

# Genomic Analysis of Yam: Understanding Its Adaptive Evolution and Medicinal Properties

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**Abstract** Yam, commonly known as Shuyu, Tushu, or Shuyao in Chinese, is a traditional Chinese medicinal and edible plant with nutritional and medicinal value. This study aims to elucidate the adaptive evolution and medicinal properties of yam through comprehensive genomic analysis. The study integrates findings from various research efforts, including transcriptome sequencing, chloroplast genome characterization, and metabolomic profiling. Transcriptome analysis has revealed key pathways and hormone activities involved in microtuber formation, highlighting the role of differentially expressed genes in the plant's development and stress responses. Chloroplast genome sequencing has provided insights into the phylogenetic relationships and potential molecular markers for species identification. Metabolomic studies have identified significant metabolites in different parts of the plant, contributing to its medicinal properties. Additionally, the structural characterization of polysaccharides and their bioactivity on gut microbiota underscores the plant's health benefits. The identification of endogenous gibberellins and  $\alpha$ -glucosidase inhibitors further supports the plant's therapeutic potential. This study consolidates current genomic and biochemical data, offering a comprehensive understanding of yam's adaptive evolution and medicinal properties, thereby providing references for future research and potential biotechnological applications.

**Keywords** Yam; Genomic analysis; Adaptive evolution; Medicinal properties; Transcriptome

## 1 Introduction

Yam, commonly known as Shuyu, Tushu, or Shuyao in Chinese, is a significant tuber crop widely cultivated in China and other parts of Asia. It is renowned for its nutritional and medicinal properties, which have been utilized in traditional Chinese medicine for over 2000 years (Yu et al., 2020). The plant is valued not only for its edible tubers but also for its bioactive compounds, which exhibit various health benefits, including immunomodulatory activities (Li et al., 2020), alleviation of antibiotic-associated diarrhea (Zhang et al., 2019), and potential therapeutic effects on erectile dysfunction (Yu et al., 2020).

Genomic analysis plays a crucial role in plant research by providing insights into the genetic makeup, evolutionary history, and adaptive mechanisms of plant species. For yam, genomic studies can reveal the genetic diversity and regulatory networks involved in key physiological processes such as tuber expansion (Zhou et al., 2020), starch composition (Zou et al., 2020), and response to environmental stressors. Understanding these genetic factors is essential for the development of improved cultivars with enhanced nutritional and medicinal properties. Moreover, genomic resources can facilitate molecular breeding efforts aimed at increasing crop yield and resilience (Cao et al., 2020; Lu et al., 2023).

The primary objective of this study is to compile and analyze the existing genomic data on yam to understand its adaptive evolution and medicinal properties. By synthesizing these findings, this study expects to provide a comprehensive understanding of the genomic basis of yam's adaptive evolution and medicinal properties, thereby offering valuable insights for future research and breeding programs.

## 2 Genomic Features of Yam

### 2.1 Genome sequencing and assembly

The genome sequencing and assembly of yam have been pivotal in understanding its genetic makeup and potential for medicinal applications. High-quality genome sequencing has been performed on related *Dioscorea* species, such as *Dioscorea zingiberensis* (Figure 1), *Dioscorea rotundata* (Ma et al., 2018; Li et al., 2022), which provides insights into the biosynthesis and evolution of important metabolites like diosgenin saponins (Ma et al., 2018; Li et al., 2022). These studies reveal that the genome of *Dioscorea* species is complex, with significant gene duplication events that have contributed to the evolution of their unique metabolic pathways. The assembly of these genomes has been anchored on multiple chromosomes, providing a comprehensive framework for further genetic and functional studies.

