboo, four Moso bamboo variants—yellow-skin Moso bamboo, golden-thread Moso bamboo, green-skin flower Moso bamboo, and flower Moso bamboo—were used as experimental materials. High-throughput resequencing technology was employed to obtain whole-genome sequences for detection and annotation of single nucleotide polymorphisms (SNPs), small insertions/deletions (InDels), and structural variations (SVs), and variant genes were functionally annotated. The results showed that the flower Moso bamboo genome exhibited the highest number of gene variants at 12,555, while the golden-thread Moso bamboo sample had the fewest variant sites at 11,923. All four samples had more than 7,000 variant genes that received functional annotation. GO annotation classification included 56 functional groups across three gene functional classification systems: cellular component, molecular function, and biological process. In terms of cellular component, there were 2,431 genes related to chlorophyll synthesis; in biological process, 75 genes participated in carotenoid synthesis, and 80 genes were involved in anthocyanin synthesis regulation and anthocyanin accumulation in tissues under UV light. COG classification indicated 369 genes involved in replication, recombination, and repair, 291 genes for signal transduction mechanisms, and 222 genes related to transcription. The KEGG database was used to systematically analyze the metabolic and biosynthetic pathways of flavonoids, carotenoids, and other substances in which variant genes participate. In-depth study of the regulatory pathways of these differential genes to explain the variation mechanism of bamboo culms at the DNA level can provide data support for in-depth research on the rich intraspecific polymorphism and genetic variation of Moso bamboo, and elucidate the genetic basis of gene families, functional genes, and other genetic elements for different variation types.

Full Text

Genomic Sequence Analysis of Four Culm Variants of Moso Bamboo (Phyllostachys edulis)

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Abstract

Moso bamboo is an important economic bamboo species in China that has generated rich variations during long-term cultivation and adaptation. To reveal the genome-wide mutation types in culm-variant forms of Moso bamboo, we conducted high-throughput whole-genome resequencing on four representative variants: Phyllostachys edulis f. holochrysa, P. edulis f. gracilis, P. edulis f. nabeshimana, and P. edulis f. huamozhu. We detected and annotated single nucleotide polymorphisms (SNPs), small insertions and deletions (InDels), and structural variations (SVs), and performed functional annotation of the variant genes. The results showed that P. edulis f. huamozhu exhibited the highest number of gene variations (12,555), while P. edulis f. gracilis had the fewest variant sites (11,923). More than 7,000 variant genes were functionally annotated in each of the four samples. GO annotation classification encompassed 56 functional groups across three gene ontology systems: cellular component, molecular function, and biological process. In the cellular component category, 2,431 genes were related to chlorophyll synthesis. In biological processes, 75 genes participated in carotenoid synthesis, while 80 genes were involved in anthocyanin synthesis regulation and anthocyanin accumulation in tissues under ultraviolet light. COG classification revealed 369 genes involved in replication, recombination, and repair; 291 genes in signal transduction mechanisms; and 222 genes in transcription. KEGG database analysis systematically examined the metabolic pathways of flavonoids, carotenoids, and other substances involving variant genes. In-depth investigation of these differential gene regulatory pathways, and interpretation of culm variation mechanisms at the DNA level, can provide data support for further exploration of rich intraspecific polymorphism and genetic variation in Moso bamboo, and elucidate the genetic basis of gene families and functional genes underlying different variation types.

Keywords: Moso bamboo (Phyllostachys edulis), variant, whole genome resequencing, gene annotation

Introduction

Moso bamboo (*Phyllostachys edulis*) is a unique traditional economic bamboo species in China with extensive distribution, and over 20 variants have been documented. These variants exhibit rich morphological polymorphism, particularly in culm color traits. For example, *P. edulis* f. *huamozhu* has yellow culms with

green longitudinal stripes of varying widths, while *P. edulis* f. *nabeshimana* has green culms with thin light-yellow longitudinal stripes. Such color variations greatly enrich ornamental varieties and enhance landscape aesthetic value. Genetic variation in Moso bamboo culm traits represents a key focus for breeding programs.

High-throughput sequencing technology enables comprehensive genome-wide analysis and has been widely applied in plants including foxtail millet, rice, soybean, okra, *Magnolia officinalis*, common bean, and tomato. In recent years, with advances in molecular biology and omics technologies, the Moso bamboo genome has been published, and several trait-related gene families—including AP2/ERF, SAUR, AQP, SBP-like, HD-Zip, Hsp, and CO-Like—have been identified and functionally validated. However, genome-level studies remain limited, particularly regarding culm color variation in Moso bamboo variants. Only preliminary explorations of genome sequence variation have been conducted for two variants (*P. edulis* f. *luteosulcata* and *P. edulis* f. *holochrysa*), which has constrained the application and development of genetic breeding in Moso bamboo.

