

Bioinformatics Analysis of the Amylase Gene Family in *Millettia speciosa* Postprint

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Abstract

Studying the biological activity of the *Millettia speciosa* amylase gene family lays a foundation for revealing the growth and development patterns of *Millettia speciosa* and screening genes related to root thickening. Based on transcriptome sequencing results of non-thickened and thickened *Millettia speciosa* roots, this study employs bioinformatics techniques to analyze 28 screened *Millettia speciosa* amylase genes. The molecular weights of amino acid sequences encoded by these 28 *Millettia speciosa* amylase-related protein genes range from 20.78 KDa to 349.39 KDa; all are acidic proteins; subcellular localization is partially in chloroplasts; they possess PLN02784 super family and AmyAc-family super family domains. In the secondary structure, except for MsAm1, 7, 8, 15, 16, 22, 23, and 28 where α -helix occupies the largest proportion, random coil accounts for the highest proportion. Tertiary structure prediction reveals α -amylase structures, β -amylase structures, isoamylase structures, etc. The amylase gene family contains a total of 86 regulatory elements, with MsAm9 having the most (42 elements). Phylogenetic tree analysis indicates that MsAm15 and 16 belong to Class 1 and both possess motif 2, motif 3, and motif 7; MsAm4, 24, and 26 belong to Class 1. Comparison with *Arabidopsis thaliana* amylases shows that AtBM4 and MsAM6 cluster together, AtAM2 and MsAM2 cluster together, AtBM8 and MsAM5 cluster together, AtBM4 and MsAM6 cluster together, AtAM10 and MsAM22 cluster together, and AtIM3 and MsAM17 cluster together. These analytical results can provide a theoretical basis for future in-depth studies on the biological functions and regulatory mechanisms of the 28 *Millettia speciosa* amylases, and offer references for research on root thickening and variety improvement in *Millettia speciosa*.

Full Text

Preamble

Bioinformatics Analysis of the Amylase Gene Family in *Millettia speciosa*

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Abstract

This study investigates the biological activity of the amylase gene family in *Millettia speciosa* to establish a foundation for elucidating its growth and development patterns and screening genes associated with root enlargement. Based on transcriptome sequencing data from both enlarged and non-enlarged roots of *M. speciosa*, we conducted a comprehensive bioinformatics analysis of 28 amylase genes. The amino acid sequences encoded by these 28 amylase-related protein genes exhibited molecular weights ranging from 20.78 kDa to 349.39 kDa. All identified proteins were acidic, with partial subcellular localization in chloroplasts, and contained conserved domains including PLN02784 superfamily and AmyAc-family superfamily. In the secondary structure, random coils predominated except in MsAm1, 7, 8, 15, 16, 22, 23, and 28, where α -helices were most abundant. Tertiary structure prediction revealed α -amylase, β -amylase, and isoamylase configurations. The amylase gene family contained 86 regulatory elements in total, with MsAm9 possessing the most (42 elements). Phylogenetic analysis demonstrated that MsAm15 and 16 clustered into one class, both containing motif 2, motif 3, and motif 7, while MsAm4, 24, and 26 formed another distinct class. Comparative analysis with *Arabidopsis thaliana* amylases revealed that AtBM4 grouped with MsAM6, AtAM2 with MsAM2, AtBM8 with MsAM5, AtAM10 with MsAM22, and AtIM3 with MsAM17. These findings provide a theoretical framework for future investigations into the biological functions and regulatory mechanisms of these 28 *M. speciosa* amylases, offering valuable references for studies on root enlargement and variety improvement.

Keywords: *Millettia speciosa*, transcriptome, amylase gene family, physicochemical characteristics

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Introduction

Millettia speciosa, belonging to the Fabaceae family, Papilionoideae subfamily, and *Millettia* genus, is a dried root used in traditional medicine. With a sweet taste and neutral properties, it tonifies deficiency, moistens the lungs, and strengthens tendons and joints, demonstrating clinical efficacy against chronic conditions including lumbar muscle strain, rheumatoid arthritis, tuberculosis, and chronic bronchitis (National Compilation Group of Chinese Herbal Medicines, 1986). The plant is primarily distributed in Fujian, Hunan, Guangdong, Guangxi, Hainan, and Guizhou provinces, serving as a renowned bone-strengthening and tendon-reinforcing herb in Guangdong and Guangxi regions. It is commonly used in medicinal diets and medicinal wines (Nanjing University of Traditional Chinese Medicine, 2005; Food and Drug Administration of Guangdong, 2004; Department of Health of Guangxi Zhuang Autonomous Region, 1992; Wei et al., 2010; Liu et al., 2009; Wei et al., 2009), establishing it as a prominent medicinal and edible plant in Lingnan area.

