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Low genetic diversity and weak population structure of *Albizia odoratissima* on Hainan Island

Zhiting Li[1], Qiaomiao Ji[1], Yong Yang[1], Meng Xu[2] and Yali Guan[1*]

Abstract

Background The increasing demand for wood owing to societal development has highlighted the potential of *Albizia odoratissima*, a valuable timber species, to address significant timber shortages in China. However, the lack of effective genetic and genomic resources has limited the development and utilization of this species.

Results In this study, we utilised 95.3 Gb of HiFi reads to assemble a draft genome of *A. odoratissima*, resulting in a genome size of 788 Mb, comprising 511 contigs. We conducted whole-genome resequencing on 106 individuals from 7 populations on Hainan Island to explore these resources. Our analysis identified 498,308 high-quality single nucleotide polymorphisms, which were used to assess the genetic diversity, structure, and demographic history of *A. odoratissima* on Hainan Island. The results indicated that the genetic diversity of *A. odoratissima* on Hainan Island is relatively low (observed heterozygosity = 0.189, expected heterozygosity = 0.189, genetic diversity = 1.319×10^{-4}) with minimal genetic differentiation (*Fst* = 0.0151) among the seven populations. Furthermore, molecular variance, principal coordinate analysis, neighbour-joining tree analysis, and genetic structure analysis revealed a shallow population structure. The linkage disequilibrium (LD) decay ranged from 11.4 kb for Jianfengling (JFL) to 39.2 kb for Wuzhishan (WZS). LD decay, demographic history, and Tajima's D analyses indicated that the WZS population has experienced a bottleneck effect.

Conclusions This study offers new insights into the genetic diversity and population structure of *A. odoratissima* on Hainan Island, providing a foundation for future resource utilization and genetic improvement strategies for this species.

Keywords *Albizia odoratissima*, Whole-genome resequencing, Population genetics, Population structure, Hainan Island

Background

Genetic diversity, a product of species evolution, is an important component of biodiversity. Many factors affect genetic diversity, including growth cycle, transmission mode, environmental changes, and human interference [1], leading to differences in genetic variation between and within different populations [2]. Genetic diversity is crucial for species survival. Generally, the higher the level of genetic diversity exhibited by a species, the greater its potential for evolution and its capacity to adapt to environmental and climate changes [3, 4]. High levels of

*Correspondence:
Yali Guan
ylguan76@sina.com
[1] Ministry of Education Key Laboratory for Ecology of Tropical Islands, Key Laboratory of Tropical Animal and Plant Ecology of Hainan Province, College of Life Sciences, Hainan Normal University, Haikou 571158, China
[2] Co-Innovation Center for Sustainable Forestry in Southern China, College of Forestry, Nanjing Forestry University, Nanjing 210037, China

genetic diversity are the basis for breeding [5]. Therefore, the determination of genetic diversity is crucial for conservation of germplasm resources.

Albizia odoratissima is an evergreen tall tree of the family Leguminosae, native to Hainan, Guangdong, Guangxi, Fujian, Guizhou, Sichuan, and Yunnan provinces in China, as well as India, Bangladesh, and Sri Lanka [6, 7]. *A. odoratissima* has high utilization value. It grows rapidly, features a straight trunk, and exhibits strong nitrogen fixation capabilities. Additionally, it is highly resistant to drought, high temperatures, and poor soil conditions, making it an ideal choice for afforestation and soil and water conservation. The yield of *A. odoratissima* is high, with significant differences between the heartwood and sapwood. The wood of *A. odoratissima* is not easily cracked or deformed, insect-and corrosion-resistant, and often used in the manufacturing of musical instruments, furniture, ships, and buildings [6]. In addition, the flowers, leaves, heartwood, bark, and roots of *A. odoratissima* contain various flavonoids [8, 9], and their extracts have strong antibacterial, antioxidant, and antidepressant pharmacological activities, which have high utilization value in the pharmaceutical field [8, 10].

Understanding the genetic diversity patterns of species provides a theoretical foundation for evaluating their genetic resources, formulating conservation strategies, and ensuring sustainable utilization. Molecular markers are powerful tools for studying genetic variability [11, 12]. Despite the high utilization value of *A. odoratissima*, there is limited availability of molecular marker resources and sequence information. An et al. [13] collected 10 populations of *A. odoratissima* from Guangxi and Hainan, totalling 280 individuals, and conducted genetic diversity analysis using 16 expressed sequence tag (EST) simple sequence repeat (SSR) markers. Furthermore, there are no existing research studies on the use of molecular markers in *A. odoratissima*.