Revealing the extent of genetic variation at the DNA level is crucial for analyzing the causes of morphological differences among Moso bamboo variants. Therefore, conducting genomic research on Moso bamboo variants to uncover genome-wide mutation types and investigate genes related to metabolic pathways such as flavonoid synthesis and nitrate reductase is essential for parsing the rich genetic diversity and trait-related genetic variation in this species. This study selected four representative culm-color variants of Moso bamboo as research subjects, using the Moso bamboo genome as a reference. Through high-throughput sequencing technology, we constructed a whole-genome database, performed bioinformatic assembly of obtained nucleotide sequences, detected and annotated SNPs, SVs, and InDels, and annotated variant gene functions to accumulate genomic sequence data. This work provides a foundation for in-depth analysis of genetic variation at the whole-genome level and offers a genetic basis for breeding applications.

Materials and Methods

1.1 Plant Materials

Experimental materials were selected from the germplasm resource nursery at the Anhui Taiping Experimental Center of the International Center for Bamboo and Rattan. Fresh young leaves were collected from four Moso bamboo variants (Table 1), snap-frozen in liquid nitrogen, and stored at -80°C.

Table 1 Brief introduction of four Moso bamboo variants

ID	Latin Name	Morphological Characteristics
R01	*Phyllostachys edulis* f. *holochrysa*	Culms and branches golden yellow
R02	*P. edulis* f. *gracilis*	Short height, thick culm walls, longer basal internodes
R03	*P. edulis* f. *nabeshimana*	Culms green, internodes with light yellow strips
R04	*Phyllostachys edulis* f. *huamozhu*	Culms yellow with green strips

1.2 Experimental Methods

1.2.1 Genome Sequencing DNA was extracted from leaves of Moso bamboo variants using the method described by Zidani et al. (2005). After fragmentation, damage repair, adapter ligation, PCR enrichment, and library quality assessment, sequencing libraries were constructed and run on the Illumina HiSeq 2500 platform to obtain raw data, which was filtered to generate high-quality clean data.

1.2.2 Alignment and Statistics Clean reads were aligned to the sequenced Moso bamboo genome using BWA software (Li & Durbin, 2009). Sequencing depth, genome coverage, and other information were statistically analyzed.

1.2.3 Detection of SNPs, InDels, and SVs After duplicate removal using Picard software (Gordon et al., 2012) and preprocessing with GATK software (McKenna et al., 2010), SNP and InDel variants were detected. SV variants were detected using BreakDancer software (Chen et al., 2009), following the methodology described in Mou et al. (2020).

1.2.4 Annotation of SNPs, InDels, and SVs SNP, InDel, and SV annotations were performed using SnpEff software (Cingolani et al., 2012), following the methodology described in Mou et al. (2020).

1.2.5 Functional Gene Annotation Using BLAST software, gene sequences of potentially functionally variant genes were compared against three major functional databases—GO (Ashburner et al., 2000), COG (Tatusov et al., 2000), and KEGG (Minoru et al., 2004)—to obtain gene annotations.

Results

2.1 Alignment to the Moso Bamboo Genome

High-throughput sequencing generated data for all four bamboo variants. *P. edulis* f. *gracilis* (R02) yielded the fewest clean reads (82,276,884 bp), while *P. edulis* f. *huamozhu* (R04) yielded the most (112,054,728 bp). The percentage of

reads mapped to the Moso bamboo reference genome exceeded 99.45% for all samples, and the percentage of properly paired reads mapped to the reference genome at expected distances was approximately 88%, indicating appropriate reference genome selection and absence of contamination in experimental procedures. The mapping rate was higher than 70%, suggesting close phylogenetic relationships between the four variants and the reference genome, high-quality genome assembly, and high read sequencing quality. The average coverage depth for all four samples was approximately 10× (Table 2).