Modern experimental studies have demonstrated that *M. speciosa* enhances immune function, protects the liver, exhibits expectorant, antitussive, and anti-asthmatic effects, and possesses antioxidant, anti-inflammatory, and anti-tumor properties (Zheng et al., 2008; Shi et al., 2008; Luo et al., 2014; Huang et al., 2014; Zhou et al., 2009; Chen et al., 2014; Wang et al., 2013). With increasing development and utilization, demand for fresh *M. speciosa* in medicinal diets has grown rapidly, driving continuous price increases. In 1999, dried *M. speciosa* was purchased at 5–6 yuan/kg at production sites. By 2007, fresh roots com-

manded 20 yuan/kg, and by 2012, premium quality fresh roots reached 80–100 yuan/kg, yet bulk supplies remain unavailable in the market (Wu, 2014).

In recent years, diminishing wild resources have highlighted the broad development prospects of cultivated *M. speciosa*. However, cultivation faces the critical challenge of non-enlarged roots that fail to form tubers, severely impacting both yield and quality. Field investigations reveal significant phenotypic variation among roots from the same plant, with distinct differences in tuberization capacity. To date, no definitive molecular mechanism studies on root enlargement in *M. speciosa* have been reported. Existing research indicates that gene expression significantly influences tuberous root development in plants, with notable changes in genes related to lignin and starch synthesis and metabolism (Gui et al., 2011; Wang et al., 2016; Hatfield et al., 1994). Studies on purple sweet potato report that in storage roots, starch content decreases while β -amylase activity increases significantly during enlargement, accelerating starch degradation and suggesting a relationship between amylase activity and storage root development. Based on transcriptome sequencing data from *M. speciosa* roots, this study conducts bioinformatics analysis of identified amylase gene family members to provide references for elucidating the molecular mechanisms of amylase function in root enlargement and storage. These findings offer theoretical foundations and genetic resources for breeding improved *M. speciosa* varieties with enlarged roots and for future transgenic research.

Materials and Methods

1.1 Materials

Millettia speciosa plants were collected in Napo County, Baise City, Guangxi, and identified as dried roots of *Millettia speciosa* (Fabaceae) by researcher Longhua Bai from Guangxi Medicinal Botanical Garden. Two-year-old plants were selected, and both enlarged roots (fleshy, soft, brittle, easily broken, diameter >2.5 cm) and non-enlarged roots (non-fleshy, highly fibrous, hard, difficult to break, diameter <1 cm) were harvested from the same individual plant for transcriptome sequencing.

1.2 Methods

Transcriptome sequencing and sequence analysis of both enlarged and non-enlarged *M. speciosa* roots were performed by Wuhan Huada Medical Laboratory Co., Ltd. using the Illumina HiSeq2500 platform. Based on the transcriptome sequencing data and annotation results, unigenes annotated as amylases were identified and validated for complete open reading frames (ORFs) using the online tools ORF Finder (<http://www.ncbi.nlm.nih.gov/orffinder>) and conserved domain prediction via CD Search (<http://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi>). Physicochemical properties of the encoded amino acid sequences were predicted using ExPASy (<https://web.expasy.org/cgi-bin/protparam/protparam>), and transmembrane domains were analyzed (<http://www.cbs.dtu.dk/services/TMHMM>).

Signal peptide prediction and subcellular localization of the 28 amylase sequences were performed using SignalP-5.0 (<http://www.cbs.dtu.dk/services/SignalP/>) and TargetP 1.1 Server (<http://www.cbs.dtu.dk/services/TargetP/>), respectively. Secondary structure prediction and tertiary structure modeling were conducted using SWISS-MODEL (<http://swissmodel.expasy.org>) and Phyre2 (Kelly et al., 2015). Cis-regulatory elements, enhancers, and suppressors were analyzed using PlantCARE (Lescot et al., 2002; <http://bioinformatics.psb.ugent.be/webtools/plantcare/html/>). A phylogenetic tree was constructed using the neighbor-joining method in MEGA7.0 (bootstrap=1,000) based on amylase amino acid sequences, and protein motifs were analyzed using the MEME online tool.

Results and Analysis

Transcriptome sequencing and analysis identified 28 amylase genes, with base sequences accessible via the QR code in Figure 1 [Figure 1: see original paper].