Hainan Island, the largest tropical island in China, covers an area of 3.54×10^4 km^2. As a global biodiversity hotspot, it boasts a species-rich flora, including a remarkable number of endemic species [14]. The genetic differentiation resulting from the long-term geographical isolation of islands is a key driving force behind the unique germplasm resources of *A. odoratissima* on Hainan Island [13]. However, the small sample size and limited number of SSR markers hinders our understanding of the genetic resources of *A. odoratissima* on Hainan Island. Therefore, this study collected 106 samples from 7 populations on Hainan Island, and mined a large number of single nucleotide polymorphism (SNP) loci using resequencing data to reveal the distribution pattern of genetic resources in *A. odoratissima*, thereby providing a theoretical basis for its protection and sustainable utilization.

Results

Sequencing of the *A. odoratissima* genome and SNPs

We selected a mature *A. odoratissima* tree grown on Meilan Internship Farm of Hainan Agricultural School for PacBio HiFi sequencing. A total of 95.3 Gb HiFi data were obtained, comprising 4,740,024 reads with an average read length of 20,110 bp (Table 1). The N50 length of the HiFi reads was > 20 kb. Using the Hifiasm software to assemble all PacBio HiFi reads, a 788 Mb genome assembly containing 511 contigs was obtained, with an N50 value of 55.51 Mb and an L50 value of 6. The 97.7% of complete BUSCOs indicated good completeness of the genome. These contigs were subsequently used as reference sequence data for SNP mining.

Whole genome resequencing was performed on the 106 collected samples, and 1413.32 Gb of data were obtained, with 9.42×10^9 reads and an average of 8.89×10^7 reads per accession (Table 1). The average sequencing depth across all samples was 16.87×, with an average alignment rate of 98.48%. The high sequencing quality was evident, as the percentage of clean reads with Q30 scores ranged from 93.28% to 97.83% (Table S1). Mapping these reads to the reference genome identified 54,296,894 SNPs, with an average density of 33.79 SNPs/kb. After stringent filtering, 498,308 SNPs were retained for further analysis.

Genetic diversity and differentiation analysis of the *A. odoratissima*

Using SNP data from whole-genome resequencing, we estimated the genetic diversity of *A. odoratissima* on Hainan Island (Table 2). The overall mean nucleotide diversity was 1.319×10^{-4}, ranging from 1.267×10^{-4} (WZS) to 1.356×10^{-4} (LMS). The overall mean values for *Ho* and *He* were both 0.189, with *Ho* ranging from 0.182 (MR) to 0.196 (LMS), and *He* ranging from 0.173 (WZS) to 0.194 (JFL and LMS), indicating that the genetic diversity of *A. odoratissima* on Hainan Island is low.

Analysis of molecular variance (AMOVA) was performed to evaluate genetic diversity among and within populations (Table 3). The results indicated that 94.576% of the total genetic variation occurred within individuals, 4.361% within populations, and only 1.063% between populations. Analyses of the seven *A. odoratissima* populations revealed *Fst* and *Nm* values of 0.003–0.042 and 5.704–81.941, respectively (Table 4).

Table 1 Summary of sequencing data for *Albizia odoratissima*

Libraries	Reads number	Total data (Gb)	Sequence coverage (×)
PacBio (HiFi) reads	4,740,024	95.3	120.9
DNBseq reads	9,422,107,348	1413.32	16.9

Table 2 Genetic diversity of seven *A. odoratissima* populations on Hainan Island

Population	Nucleotide diversity (π)	*Ho*	*He*	Tajima's D
BWL	1.328×10^{-4}	0.189	0.189	−0.074
JFL	1.310×10^{-4}	0.187	0.194	−0.001
LMS	1.356×10^{-4}	0.196	0.194	−0.047
MR	1.297×10^{-4}	0.182	0.191	0.001
SY	1.304×10^{-4}	0.189	0.191	0.047
WZS	1.267×10^{-4}	0.188	0.173	0.292
YGL	1.338×10^{-4}	0.193	0.190	−0.036
mean	1.319×10^{-4}	0.189	0.189	0.026

The *Fst* value between the WZS and SY populations was the highest (0.042), while the lowest *Fst* value (0.003) occurred between the LMS and BWL populations. Overall, the *Fst* values among different populations on Hainan Island were very low, indicating significant gene flow and a very low level of genetic differentiation. Notably, the WZS population exhibited relatively higher *Fst* values and lower gene flow compared with those of other populations.

A number of factors influence LD decay, including genetic drift, recombination, selection, and population structure. The WZS population exhibited the highest LD level and slowest decay rate (39.2 kb), whereas the JFL population had the lowest LD and the fastest decay rate (11.4 kb) (Fig. 1).