Table 2 Output statistics among four samples

Sample	Clean_{reads}(%)	Mapped_{ratio}(%)	properly_{mapped_ratio}(%)	Average_{depth}	Coverage_{1X}_{ratio}(%)	Coverage_{5X}_{ratio}(%)	Coverage_{10X}(%)

2.2 SNP Analysis

2.2.1 SNP Detection SNP loci statistics for the four Moso bamboo samples are presented in Table 3 . *P. edulis* f. *huamozhu* (R04) exhibited the highest number of SNPs (1,691,715), while *P. edulis* f. *nabeshimana* (R03) had the fewest (1,534,648). Across all four samples, the transition/transversion (Ti/Tv) ratio ranged from 3.05 to 3.10, indicating that transitions occurred more readily than transversions. Heterozygous SNP numbers were approximately 10 times higher than homozygous SNPs, with heterozygosity rates ranging from 88.53% to 92.01%. *P. edulis* f. *huamozhu* (R04) showed the highest heterozygosity rate (92.01%), while *P. edulis* f. *nabeshimana* (R03) showed the lowest (88.53%).

Table 3 SNP loci statistics in four samples

Sample	Transition	Transversion	Ti/Tv	Het-ratio

Based on alignment results between the four Moso bamboo samples and the reference genome, pairwise SNP statistics are summarized in Table 4 , with values representing SNP numbers between corresponding samples. The highest number of SNPs was observed between *P. edulis* f. *gracilis* (R02) and *P. edulis* f. *nabeshimana* (R03).

Table 4 Summary of SNPs detected between four samples

ID	R01	R02	R03	R04

2.2.2 SNP Annotation SNP annotation for the four samples identified variant locations and types (Figure 1 [Figure 1: see original paper]). Across all four Moso bamboo variants, approximately 2% of SNPs occurred within CDS regions,

with synonymous mutations accounting for about 48% and non-synonymous mutations for about 51%. A non-synonymous/synonymous mutation ratio greater than 1 suggests positive selection effects.

Figure 1 SNP annotations pie of *Phyllostachys edulis* f. *holochrysa* (R01)

2.3 InDel Analysis

2.3.1 InDel Detection InDel statistics for the four Moso bamboo variants (Table 5) revealed that total InDels detected genome-wide ranged from 271,648 to 292,253, with insertion mutations slightly fewer than deletion mutations. In coding regions, total InDels ranged from 4,711 to 4,877, with insertion mutations accounting for approximately 67% of deletion mutations. Genome-wide, homozygous mutations were about twice as frequent as heterozygous mutations, while in coding regions, homozygous mutations were slightly less frequent than heterozygous mutations.

Table 5 Summary of InDels detected in four samples

Sample | Genome (Insertion/Deletion/Total) | CDS (Insertion/Deletion/Total) |

Analysis of InDel lengths across different regions revealed that coding regions contained more +1, -1, +3, and -3 mutations, while the genome-wide range showed more +1, -1, +2, and -2 mutations (values represent InDel lengths within 10 bp; positive values indicate insertions, negative values indicate deletions).

Pairwise InDel comparisons among the four samples are summarized in Table 6 , with values representing InDel numbers between corresponding samples.

Table 6 Summary of InDels detected between variants of Moso bamboo

ID	R01	R02	R03	R04

2.3.2 InDel Annotation Based on gene and CDS position information from the Moso bamboo reference genome, InDel locations and frameshift mutations were annotated (Figure 2 [Figure 2: see original paper]). Approximately 1.7% of InDels occurred in coding regions across all four Moso bamboo variants. Frameshift InDels may cause alterations in gene function.

Figure 2 InDel annotations pie of *Phyllostachys edulis* f. *holochrysa* (R01)

2.4 SV Analysis

2.4.1 SV Detection Detection of insertions (INS), deletions (DEL), inversions (INV), intra-chromosomal translocations (ITX), and inter-chromosomal translocations (CTX) between the four samples and the reference genome revealed that deletion-type SVs were most abundant across all four Moso bamboo variants, followed by intra-chromosomal translocation types (Table 7).

Table 7 Summary of SVs detected in four samples

Sample | Insertion | Deletion | Inversion | Internal chromosomal translocation | Translocation between chromosomes | Total |

2.4.2 SV Annotation SV location information was detected for all samples, and annotations for three SV types—deletion (DEL), insertion (INS), and inversion (INV)—were performed. The results (Table 8) indicated consistent SV distribution patterns across all four Moso bamboo variants, with the highest number of variant genes annotated in intergenic regions, particularly for deletion types, followed by insertion types.