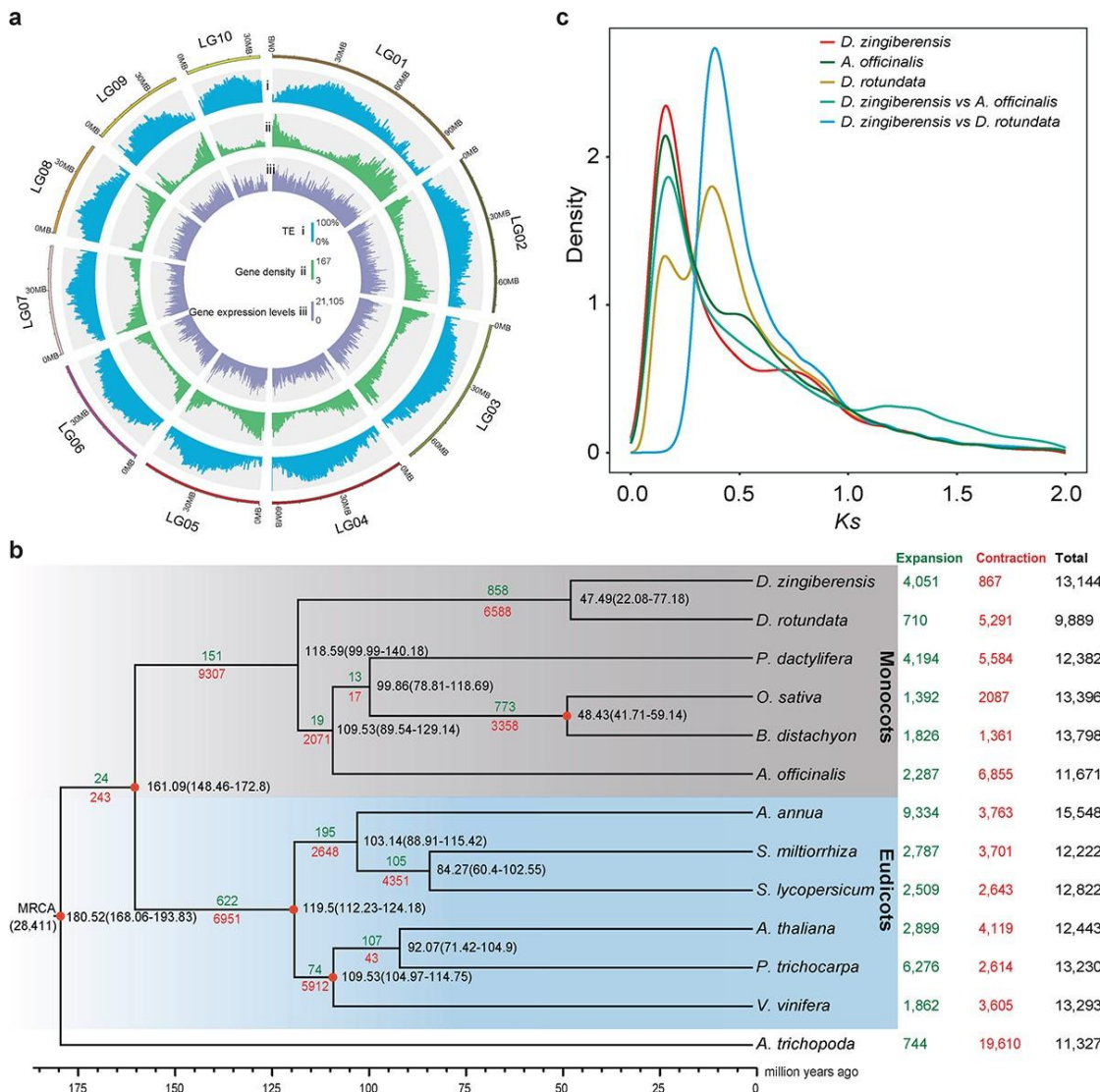


Figure 1 Genome assembly characterization and genome evolution of *D. zingiberensis* (Adopted from Li et al., 2022)  
 Image caption: (a) Circos view of the *D. zingiberensis* genome. (i) TE density distributions in each linkage group. (ii) Gene density: numbers of genes in 1-Mb non-overlapping windows. (iii) Gene expression levels: gene expression levels of each gene in leaves, stems, and rhizomes of *D. zingiberensis*. The distribution of TE density shows a peak in the middle, while that of gene density shows two peaks, with one at each end. (b) Phylogenetic tree showing the divergence times and evolution of gene family sizes for 13 plant species. The value at each node represents the divergence time in millions of years ago (Mya) relative to the present. Expansion: number of gene families expanded (green); Contraction: number of gene families contracted (red); Total: total number of gene families (black). (c) WGD events detected in *D. zingiberensis*. Frequency plot of Ks distributions of paralogs identified from *D. zingiberensis*, *D. rotundata*, and *A. officinalis* (Adopted from Li et al., 2022)

As of March 2024, there have been no complete reports on the genomic information of *Dioscorea* species, severely limiting both basic research and industrial development of yams. Genome data deficiency significantly hampers various fields of study, including taxonomy and evolutionary analysis (Kron et al., 2007), particularly in gene cloning and genome sequencing initiatives (Rabinowicz and Bennetzen, 2006). The *Dioscorea* genus exhibits a complex genome characterized by high repeat content, heterozygosity, and large genome size, posing challenges for de novo sequencing and assembly of the yam genome. Currently, PCR-based sequencing of the 18S rRNA gene sequence and comparative sorting can serve as a method for yam germplasm identification (Liu et al., 2001). The chloroplast genome of yams is highly conserved in gene content, structure, and gene order, containing numerous functional chloroplast genes, suggesting future research avenues in chloroplast genome and genetic studies through high-throughput sequencing.

## 2.2 Structural genomic features

The structural genomic features of yam include various elements that contribute to its functional and adaptive evolution. For instance, the presence of low methyl-esterified pectin in the tuber of yam indicates a complex polysaccharide structure, which includes homogalacturonan and highly branched rhamnogalacturonan I regions (Ma et al., 2018). The genetic resources of Chinese yam (*Dioscorea opposita*) constitute a monophyletic group that evolved from *Dioscorea* species with diploid rhizome compositions in different directions. The Asian and African groups have a chromosome base number  $X=10$ , while the American group has  $X=9$  chromosomes (Chin et al., 1985). RNA-Seq analysis of various tissues of Guinea yam (*Dioscorea rotundata*) predicted a genome containing 26,198 genes. Approximately 5,557 genes were found to have orthologs in maize, rice, and Arabidopsis, while 12,625 genes did not show direct or paralogous orthologs in these species. Furthermore, QTL-seq analysis of genomic regions determining plant sex in 253 plants revealed that a segment on pseudo-chromosome 11 is homozygous in male plants but heterozygous in females. This suggests that the ZZ genotype consistently produces male plants, whereas the ZW genotype is less stable, typically producing female plants but occasionally hermaphroditic or male plants as well (Tamiru et al., 2017).