Genetic structure analysis of the *A. odoratissima*

To confirm the clustering of *A. odoratissima* from Hainan Island, principal components analysis (PCA) was performed using the SNPs obtained from all 106 individuals. The first two principal components explained 15.83% of the total genetic variance of the 106 individuals, with 8.65% attributed to component 1 and 7.18% to component 2. Except for individuals from WZS and some individuals from SY, all other individuals were closely clustered and overlapped, suggesting high genetic similarity among them (Fig. 2).

To further understand the relationships among *A. odoratissima* populations and visualize their genetic distances, a phylogenetic tree was constructed based on 498,308 SNPs, which grouped the samples into distinct branches. Generally, except for the samples from the WZS, which clustered together, individuals from different populations were interspersed (Fig. 3a), indicating small genetic distances between populations.

To better understand the population structure of *A. odoratissima* on Hainan Island, genetic structure analysis was performed based on the obtained SNP dataset. The number of clusters was determined using the K value with the minimum cross-validation (CV) error. In this study, the CV was the minimum at K = 1 (Fig. 3b), indicating that *A. odoratissima* on Hainan Island shares a

Table 3 Results of Analysis of molecular variance (AMOVA) for seven populations of *A. odoratissima* on Hainan Island

Source of variation	Degrees of freedom	Sum of Squares	Mean Squares	Estimate of variance	Percentage of total variation (%)
Within individuals	106	4,992,138	47,095.64	47,095.64	94.576
Between individuals	99	5,092,425	51,438.64	2171.499	4.361
Between populations	6	401,532.4	66,922.07	529.6612	1.063
Total	211	10,486,096	49,697.14	49,796.8	100

Table 4 Pairwise matrices of *Fst* (below the diagonal) and *Nm* (above the diagonal) among seven populations of *A. odoratissima* on Hainan Island

Population	BWL	JFL	LMS	MR	SY	WZS	YGL
BWL		76.4771	81.9409	38.8859	22.8404	5.8255	34.8111
JFL	0.0033		58.0441	34.9365	54.8149	6.2660	39.1343
LMS	0.0030	0.0043		65.6209	28.4263	6.7548	65.1899
MR	0.0064	0.0071	0.0038		38.1755	6.4749	80.2705
SY	0.0108	0.0045	0.0087	0.0065		5.7041	34.9677
WZS	0.0411	0.0384	0.0357	0.0372	0.0420		6.4200
YGL	0.0071	0.0063	0.0038	0.0031	0.0071	0.0375	