Table 8 SV annotations in four variants of Moso bamboo

Region	Deletion	Insertion	Inversion
Exon			
Intron			
Intergenic			

2.5 Functional Annotation and Analysis of Variant Genes

2.5.1 Variant Gene Mining Genes with non-synonymous SNPs and InDels/SVs occurring in CDS regions were statistically analyzed for all four samples (Table 9) to identify potentially functionally variant genes. *P. edulis* f. *huamozhu* (R04) exhibited the highest number of gene variations (12,555), including 5,563 genes with non-synonymous SNPs, 4,006 genes with InDels, and 2,986 genes with SVs, showing the highest totals for both overall differential genes and SV-mutated genes. Among the three variant types, non-synonymous SNP genes were most abundant, followed by InDel genes, with SV-mutated genes being the least common.

Table 9 Summary of gene variations in four variants

Sample | Genes with Non-synonymous SNP | Genes with InDel | Genes with SV | Total |

2.5.2 Functional Annotation of Variant Genes Variant gene numbers annotated in databases for *P. edulis* f. *holochrysa*, *P. edulis* f. *gracilis*, *P. edulis* f. *nabeshimana*, and *P. edulis* f. *huamozhu* were 7,575, 7,538, 7,476, and 7,728, respectively. GO classification results (Figure 3 [Figure 3: see original paper]) displayed gene numbers and percentages across 56 functional categories within the three major classification systems (molecular function, cellular component, and biological process). In the cellular component category, 2,431 genes were related to chlorophyll synthesis. In biological processes, 75 genes participated in carotenoid synthesis, and 80 genes were involved in anthocyanin synthesis regulation and accumulation under ultraviolet light. The four Moso bamboo

variants showed differences in variant gene numbers within specific functional categories. For instance, *P. edulis* f. *huamozhu* had 21 carotenoid synthesis-related genes, while *P. edulis* f. *nabeshimana* had 17 and *P. edulis* f. *holochrysa* had 18. These differences in gene number and type may cause corresponding functional changes. In-depth investigation of chlorophyll, carotenoid, and anthocyanin synthesis-related genes and their regulatory pathways facilitates interpretation of culm color variation at the DNA level.

Figure 3 Classification of *Phyllostachys edulis* f. *holochrysa* (R01) gene variations compared with GO database

COG annotation classification (Figure 4 [Figure 4: see original paper]) visually displayed frequencies across COG functional categories, with high values corresponding to functional annotation, transcription, replication/recombination/repair, and signal transduction mechanisms. A total of 1,630 genes received functional annotation, including 369 genes involved in replication, recombination, and repair; 291 genes in signal transduction mechanisms; and 222 genes in transcription.

Figure 4 Classification of *Phyllostachys edulis* f. *holochrysa* (R01) gene variations compared with COG database

KEGG database analysis systematically examined the functions of gene products from the four Moso bamboo variants in biological processes. Using the valine, leucine, and isoleucine biosynthesis pathway in *P. edulis* f. *holochrysa* (R01) as an example (Figure 5 [Figure 5: see original paper]), 57 genes were annotated in this pathway, including 23 variant genes. The entire pathway involves a series of biochemical reactions linked by different enzymes, where numbers within boxes represent enzyme codes and red boxes indicate pathway-related variant genes.

Figure 5 Pathway of *Phyllostachys edulis* f. *holochrysa* gene variations compared with KEGG database

Discussion

Whole-genome resequencing enables sequencing of different varieties based on known plant genome sequences, thereby identifying individual differences from the species (Ley et al., 2008). With the public release of the Moso bamboo genome sequence (Peng et al., 2013), investigating genomic sequence differences among Moso bamboo varieties or variants has become feasible. Whole-genome resequencing can detect complete individual genome sequences and scan for variation sites closely related to growth traits (Song et al., 2017). Moso bamboo has a monopodial rhizome system, and all its different variant types are scattered bamboos. Under the influence of genetic drift, long-term cultivation practices, and natural environmental changes, Moso bamboo has generated substantial intraspecific genetic variation, producing various unique structural forms and exhibiting rich ornamental traits. Specifically, *P. edulis* f. *holochrysa*, *P. edulis*

f. *huamozhu*, and *P. edulis* f. *nabeshimana* show varying degrees of culm color variation, enhancing their landscape ornamental value.