## 2.3 Functional genomic elements

Functional genomic elements in *Dioscorea opposita* play a critical role in its medicinal properties and adaptive evolution. Transcriptome analysis has identified key pathways and hormone activities involved in microtuber formation, which is essential for the plant's growth and development (Terauchi et al., 1991). Transcription factors (TFs) are key components regulating signal transduction pathways in organisms, capable of modulating the expression of downstream stress-responsive genes (Zhu et al., 2020). WRKY, a plant-specific transcription factor, plays crucial roles in responses to abiotic stresses, regulating processes such as adventitious root development (McGregor, 2006), seed germination and dormancy (Huang et al., 2019), leaf senescence (Tian and Zhang, 2024), and flowering time (Yu et al., 2013). It contains highly conserved sequences like WRKYGQK and a zinc-finger motif (CX4-7CX22-23HXH/C) (Jang et al., 2010). The first WRKY gene family member *SPF1* was cloned from sweet potato in 1994 (Ishiguro and Nakamura, 1994), and subsequent systematic explorations and functional identifications of WRKY transcription factor families have been conducted in various species including *Arabidopsis thaliana* (Eulgem et al., 2000), strawberry (*Fragaria×ananassa* Duch.) (Wei et al., 2016), kiwifruit (*Actinidia chinensis* Planch.) (Jing and Liu, 2018), rice (*Oryza sativa*) (Wu et al., 2005), and tobacco (*Nicotiana tabacum* L.) (Xiang et al., 2016) based on genomic and transcriptomic data. In yam research, four proteins interacting with DoWRKY40 were identified using yeast two-hybrid technology, involved in plant growth and development, cell cycle regulation, cell proliferation, signal transduction, and environmental stress responses. These proteins include the transcription factor EGL1, DNA-binding protein BIN4, protein phosphatase 2C, and BAG family molecular chaperone regulator 7 (Analysis of Yam *DoWRKY40* Gene Expression Characteristics and Interacting Proteins). Research on the mechanism of anthocyanin accumulation in purple yam involves studying aspects such as the expression of anthocyanin synthesis-related genes, exploration of key genes, expression of transcription regulatory factors, and cloning of anthocyanin synthesis-related genes from four perspectives. The process of anthocyanin accumulation is dynamic and regulated by multiple genes; genes involved in anthocyanin synthesis such as F3' H and F3' 5' H may be related to plant growth and development (Yan Ruixia, 2014, Nanjing

Agricultural University). Expression analysis using RT-qPCR revealed that ATPase and chlorophyll content in yam regulate starch and sucrose content, with B1 showing outstanding qualities in dry matter and starch content. It is hypothesized that the gene encoding V-ATPase (*Unigene0030095*) and chloroplast gene (*Unigene0036091*) play significant roles in the growth and development of yam (Shao Ying, 2021, Inner Mongolia Agricultural University).

ABA regulation of tuber formation highlights the complex interactions of genetic and environmental factors in yam functional genomics. Furthermore, the identification of specific metabolites and their distribution characteristics (such as those found in the skin and non-skin parts of *Dioscorea opposita* Thunb. cv. Tiegun) provides valuable insights into the functional roles of these genomic elements in overall plant physiology and medicinal effects (An et al., 2019).

By constructing an *in vitro* foam cell model, the effects of dioscin metabolites on lipid metabolism of foam cells, levels of pro-inflammatory cytokines, and expression of key targets were investigated. A total of 588 dioscin targets and 5,489 targets related to atherosclerosis (AS) were identified, with 275 overlapping targets between dioscin and AS. Through PPI network screening, 52 key targets including Src, signal transducer and activator of transcription 3 (STAT3), and others were identified. GO functional enrichment analysis indicated that these targets are mainly involved in processes such as protein phosphorylation, cellular response to lipid, positive regulation of cell migration, and inflammatory response (Wang and Wang, 2022).

In summary, the genomic features of yam, including its sequencing and assembly, structural elements, and functional genomic components, provide a comprehensive understanding of its adaptive evolution and medicinal properties. These insights are crucial for the continued exploration and utilization of yam in both food and pharmaceutical applications.

### 3 Adaptive Evolution of Yam

#### 3.1 Environmental adaptations

Yam exhibits significant adaptability to various environmental conditions. This adaptability is crucial for its survival and medicinal properties. The plant's ability to thrive in diverse environments can be attributed to its genetic diversity and physiological mechanisms. For instance, the transcriptome analysis of yam revealed a substantial number of differentially expressed genes (DEGs) between leaf and rhizome tissues, indicating tissue-specific adaptations that may contribute to its overall environmental resilience (Hou et al., 2020). Additionally, the presence of various metabolites in different parts of the plant, such as higher levels of  $\alpha$ -glucose and batatasin compounds in the peel, suggests a complex metabolic adaptation to environmental stressors (An et al., 2019).

Yam genetic differentiation in ecological environments is primarily influenced by environmental changes associated with altitude and latitude. Altitudinal variation results in significant morphological differences between populations in mountainous and low-altitude regions, forming distinct genetic clusters due to differing geographic features. Latitude also correlates with genetic divergence in yam populations, showing lineage differentiation across different latitudinal regions. Genetic differentiation correlates positively with geographical distance but is also influenced by physical barriers. For instance, in varying drought conditions, *Dioscorea* species exhibit trends in Superoxide Dismutase (SOD) activity, Malondialdehyde (MDA), Proline (Pro), soluble sugars (SS), and soluble proteins (SP) content (Liu et al., 2020). The content of photosynthetic products in different forms of *Dioscorea polystachya* leaflets varies significantly: soluble proteins, soluble sugars, starch, and reducing sugars show notable differences. Dark green leaflets are significantly higher than light green ones, trifoliate leaflets are significantly higher than other leaflet numbers, and leaflet angle is strongly positively correlated with photosynthetic product content (Wen Jinming, 2018, Shanxi Agricultural University). Additionally, studies on soil moisture conditions reveal that optimal economic benefits for yam root and tuber yield and saponin content are achieved under conditions where soil moisture constitutes 50% of field water holding capacity (Xu Guixin, 2006, Northwest A&F University).

### 3.2 Genetic basis of stress resistance

The genetic basis of stress resistance in yam is multifaceted, involving numerous genes and pathways. The identification of endogenous gibberellins in dormant bulbils of yam highlights the role of these hormones in dormancy and stress resistance (Tanno et al., 1992). Gibberellins are known to regulate various aspects of plant growth and development, including responses to environmental stress. Furthermore, the transcriptome assembly and gene expression analysis of yam identified a significant number of simple sequence repeats (SSRs) and differentially expressed genes, which are likely involved in stress response mechanisms (Hou et al., 2020). These genetic elements provide a foundation for understanding how yam copes with environmental stress and maintains its medicinal properties.