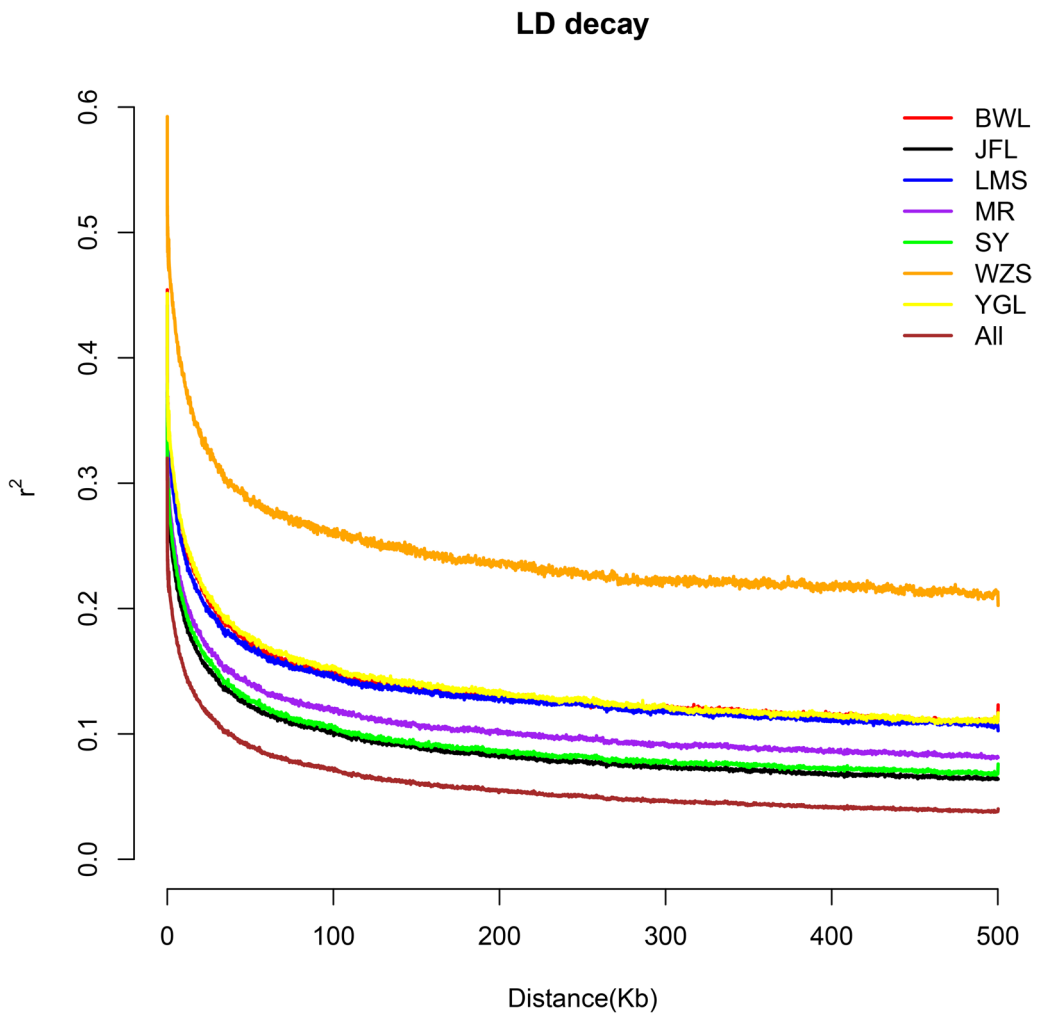

Fig. 1 Linkage disequilibrium (LD) decay of *Albizia odoratissima* on Hainan Island measured using r^2 against distance