2.1.1 Identification and Physicochemical Property Analysis of *M. speciosa* Amylase Gene Family Members

Based on root transcriptome sequencing results, 28 unigenes annotated as amylase genes were identified and confirmed to contain complete ORFs using ORF Finder and CD Search (Table 2). These 28 amylase unigenes were designated MsAm1 through MsAm28 (Table 1). ORF Finder predicted that MsAm28 encoded the smallest amylase precursor with 256 amino acids, while MsAm12 encoded the largest with 4,141 amino acids. Physicochemical property prediction using ExPASy revealed that *M. speciosa* amylases ranged from 20.78 kDa to 349.39 kDa in molecular weight, all classified as acidic proteins. Positively charged residues (Arg+Lys) and negatively charged residues (Asp+Glu) were present in all sequences. Instability coefficient analysis indicated that MsAm1, MsAm8, MsAm15, MsAm16, MsAm18, MsAm21, MsAm25, MsAm27, and MsAm28 were stable proteins, while the remainder were unstable. Grand average of hydropathicity and aliphatic index calculations confirmed that all family members were hydrophilic proteins (Table 1).

2.1.2 Gene Sequence Prediction of *M. speciosa* Amylases

Analysis of cis-regulatory elements, enhancers, and suppressors using PlantCARE identified 86 regulatory elements across the amylase gene family. MsAm9 contained the most elements (42), followed by MsAm10 (41), while MsAm28 had the fewest (7). All 28 amylases contained the Unnamed__4 element, and all except MsAm11 contained CAAT-box elements. Except for MsAm1, all sequences contained STRE elements. MYB elements were abundant, present in all sequences except MsAm8 and MsAm28, followed by MYC, ARE, MBS, as-1, MYB-like sequence, Unnamed__1, and TGACG-motif (Figure 3 [Figure 3: see original paper]).

2.2.1 Structural Domain Prediction of *M. speciosa* Amylases

Domain analysis revealed 11 structural domains within the *M. speciosa* amylase gene family (Figure 4 [Figure 4: see original paper]), including PLN02784 superfamily, AmyAc-family superfamily, E-set-GDE-Isoamylase-N, PUA superfamily, AmyAc-plant-IsoA, and GH-D superfamily. Different amylase types exhibited distinct domain compositions. For instance, sequences containing the PLN02784 superfamily domain, including MsAm5, MsAm6, MsAm10, MsAm11, MsAm12, MsAm13, MsAm14, MsAm15, MsAm16, MsAm17, MsAm18, MsAm19, MsAm23, and MsAm27, were predicted to be α -amylases.

2.2.2 Secondary Structure Analysis of *M. speciosa* Amylases

Secondary structure prediction using SOPMA demonstrated that random coils predominated in most amylases, comprising approximately 34.15%–55.56% of the structure, except in MsAm1, MsAm7, MsAm8, MsAm15, MsAm16, MsAm22, MsAm23, and MsAm28, where α -helices were most abundant (38.46%–75.86%). MsAm28 exhibited the highest α -helix proportion (75.86%), followed by MsAm7, MsAm22, MsAm15, MsAm8, MsAm23, MsAm19, MsAm1, and MsAm17 (38.15%–58.00%). Five sequences lacked α -helices entirely, while MsAm6 had the lowest proportion (8.16%). β -sheet content was highest in MsAm23 (12.25%) and lowest in MsAm2 (4.34%). Extended strand proportion peaked in MsAm5 (40.00%), followed by MsAm8, MsAm6, MsAm23, and MsAm25 (34.15%–37.78%), with MsAm22 showing the minimum (13.58%) (Figure 5 [Figure 5: see original paper]).

2.3.1 Signal Peptide Prediction and Subcellular Localization

Transmembrane prediction indicated that all gene family members could be transported across the extracellular membrane. Signal peptide analysis revealed potential signal peptides in MsAm5, MsAm8, and MsAm14, while the remaining sequences lacked signal peptides. Subcellular localization demonstrated that all amylases were targeted to the cell wall exterior, with MsAm3, MsAm9, MsAm11, MsAm12, MsAm13, MsAm21, MsAm22, MsAm23, and MsAm27 showing significant chloroplast localization (Figure 6 [Figure 6: see original paper]).