Whole-genome resequencing of the four Moso bamboo variants enabled preliminary statistical analysis of genomic data, alignment to the reference genome, and detection of SNPs, InDels, and SVs. SNP variations are classified as transitions or transversions, with Ti/Tv ratios around 3 for all four variants, indicating that transitions occur more readily than transversions. SNP heterozygosity rates of approximately 90% suggest high heterozygosity levels, meaning a high proportion of SNP loci on homologous chromosomes contain different base types. InDel numbers similarly reflect differences between samples and the Moso bamboo genome, and InDels in coding regions can cause frameshift mutations affecting gene function. SV numbers for deletion, insertion, inversion, and translocation types reflect large-scale sequence differences at the genome level. Bioinformatic analysis comparing structural differences among variants with different culm colors and performing differential annotation provides a genetic foundation for Moso bamboo breeding and offers valuable basis for functional studies of important genes.

Color variation is a common phenotypic variation in plants, with leaf color mutants reported in rice, *Arabidopsis*, chrysanthemum, and other species. According to incomplete statistics, more than 140 genes are associated with chloroplast content in rice (Zhao et al., 2018). Bamboo pigments are divided into three major categories: chlorophyll, anthocyanin, and carotenoid. Functional database comparison enabled annotation and analysis of variant genes from the four Moso bamboo variants. GO classification clustering reflected gene numbers and product properties across different functional group categories, with pigment synthesis-related genes associated with culm color variation—chlorophyll, carotenoid, and anthocyanin synthesis genes—analyzed as priority targets. COG classification annotated orthologous categories of gene products, with substantial differences in gene numbers across categories reflecting physiological or metabolic preferences under different conditions. KEGG database analysis organized genes and enzymes into pathways, with significant enrichment in amino acid biosynthesis, carotenoid biosynthesis, flavonoid biosynthesis, terpenoid biosynthesis, plant hormone signal transduction, and porphyrin and chlorophyll metabolism. Among these, pigment synthesis-related pathways for chloroplasts, carotenoids, and anthocyanins represent the primary metabolic pathways associated with culm color.

Integrating biological and physiological characteristics of different culm-color Moso bamboo variants with whole-genome sequence analysis of pigment synthesis-related genes facilitates interpretation of culm color variation causes at the genetic level. Studies have shown significant differences in physiological indicators such as chlorophyll content and β-carotene content among different Moso bamboo variants (Chen et al., 2011), with larger variants like *P. edulis* f. *huamozhu* showing higher physiological indicator values than smaller variants like tortoise-shell bamboo and green-sulcus bamboo (Yan, 2011). ISSR

and AFLP molecular marker analyses of Moso bamboo variants indicated relatively low genetic variation among variants (Ruan, 2008). Building upon previous research on two culm-color variants (*P. edulis* f. *luteosulcata* and *P. edulis* f. *holochrysa*) (Mou et al., 2020), this study performed whole-genome resequencing on four Moso bamboo variants including *P. edulis* f. *holochrysa*, enabling functional annotation of variant genes at the DNA level. This approach allows analysis of gene product metabolic pathways and functions in cells, particularly through in-depth analysis of flavonoid, carotenoid, and nitrate reductase synthesis pathways, providing important theoretical basis for revealing related metabolic pathway genes and offering significant insights for investigating culm color variation in Moso bamboo variants. Additionally, color variation is typically an unstable trait. For example, *P. edulis* f. *huamozhu* may revert to all-green or transform into *P. edulis* f. *nabeshimana* under different environmental conditions, suggesting that color variation in bamboo is not genetically stable. Therefore, exploring the molecular mechanisms of color variation involves considerable complexity, and its metabolic regulation requires further investigation.

Conclusion

Using second-generation high-throughput resequencing technology, we conducted whole-genome resequencing of four Moso bamboo variant materials, analyzing and annotating SNPs, InDels, and SVs to screen for genes with potential functional variations. Comparison of variant genes against functional databases (GO, COG, KEGG) yielded functional annotation for over 7,000 variant genes per sample. GO annotation classification encompassed 56 functional groups across three systems: cellular component, molecular function, and biological process. In cellular components, 2,431 genes were related to chlorophyll synthesis. In biological processes, 75 genes participated in carotenoid synthesis, and 80 genes were involved in anthocyanin synthesis regulation and tissue accumulation under ultraviolet light. COG classification identified 369 genes in replication, recombination, and repair; 291 genes in signal transduction mechanisms; and 222 genes in transcription. KEGG database analysis systematically examined metabolic synthesis pathways for flavonoids, carotenoids, and other substances involving variant genes. Subsequent in-depth data analysis will parse gene families and functions across different variant types, providing preliminary elucidation of the molecular genetic basis underlying different culm variations in Moso bamboo.

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Note: Figure translations are in progress. See original paper for figures.