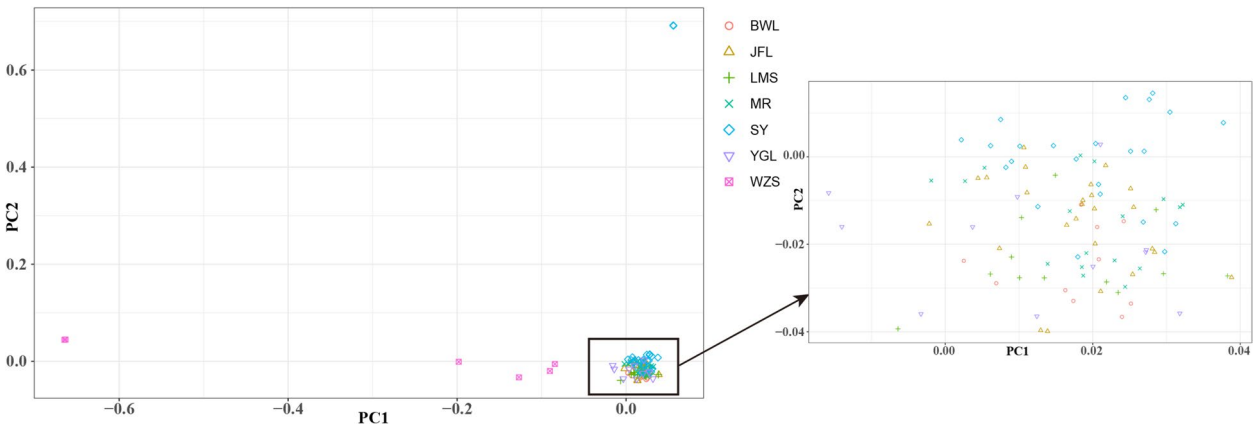

Fig. 2 Principal coordinate analysis among *A. odoratissima* on Hainan Island

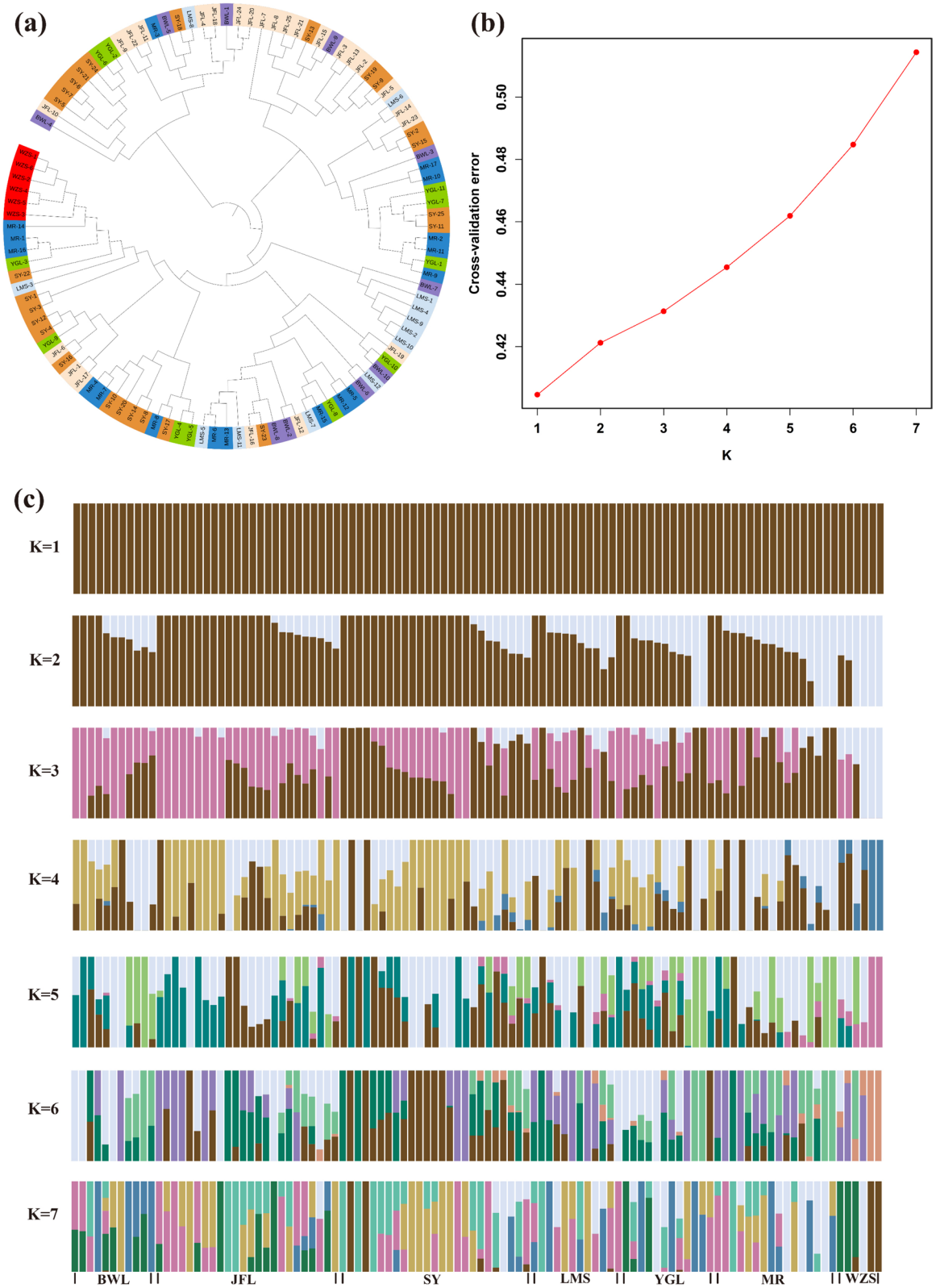

Fig. 3 Population relationship and structural analysis of *A. odoratissima* on Hainan Island. **a** Neighbour-joining tree constructed based on genetic distance. **b** Cross-validation (CV) error for K values ranging from 1 to 7, with the minimum CV (0.40462) observed at K = 1. **c** ADMIXTURE results for 106 *A. odoratissima* individuals based on the SNP dataset, showing population structure for K = 1, 2, 3, 4, 5, 6, and 7

common ancestral origin. When K increased to two, the populations were classified into two clusters: cluster 1 mainly included BWL, JFL, SY, LMS, YGL, and MR and cluster 2 predominantly consisted of WZS. As K continued to increase, significant genetic admixture was observed across all populations (Fig. 3c). Additionally, TreeMix analysis identified frequent migration events between these *A. odoratissima* populations (Fig. 4).

Demographic history of the *A. odoratissima*

Inferring demographic history can help reveal the genetic structure of *A. odoratissima*. We selected three representative individuals from each population to reconstruct the population history of *A. odoratissima* on Hainan Island (Fig. 5). The results indicated that all populations initially expanded rapidly, reaching a peak size at approximately 1 million years ago. However, between 1 million and 100,000 years ago, the population size began to decline sharply. Over the past 10,000 years, all populations, except the WZS population, experienced rapid expansion.

Additionally, Tajima's D test results showed that, with the exception of the WZS population, the values for the other populations were close to 0, while the WZS