2.3.2 Tertiary Structure Analysis of *M. speciosa* Amylases

Tertiary structure prediction and visualization using SWISS-MODEL revealed distinct structural configurations (Table 2). α -Amylase structures were predicted for MsAm3, MsAm10, MsAm11, MsAm16, MsAm18, MsAm19, and MsAm27. β -Amylase structure was identified in MsAm22. Isoamylase structures were found in MsAm2 and MsAm20. Sequences exhibiting both α - and β -amylase structures included MsAm1, MsAm14, MsAm21, and MsAm28, while methyltransferase structures were predicted for MsAm4, MsAm24, and MsAm26. Notably, MsAm1, MsAm2, MsAm3, MsAm4, MsAm10, MsAm11,

MsAm16, MsAm17, MsAm18, MsAm20, MsAm21, MsAm22, MsAm24, MsAm26, and MsAm27 showed 100% sequence homology (Figure 7 [Figure 7: see original paper]).

2.4 Phylogenetic Analysis and Classification of *M. speciosa* Amylases

The neighbor-joining phylogenetic tree based on amylase amino acid sequences revealed that among the 28 *M. speciosa* amylases, MsAm15 and MsAm16 clustered into one class, both containing motif 2, motif 3, and motif 7, while MsAm4, MsAm24, and MsAm26 formed another class containing motif 1, motif 2, motif 3, motif 4, motif 5, motif 7, and motif 8 (Figure 8 [Figure 8: see original paper]). Comparative phylogenetic analysis with 15 *Arabidopsis thaliana* amylase genes demonstrated that AtBM4 grouped with MsAM6, AtAM2 with MsAM2, AtBM8 with MsAM5, AtAM10 with MsAM22, and AtIM3 with MsAM17 (Figure 9 [Figure 9: see original paper]).

Conclusion and Discussion

This bioinformatics analysis of 28 *M. speciosa* amylases revealed that the encoded amino acid sequences ranged from 20.78 kDa to 349.39 kDa, all representing acidic proteins with partial chloroplast localization. The family possessed PLN02784 superfamily and AmyAc-family superfamily domains, with random coils predominating in secondary structures. Tertiary structure predictions indicated α -amylase, β -amylase, and isoamylase configurations. The gene family contained 86 regulatory elements total, with phylogenetic analysis revealing that MsAm15 and 16 clustered into one class containing motif 2, motif 3, and motif 7, while comparative analysis with *Arabidopsis* showed AtBM4 grouping with MsAM6. Notably, all these genes exhibited significantly increased expression levels in enlarged root transcriptomes, suggesting a potential correlation between amylase activity and root enlargement. These bioinformatics results establish a foundation for investigating the mechanisms underlying *M. speciosa* root enlargement and provide direction for future research.

Previous studies have demonstrated that starch content and β -amylase activity during the late enlargement and storage stages affect sweet potato tuberization and yield (Tao et al., 2010; Xie et al., 2008). Significant differences in β -amylase activity and starch content among sweet potato varieties correlate with tuberization capacity (Chen et al., 2013; Dzedzoave et al., 2010; Sundarram, 2014). Additionally, Tan (2018) performed transcriptome sequencing on *M. speciosa* seedlings with different tuberization capacities, obtaining 64,036 unigenes and identifying 213 root growth-related genes, 358 starch metabolism-related genes, and 383 hormone metabolism-related genes, with 61 genes showing significant differential expression including expansins, cellulose synthases, key starch synthesis enzymes, and metabolism-related genes for cytokinin, ethylene, auxin, strigolactone, and brassinosteroid. These findings exhibit consistency with our study, though further in-depth research and validation are required. Therefore, whether *M. speciosa* root enlargement is associated with these genes and

which specific genes regulate root growth and tuberization remain unresolved questions, leaving the molecular mechanism of root enlargement unclear and necessitating further investigation.

Beyond root enlargement, amylases exhibit broad biological activities. α -Amylase cleaves internal α -1,4 glycosidic bonds in starch, glycogen, or polysaccharides, producing short-chain dextrans, oligosaccharides, glucose, and maltose, thereby rapidly reducing starch viscosity. While α -amylases from plant, animal, or microbial sources share similar functions, they differ in optimal temperature, pH, and other application conditions (Li et al., 2017). Modern research indicates that amylase significantly reduces gelatinization properties in wheat (Liu et al., 2017), thereby affecting wheat quality. Radish, rich in amylase, serves as an ultra-low-calorie vegetable that promotes gastric mucosal repair, prevents hyperacidity, gastritis, and gastric ulcers, and enhances digestive function (Ren et al., 2012). β -Amylase may strengthen photosynthate transport to seeds by promoting starch degradation in leaves and pod walls and participates in starch regulation in rapeseed (Jin et al., 2019), while also affecting brown rice germination (Tao et al., 2018). Therefore, investigating plant amylases will provide scientific references for elucidating plant growth, development, and substance conversion mechanisms, offering theoretical foundations for future genetic engineering breeding programs.

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