Calcium-dependent protein kinases play important roles in plant growth, development, and responses to stress. The cloned calcium-dependent protein kinase gene *DoCDPK1* shows 97% similarity with the CDPK protein sequence of *Dioscorea rotundata*. *DoCDPK1* contains the STKc\_CAMK domain. Following cold stress at 4 °C, CDPK activity decreases while *DoCDPK1* expression increases, with expression levels varying at different time points of treatment. *DoCDPK1* is likely involved in regulating growth and development during the late stages of yam tuber enlargement and in response to cold stress (<https://doi.org/10.16861/j.cnki.zggc.2024.0164>). Yam polysaccharides possess anti-aging pharmacological activities. Transcriptomic data reveal that this anti-aging effect may be related to autophagy, mTOR, and insulin signaling pathways (<https://mall.cnki.net/magazine/article/SJZA202404004.htm>). In yam anthracnose, transcriptomic analysis shows that WRKY, MYB, and TIFY transcription factors positively or negatively regulate the expression of disease resistance genes. Transcriptionally regulated proteins include PR proteins, NBS-LRR disease resistance genes, and receptor kinases, with increased expression of antioxidant protective enzyme systems CAT and SOD under oxidative stress stimuli (Han et al., 2022).

### 3.3 Evolutionary comparison with related species

Comparative genomic studies between yam and related species offer insights into the evolutionary processes that have shaped its adaptive traits. For example, the molecular phylogenetic analysis of *D. opposita* using 18S rDNA and chloroplast 16S rDNA sequences revealed significant genetic similarities and differences with other species in the Dioscoreaceae family (Hou et al., 2011). This phylogenetic information is crucial for understanding the evolutionary history and adaptive evolution of yam. Additionally, the study of NBS-LRR genes in *Dioscorea rotundata*, a related species, provides a comparative framework for investigating disease resistance genes in yam (Zhang et al., 2020). The evolutionary analysis of these genes suggests that yam may share similar mechanisms of pathogen resistance, further highlighting the adaptive evolution of this species.

In summary, the adaptive evolution of yam is characterized by its environmental adaptations, genetic basis of stress resistance, and evolutionary comparisons with related species. These factors collectively contribute to the plant's resilience and medicinal properties, making it a valuable subject for further research in plant genomics and evolutionary biology.

## 4 Medicinal Properties of Yam

### 4.1 Overview of medicinal uses in traditional medicine

Yam has been extensively utilized in traditional Chinese medicine (TCM) for its beneficial effects on the spleen and stomach. It is often employed to treat conditions such as diarrhea, fatigue, and loss of appetite. The rhizome of yam is particularly valued for its ability to regulate digestive functions and enhance overall vitality (Zhang et al., 2019; Yu et al., 2020). Additionally, it has been used in various oriental countries, including Japan and Korea, as a traditional herbal remedy for its neuroprotective properties (Yu et al., 2020).

### 4.2 Bioactive compounds and their biosynthesis

The medicinal properties of yam are attributed to its rich content of bioactive compounds, including polysaccharides, steroidal saponins, and phenanthrenes. A novel polysaccharide, DOP0.1-S-1, isolated from the rhizome, has shown significant bioactivity by promoting the growth of beneficial gut bacteria and producing

short-chain fatty acids, which are crucial for gut health (Zhang et al., 2019). Additionally, compounds such as chrysoeriol glucosides and alternanthin have demonstrated neuroprotective and antioxidant activities, which contribute to the plant's therapeutic potential (Shan et al., 2020).

The chemical composition varies significantly among different varieties of yam, with the peel of Huai yam containing predominantly phenolic compounds that promote  $\alpha$ -glucosidase activity, while other compounds exhibit enzyme inhibitory effects, indicating the regulatory role of various small molecules in blood glucose levels (<https://mall.cnki.net/magazine/article/CDMD/1022690095.htm>). Wencheng yam polysaccharides consist of glucose, mannose, and galactose in a molar ratio of 36.5:1.63:1. These polysaccharides may adopt a helical conformation with a granular surface, demonstrating notable in vitro antioxidant and blood glucose-lowering activities that correlate positively with concentration (<https://wap.cnki.net/touch/web/Dissertation/Article/1022778900.nh.html>). The antioxidant activity of Wencheng yam polysaccharides primarily involves scavenging free radicals, activating antioxidant enzymes, regulating the expression of the anti-aging gene *klotho*, and modulating the p53/p12 signaling pathway to exert anti-aging effects. Furthermore, they enhance their in vitro antioxidant activity by scavenging hydroxyl radicals, superoxide anions, and 1,1-diphenyl-2-picrylhydrazyl (DPPH) radicals (Sun et al., 2019). The chemical composition of *Dioscorea nipponica* is relatively simple, primarily consisting of steroidal saponin compounds. *Dioscorea nipponica* has become an important starting material for the synthesis of synthetic contraceptives and steroid hormone drugs. Hormonal products such as progesterone, oxytocin, and cortisone acetate synthesized based on it have been widely used clinically, making it the second largest category of drugs in the international pharmaceutical market after antibiotics. Currently, diosgenin is widely used as a raw material for steroid hormone drugs, especially corticosteroids and contraceptive steroids, in countries worldwide. In addition to being a critical raw material for synthesizing hormone drugs, diosgenin also exhibits various biological activities such as anti-tumor, anti-inflammatory, lipid-lowering, and anti-aging effects on the skin.

The biosynthesis of these bioactive compounds involves complex metabolic pathways. For instance, the production of steroidal saponins like diosgenin, a precursor to many pharmacologically active compounds, is a multi-step process involving the conversion of cholesterol through site-specific oxidation and glycosylation (Ge et al., 2023). Transcriptomic studies have identified key enzymes, such as cytochrome P450s (CYPs) and UDP-glycosyltransferases (UGTs), that play crucial roles in these biosynthetic pathways (Wang et al., 2020; Ge et al., 2023).