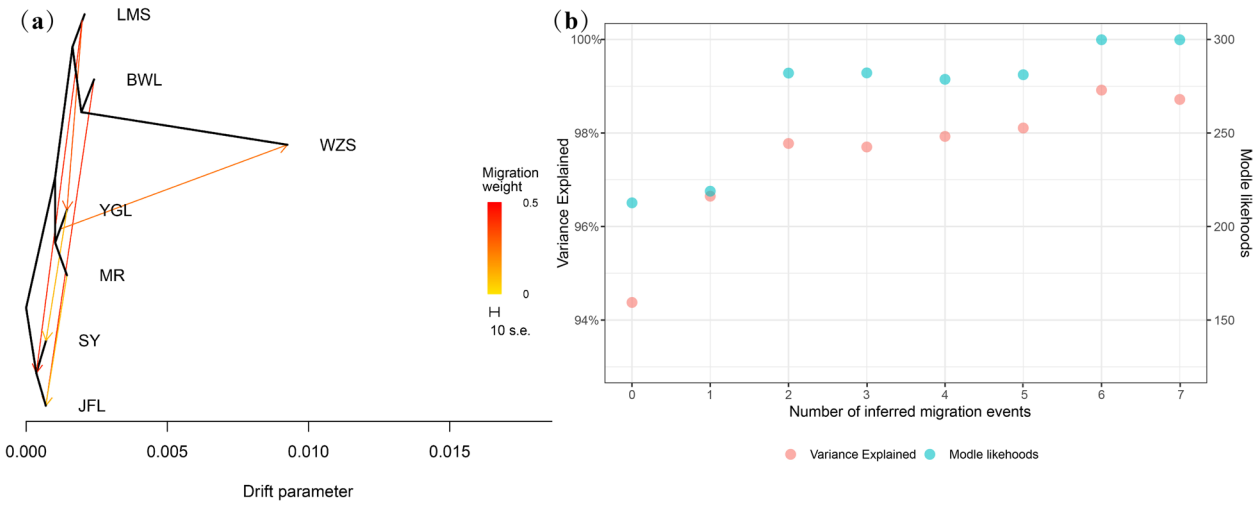

Fig. 4 Detection of gene flow between *A. odoratissima* on Hainan Island. **a** Six migration events among seven populations. Arrows indicate the direction of gene flow, while coloured bars represent migration weights: red indicates strong gene flow and yellow indicates weak gene flow. **b** Log-likelihoods and variance for each model, with the number of migration events specified from 0 to 7

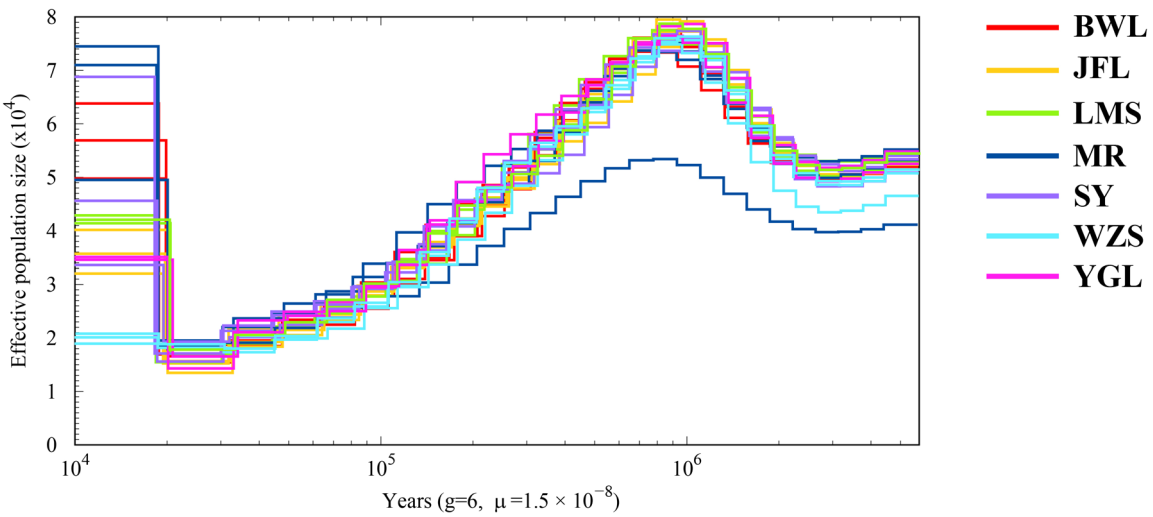

Fig. 5 Inferred demographic history for *A. odoratissima* on Hainan Island based on the pairwise sequentially Markovian coalescent (PSMC) method

population had a value of 0.292, suggesting a significant bottleneck effect.

Discussion

A. odoratissima is a valuable timber species with significant potential for development. Assessing population genetic diversity and structure is crucial for the effective conservation and utilization of the species [15]. In this study, a large number of SNP markers were developed for *A. odoratissima* using whole-genome resequencing technology for the first time. The genetic diversity and structure of *A. odoratissima* on Hainan Island were analysed to obtain important insights for its conservation, management, and utilization.

Genetic diversity

In this study, the *He* value for *A. odoratissima* on Hainan Island was 0.189, with a nucleotide diversity of 1.319×10^{-4}. Compared with *He* values reported in previous studies using 16 pairs of EST–SSR markers, the *He* value in this study is distinctly low (*Ho* = 0.208 and *He* = 0.448) [13]. *He* is a key indicator of genetic diversity within populations, reflecting the evolutionary pressures and mutation rates experienced over time [16, 17]. This difference may be attributed to variations in sample size and marker type, which can lead to discrepancies in the analysis results.

Despite its wide natural distribution in South and Southeast Asia, *A. odoratissima* on Hainan Island exhibited unexpectedly low genetic diversity. Typically, species with such broad distribution are expected to have a higher genetic diversity. However, island populations often exhibit reduced genetic diversity owing to barriers to gene flow and/or population bottlenecks [18–20]. On Hainan Island, *A. odoratissima* shows lower genetic diversity than that of species such as *Hopea hainanensis* (*Ho* = 0.198; [21]), *Haworthia reticulata* (*Ho* = 0.227, *He* = 0.267, nucleotide diversity = 9.1×10^{-4}, [22]), and *Horsfieldia hainanensis* (nucleotide diversity = 10.0×10^{-4}, [23]), and only slightly higher than that of the endangered *Chieniodendron hainanense* (*Ho* = 0.132; [24]).

Over the past 1 million years, the population size of *A. odoratissima* has steadily declined (Fig. 5). This period coincides with the Quaternary ice age, characterised by frequent volcanic activity on Hainan Island [25]. Following the end of the Quaternary glaciation over 10,000 years ago, geological activity on Hainan Island stabilised, leading to a rapid population expansion of *A. odoratissima*. The population bottleneck effect caused by these environmental shifts may also explain the low genetic diversity observed in the species. In addition, *A. odoratissima*, as a timber tree, has been frequently harvested by local residents for furniture making, and its natural habitats have been damaged. Furthermore, the seeds of *A. odoratissima* are hard and have a low germination rate under natural conditions. Field investigations have revealed that the natural regeneration of *A. odoratissima* is challenging, which may also contribute to its low genetic diversity.

Population structure and gene flow

This study detected a very low level of genetic differentiation (*Fst* = 0.0151) among *A. odoratissima* populations on Hainan Island, as supported by AMOVA analysis, with only 1.063% of the total variation attributable to differences among populations. The results of structural analysis and neighbour-joining (NJ) tree also indicate that the genetic backgrounds of the different populations are highly similar, suggesting extensive gene flow among *A. odoratissima* populations on Hainan Island.

Considering that *A. odoratissima* seeds primarily propagate by gravity, with occasional water dispersal, gene flow via seeds is very limited. However, *A. odoratissima* is an entomophilous species, and while little is known about its pollination mode, it has been reported that *Acacia* species are primarily pollinated by nocturnal insects, such as hawkmoths [26]. Therefore, it is plausible that the strong flight ability of sphingids [27] contributes to the excessive pollen flow observed among *A. odoratissima* on Hainan Island.

PCA and structural analysis revealed that the genetic differentiation between the WZS population and other populations is the highest. WZS, located in the central area of Hainan Island, is known for its high species diversity [28]. Although there is no direct evidence of restricted gene flow between WZS and other populations, the WZS population exhibits the slowest LD decay rate. Combined with historical population dynamics, this suggests that it may have experienced a bottleneck effect. This is further supported by the genetic diversity and Tajima's D analysis, with the *He* value of WZS significantly lower than that of the other populations, and the Tajima's D value being positive. These factors may account for the slight genetic differentiation observed between the WZS population and the others.

Conservation recommendations

Understanding the genetic diversity and structure of populations is critical for developing strategies for the conservation and utilization of genetic resources. Given the significant bottlenecks that *A. odoratissima* populations have encountered in the past, this study found that the genetic diversity and differentiation of *A. odoratissima* on Hainan Island are very low. Therefore, we recommend preserving all extant populations to maintain the

remaining genetic variation. To further enhance resource utilization, seed orchards should be established, and *A. odoratissima* from other regions should be introduced to increase the genetic diversity within these orchards.

Conclusions

This study used whole-genome resequencing to explore the genetic diversity and structure of *A. odoratissima* on Hainan Island. The findings indicate low genetic diversity and differentiation among *A. odoratissima* populations on the island, with significant gene flow. These insights enhance our current understanding of the genetic diversity and structure of *A. odoratissima* on Hainan Island and provide a theoretical foundation for the development, utilization, and conservation of genetic resources.

Materials and methods

Plant materials

A. odoratissima sample material used for genome assembly was obtained from the Meilan Internship Farm of Hainan Agricultural School, located in Meilan District, Haikou City, Hainan Province. Fresh leaves were collected for PacBio HiFi sequencing.