#### 4.3 Genomic insights into medicinal compound production

Recent genomic and transcriptomic analyses have provided deeper insights into the biosynthesis of medicinal compounds in yam. High-throughput sequencing of leaf and rhizome tissues has revealed a wealth of genetic information, including differentially expressed genes (DEGs) that are involved in the synthesis of terpenoids and other bioactive metabolites (Li et al., 2020). These studies have identified numerous candidate genes that are potentially involved in the biosynthesis of key medicinal compounds, thereby providing references for future functional investigations (Li et al., 2020).

With the development of genomics and functional genomics, significant advances have been made in exploring cholesterol pathways in plants, such as the discovery of steroidal saponin synthesis pathways and the identification of downstream synthetic genes. The value of genomics is increasingly highlighted as it combines with functional genomics and even metabolomics, greatly promoting the elucidation of important secondary metabolite synthesis pathways in plants. The application of high-throughput sequencing technologies plays a crucial role in medicinal plant research, particularly in deeply exploring genes related to the biosynthesis of secondary metabolites. Understanding these genes, their characteristics, and predicting their functions contribute to further biochemical studies on medicinal component biosynthesis pathways. This enhances our understanding of the biosynthesis or regulatory networks of medicinal components, thereby promoting biotechnological methods to increase their yield to meet medicinal demands. However, genetic information on medicinal plants, especially non-model species, is relatively limited. Medicinal plant genomes are often complex, with high heterozygosity,

high repetitive sequence content, polyploidy, and large genomes, which hinder comprehensive whole-genome sequencing and analysis. Moreover, the complexity and diversity of medicinal components make it difficult to infer biosynthetic pathways, posing challenges for in-depth research. In particular, genes in major secondary metabolism pathways, such as those in the phenylpropane metabolism pathway, are often multi-copied, and enzymes encoded by different gene copies may participate in different metabolic branches. Systematic exploration and analysis of these gene family members provide valuable references for accurately locating enzymes catalyzing these steps in further functional studies.

Moreover, comparative genomic studies with other *Dioscorea* species have highlighted the evolutionary aspects of these biosynthetic pathways. For example, the genome of *Dioscorea zingiberensis*, a closely related species, has shed light on the origin and evolution of diosgenin saponin biosynthesis (Figure 2), suggesting that similar mechanisms may be at play in yam (Wang et al., 2020). These genomic insights not only enhance our understanding of the plant's medicinal properties but also open up possibilities for metabolic engineering to optimize the production of valuable bioactive compounds.

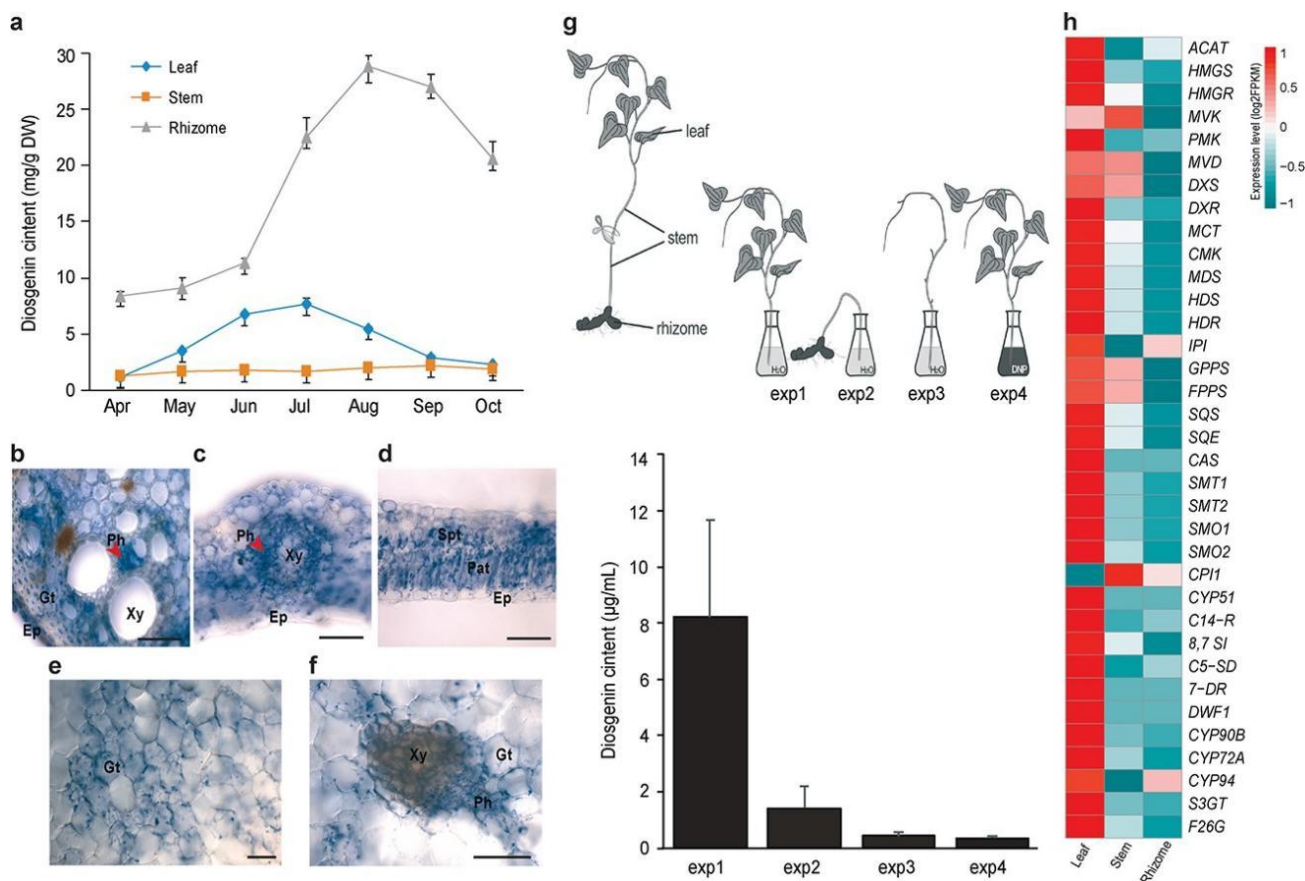


Figure 2 Diosgenin distributions and gene expression levels in different tissues of *D. zingiberensis* (Adopted from Li et al., 2022)  
 Image caption: (a) Diosgenin contents in different tissues of *D. zingiberensis* during the development period of 7 months. (b-f) Immunohistochemical localization of diosgenin in stem (b), leaf (c, d), and rhizome (e, f) tissues. Blue color in sections represents the diosgenin signal. Diosgenin is detected in the epidermis (Ep), ground tissue (Gt), and phloem (Ph) of the stem cross-section. Blue signals localized in the phloem are observed. The diosgenin signal is concentrated in palisade tissue (Pat), spongy tissue (Spt), and phloem in the leaf. Xy represents the xylem. Scale bar = 100 µm. (g) Schematic diagram of the transport assay. The aerial part of the plant with leaves attached (exp1), stem connected to the rhizome (exp2), and stem of the aerial part with leaves detached were immersed in flasks containing deionized water (exp3). The aerial part with leaves attached was also inserted into a flask containing 1.5 mM dinitrophenol (exp4). The diosgenin content secreted into the water in each treatment is shown in the histogram. (h) Expression profiles of pathway genes based on RNA-seq data from three tissues (leaves, stems, and rhizomes). Gene expression values (FPKM) were normalized by log<sub>2</sub>, and the expression pattern was visualized using the R package pheatmap. Three biological replicates for each sample were collected in this study, and the error bar represents the standard error (Adopted from Li et al., 2022)

The medicinal properties of yam are deeply rooted in its traditional uses and are supported by a rich array of bioactive compounds. Advances in genomic research are providing valuable insights into the biosynthetic pathways of these compounds, paving the way for enhanced utilization and conservation of this important medicinal plant.

## 5 Genomic Analysis Techniques

### 5.1 Genomic sequencing technologies

For medicinal plants, the advancement of genome sequencing projects will drive the application of cutting-edge technologies in medicinal plant research. This progress provides a theoretical basis for elucidating the synthesis and regulation of effective components in medicinal plants, facilitating the screening of plant-derived natural medicines and the study of important secondary metabolite biosynthesis. Currently, research on biosynthetic pathways and regulation of secondary metabolites in medicinal plants remains relatively weak, often employing single-gene research strategies. Genomic studies will promote the application of multi-omics approaches in the study of secondary metabolic pathways and their regulation, providing references for the "batch" discovery of relevant genes in these pathways. This will have a positive impact on the application research of biosynthesis and metabolic engineering of secondary metabolites with significant medicinal value (Chen et al., 2010). The advent of high-throughput sequencing technology represents a significant milestone in genomics research, drastically reducing the cost per base of nucleotide sequencing and providing a new platform and developmental opportunities for genomic research (Chen et al., 2010). The low cost of sequencing enables the sequencing of more species' genomes and decoding of genomic genetic codes, with next-generation high-throughput sequencing technologies increasingly chosen by researchers for whole-genome sequencing studies.

Genomic sequencing technologies have significantly advanced our understanding of yam, providing insights into its adaptive evolution and medicinal properties. High-throughput sequencing platforms, such as the Illumina HiSeq 4000, have been employed to sequence the transcriptomes of leaf and rhizome tissues of yam, yielding millions of clean reads and thousands of unigenes (Hou et al., 2020). Additionally, low-coverage whole genome sequencing has been utilized to develop genomic resources for related *Dioscorea* species, such as *D. nipponica*, revealing key mutational hotspots and polymorphic nuclear SSRs (Hu et al., 2023). These technologies enable comprehensive genomic surveys, facilitating the identification of genetic variations and the development of molecular markers essential for phylogenetic and population genetic studies (Luo et al., 2023).

### 5.2 Bioinformatics tools for genome analysis

Bioinformatics tools play a crucial role in analyzing the vast amount of genomic data generated from sequencing technologies. In the study of yam, bioinformatics software was used to analyze transcriptome data, identify differentially expressed genes (DEGs), and validate expression patterns through qRT-PCR analysis (Hou et al., 2020). Comparative genomic analyses have also been conducted using tools to align and compare plastome sequences, identify divergent regions, and develop DNA barcodes for species delimitation (Xia et al., 2019; Lu et al., 2023). Furthermore, tools such as Automatic Barcoding Gap Discovery (ABGD), Poisson Tree Processes (PTP), and Generalized Mixed Yule Coalescence (GMYC) analysis have been applied for species delimitation based on variable loci derived from plastid genome sequences (Xia et al., 2019).

Completion of whole genome sequencing for various *Dioscorea* species facilitates the use of bioinformatics tools for electronic cloning, structural and functional analysis of genes, and molecular evolutionary analysis within the *Dioscorea* genus. Starch is a crucial component of underground tubers in *Dioscorea* species, with Granule-Bound Starch Synthase (GBSS) playing a key role in controlling amylose synthesis. Using the GBSS gene sequence of *Dioscorea polystachya* as a probe, electronic cloning methods obtained GBSS gene sequences from four *Dioscorea* species: *Dioscorea alata*, *Dioscorea rotundata*, *Dioscorea bulbifera*, and *Dioscorea zingiberensis*. Bioinformatics analysis compared and analyzed the GBSS gene structures, protein structures, and phylogenetic characteristics across these species. Identification and characterization of *Dioscorea* gene family members based on conserved domains provide insights into their sequence features, gene structure, chromosome localization, gene collinearity, cis-acting elements, interspecies collinearity, and phylogenetic relationships, facilitating comprehensive studies of gene family characteristics and functions in *Dioscorea* species.



### 5.3 Comparative genomics and phylogenetics

Comparative genomics and phylogenetic analyses are essential for understanding the evolutionary relationships and genetic diversity within *Dioscorea* species. The pan-plastome of *D. alata*, for instance, was constructed to investigate genetic variations and phylogenetic relationships among different accessions, revealing distinct clades and potential DNA barcodes (Lu et al., 2023). Similarly, the complete chloroplast genomes of various *Dioscorea* species have been sequenced and compared, identifying highly variable regions and constructing phylogenetic trees to resolve relationships within the genus (Wonok et al., 2023). These studies highlight the importance of comparative genomics in elucidating the evolutionary history and adaptive mechanisms of *Dioscorea* species, contributing to their conservation and utilization in medicinal and agricultural applications.

By integrating genomic sequencing technologies, bioinformatics tools, and comparative genomics, researchers can gain a comprehensive understanding of the genetic basis underlying the adaptive evolution and medicinal properties of yam and related species. This knowledge is crucial for the development of molecular-assisted breeding programs and the sustainable use of these valuable plants in traditional medicine and agriculture.

## 6 Case Studies

### 6.1 Identification of key genes involved in adaptation

Recent genomic studies have provided significant insights into the adaptive evolution of *Dioscorea* species. For instance, the study on *Dioscorea zingiberensis* revealed that tandem duplication coupled with a whole-genome duplication event provided key evolutionary resources for the diosgenin saponin biosynthetic pathway, which is crucial for the plant's adaptation and survival (Li et al., 2022). Furthermore, using chloroplast and mitochondrial DNA sequences, the phylogenetic relationships of *Dioscorea* species were reconstructed, revealing evolutionary patterns of reproductive traits that play significant roles in species adaptation and diversification (Chen et al., 2022). These findings underscore the importance of specific gene expression patterns and genetic variations in the adaptive evolution of *Dioscorea* species.

Steroidal saponins are not only the main raw materials for synthetic steroids but also have significant medicinal value, now acclaimed as "medicinal gold" in the pharmaceutical industry. However, due to the complex and diverse structures of steroidal compounds, apart from a few steroid hormones that have received widespread attention, little is known about the biosynthetic pathways of other compounds. Preliminary genome sequencing and analysis of *Dioscorea nipponica*, rich in steroidal saponins, were conducted to evaluate genome size and complexity. This study provides a basis for further research on the genomes of *Dioscorea* species, including *Dioscorea nipponica*. Transcriptomic sequencing and chemical component analysis were employed to predict and analyze the biosynthetic pathways of steroidal saponins. Through transcriptome assembly and annotation, genes potentially involved in the biosynthesis of steroidal saponins were identified and analyzed for their expression, revealing 21 candidate genes likely involved in the biosynthesis pathway (Wang Bo, 2015, Peking Union Medical College).

### 6.2 Genetic research related to the pharmacological effects and biosynthesis of yam

Yam is renowned for its medicinal properties, which are attributed to its rich chemical composition, including polysaccharides, stilbenes, diarylheptanoids, steroids, lignans, and terpenoids. These compounds exhibit various biological activities such as anti-oxidation, immune enhancement, and hypoglycemic effects (Ge et al., 2023). Genomic studies on *Dioscorea nipponica*, a closely related species, have developed extensive genomic resources, including plastome-derived SSRs and polymorphic nuclear SSRs, which can be instrumental in understanding the genetic basis of these medicinal properties (Hu et al., 2023). Furthermore, the pan-plastome analysis of *Dioscorea alata* has revealed significant genetic variations and potential DNA barcodes that could be utilized for molecular-assisted breeding and industrial utilization of *Dioscorea* species (Lu et al., 2023).

The main component of yam, diosgenin saponin, possesses various beneficial effects including anti-inflammatory, anti-tumor, antiviral, cholesterol-lowering, blood pressure-reducing, molluscicidal, and contraceptive properties. It is used in the treatment of tracheitis and has insecticidal and antifungal effects against dermatophytes. Its

contained peroxidase enzyme exhibits significant anti-aging effects. Long-term consumption can eliminate facial scars and promote smooth and tender skin. It also serves as a raw material for synthesizing steroidal hormones and contraceptives. The biosynthesis of diosgenin saponins can be divided into three stages: the first stage involves the biosynthesis of upstream terpene skeletons, from which steroidal saponins derive. This pathway proceeds through the mevalonate (MVA) pathway, ultimately synthesizing isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAPP). Hydroxymethylglutaryl-CoA reductase (HMGCR) acts as a key enzyme catalyzing the rate-limiting step in terpene skeleton biosynthesis. Expression analysis of the HMGCR gene in *Dioscorea nipponica* roots induced by methyl jasmonate treatment revealed a positive response to methyl jasmonate stimulation. The second stage involves the biosynthesis of cholesterol, a precursor of diosgenin saponins. A crucial rate-limiting step in this stage is the catalysis of squalene to 2,3-oxidosqualene by squalene epoxidase (SE). The SE gene is critical during this phase, and its expression pattern induced by methyl jasmonate correlates highly with the expression patterns of genes involved in terpene skeleton synthesis. The third stage is the conversion of cholesterol into diosgenin saponins, which includes two important rate-limiting steps: the catalytic process of cholesterol to diosgenin saponin precursors involving P450, and the glycosyltransferase-mediated conversion of diosgenin saponin precursors to diosgenin saponins. Methyl jasmonate, phytosteroid hormones brassinosteroids and campesterol maintain a balance between plant growth, development, and defense mechanisms, representing an antagonistic relationship (Kim et al., 2013). A critical step in regulating phytosterol metabolism towards secondary metabolites derived from cholesterol or plant steroid hormones involves the catalysis process of C-24 methyltransferase (Diener et al., 2000; Holmberg et al., 2002).

### 6.3 Functional studies on bioactive compounds

Functional studies on the bioactive compounds of *Dioscorea* species have highlighted the pharmacological potential of these plants. For example, the metabolome and transcriptome profiling of *Dioscorea cirrhosa* identified 531 metabolites, including 62 flavonoids, and revealed the regulatory network and mechanism of flavonoid biosynthesis, which is crucial for the plant's medicinal properties (Yan et al., 2022). Additionally, a narrative analysis on the pharmacological activities of various *Dioscorea* species, has compiled evidence of their anti-inflammatory, antimicrobial, anticancer, antioxidant, anti-diabetic, antihypertensive, and estrogenic effects (Jamaludin et al., 2023). These studies provide a scientific basis for the further development and utilization of yam as a medicinal plant.

## 7 Future Perspectives

### 7.1 Potential for genomic-driven breeding programs

The genomic analysis of yam has opened new avenues for breeding programs aimed at improving desirable traits. For instance, the identification of genomic regions linked to sex determination and cross-compatibility in *Dioscorea alata* can be leveraged to enhance hybridization success in breeding programs (Mondo et al., 2021). Additionally, the development of high-resolution DNA barcodes for *Dioscorea* species discrimination and phylogenetic analysis provides a robust framework for identifying and selecting superior genotypes (Xia et al., 2019). The comprehensive characterization of yam tuber nutrition and medicinal quality across different geographic groups further supports the potential for targeted breeding strategies to enhance both nutritional and medicinal properties (Shan et al., 2020). These genomic tools and insights will enable breeders to unlock the potential of *Dioscorea* species, and take full advantage of its adaptability to varied environments (Bredeson et al., 2021).

### 7.2 Integrating genomic data with traditional knowledge

Integrating genomic data with traditional knowledge of yam's medicinal properties can significantly enhance the understanding and utilization of this species. Traditional Chinese medicine has long recognized the benefits of yam, particularly its role in regulating spleen and stomach functions (Zhang et al., 2019). By combining this traditional knowledge with modern genomic insights, such as the identification of key pathways and hormone activities involved in microtuber formation (Li et al., 2020), researchers can develop more effective and targeted medicinal applications. Furthermore, the structural characterization of bioactive compounds, such as galactan from yam, and their effects on human gut microbiota, provides a scientific basis for the traditional uses of this

plant (Zhang et al., 2019). This holistic approach can lead to the development of new therapeutic agents and functional foods that are both scientifically validated and culturally relevant.

### 7.3 Implications for conservation and sustainable use

The genomic analysis of yam also has important implications for conservation and sustainable use. The identification of genetic variations and phylogenetic relationships within and among *Dioscorea* species can inform conservation strategies aimed at preserving genetic diversity (Lu et al., 2023). For example, the pan-plastome analysis of *D. alata* revealed significant genetic variations among Chinese accessions, which can be used to guide the conservation of diverse genetic resources (Lu et al., 2023). Additionally, understanding the genetic basis of agronomically important traits, such as disease resistance and tuber quality, can support the development of sustainable agricultural practices that minimize environmental impact (Bredeson et al., 2021). By integrating genomic data with traditional knowledge and conservation efforts, researchers can ensure the sustainable use of yam and related species for future generations.

In summary, the future perspectives for the genomic analysis of yam encompass the potential for genomic-driven breeding programs, the integration of genomic data with traditional knowledge, and the implications for conservation and sustainable use. These efforts will not only enhance the understanding and utilization of this important species but also contribute to its long-term sustainability and resilience.

## 8 Concluding Remarks

The genomic analysis of yam has provided significant insights into its adaptive evolution and medicinal properties. Key findings include the identification of various bioactive polysaccharides and metabolites, such as DOP0.1-S-1, which promotes the growth of beneficial gut bacteria and produces short-chain fatty acids. Metabolomic studies have revealed the distribution of essential metabolites in different parts of the plant, highlighting the nutritional value of both the peel and the flesh. Enzymatic hydrolysis has been shown to alter the structural characteristics of mucilage polysaccharides, which could have implications for food processing. Transcriptome analysis has identified numerous differentially expressed genes (DEGs) and pathways involved in the plant's development and stress responses, enriching the genetic data available for this species. Additionally, the identification of endogenous gibberellins and their role in dormancy induction has provided a deeper understanding of the plant's growth regulation mechanisms.

Genomic analysis plays a crucial role in advancing our understanding of yam. It allows for the identification of key genetic markers and pathways that contribute to the plant's medicinal properties and adaptive evolution. For instance, the development of high-resolution DNA barcodes has improved species discrimination and phylogenetic analysis, which is essential for the accurate classification and conservation of *Dioscorea* species. Transcriptome sequencing has provided valuable data on gene expression patterns, aiding in the identification of genes involved in important biological processes such as tuber formation and stress response. These insights are not only vital for the genetic improvement of yam but also for its sustainable cultivation and utilization in traditional medicine and functional foods.

Future research on yam should focus on several key areas to further elucidate its genomic and medicinal properties. First, more comprehensive genomic and transcriptomic studies are needed to identify additional bioactive compounds and their biosynthetic pathways. This could involve the use of advanced techniques such as CRISPR/Cas9 for gene editing to validate the functions of specific genes. Second, there is a need for more in-depth studies on the interaction between yam polysaccharides and the human gut microbiota to better understand their health benefits. Third, research should explore the potential of yam in biotechnological applications, such as the development of novel functional foods and pharmaceuticals. Finally, conservation efforts should be strengthened through the use of molecular markers to ensure the genetic diversity and sustainability of yam populations. By addressing these research needs, we can unlock the full potential of yam as a valuable medicinal and nutritional resource.

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## Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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