The fresh leaves used for whole genome resequencing were collected from 106 individuals from 7 natural populations, covering almost the entire natural distribution area of *A. odoratissima* on Hainan Island (Table 5). To avoid collecting samples from the same parent in the same population, the interval between samples was maintained at 1 km. Fresh leaf tissues were flash-frozen in liquid nitrogen and stored at − 80 °C. DNA was extracted by the cetyltrimethylammonium bromide method [29], and the quality of each extracted DNA sample was assessed by spectrophotometer (Thermo Fisher Scientific) and agarose gel electrophoresis.

De novo whole genome sequencing and assembly

The HiFi sequencing library was constructed using the SMRTbell® prep kit 3.0 (PacBio, 102–182–700). The PacBio Binding Kit was used to bind the primer (PacBio, USA) and polymerase (PacBio, USA) to the library. After purification with AMPure PB beads (PacBio, USA), the library was sequenced on the PacBio Revio system. All sequencing was performed at Wuhan Benagen Technology Co. Ltd., based in Wuhan, China. A total of 4,740,024 PacBio HiFi reads were generated, with a total length of 95.3 Gb. After sequencing, the SMRT Link software v25.1 was used for CCS analysis to generate HiFi reads in FASTA format. HiFi reads were assembled into contigs using Hifiasm with default parameter values [30]. The genome completeness was evaluated by BUSCO using the embryophyta_odb10 database [31].

Whole-genome resequencing and SNP determination

DNA library construction and resequencing were performed using the DNBseq platform, generating 1.41 Tb reads with 150 bp paired-ends. Raw resequenced data were filtered using Fastp software with the following parameters: "–average_qual 20 –length_required 50" [32]. The BWA-mem algorithm of the BWA software [33] was used to map clean reads to the contigs in the *A. odoratissima* genome generated in the previous step. Samtools [34] was used to sort the alignment results, convert them into BAM files, and remove polymerase chain reaction duplicates for subsequent analyses. Afterwards, we used the "HaplotypeCaller," "CombineGVCFs," and "GenotypeGVCFs" modules in the Genome Analysis Toolkit [35] to detect SNPs and used the "VariantFiltration" module to filter SNPs with the parameters (QD < 2.0 || QUAL < 30.0 || SOR > 3.0 || FS > 60.0 || MQ < 40.0 || MQRankSum < − 12.5 || ReadPosRankSum < − 8.0). We used Bcftools [36] to remove SNP sites near Indel using the parameter "– SnpGap 50," and remove multiple SNPs with the parameter "view M2." Subsequently, we used VCFtools [37] to remove SNP markers with a minor allele frequency of < 1% and missing data rates of < 10%. Subsequently, the obtained high-quality SNP data were analysed.

Table 5 Sampling information of seven populations of *A. odoratissima* on Hainan Island

Population code	Population location	Geographical coordinate		Altitude (m)	Population size
		Longitude	Latitude		
WZS	Wuzhi Mountain	109°44′ N	18°52′ E	289–427	6
SY	Sanya District	109°19′ N	18°21′ E	9–243	25
MR	Maorui District	109°25′N	18°42′ E	308–806	17
JFL	Jianfeng Mountain	108°47′ N	18°41′ E	66–537	25
LMS	Limu Mountain	109°39′ N	19°2′ E	258–464	12
YGL	Yingge Mountain	109°30′ N	18°58′ E	265–451	11
BWL	Bawang Mountain	109°5′ N	19°7′ E	210–687	10

Genetic diversity and differentiation analysis

Nucleotide diversity, Tajima's D, and genetic differentiation (*Fst*) analyses were performed using VCFtools with a sliding window of 500 kb and step size of 50 kb. Observed heterozygosity (*Ho*) and expected heterozygosity (*He*) were calculated using the Plink2 software [38]. The gene flow values between populations were estimated using the following formula: $Nm \approx (1-Fst)/(4\times Fst)$. We estimated the genetic divergence of the populations using an AMOVA with vcfpop [39]. We also measured and compared the patterns of linkage disequilibrium (LD) among the seven populations using PopLD decay [40] with default parameters. The LD decayed was defined as the distance of half of the maximum r^2.

Genetic structure analysis

The pairwise distance matrix was calculated using VCF2Dis and the NJ tree was constructed using FastME [41]. iTOL was used to visualised the tree [42]. ADMIXTURE [43] was used to analyse the genetic structure of the 106 samples. The number of ancestral clusters (K) was set from 1 to 7, and the K value was selected based on the minimum CV error rate. PCA of the obtained SNP markers was performed using Plink2 [38], and the two most influential feature vectors were visualised. Additionally, the TreeMix v1.13 software was used to analyse population splits and gene flow among *A. odoratissima* populations on Hainan Island, allowing for migration events ranging from 0 to 7 [44]. The analysis results of ADMIXTURE, PCA, and TreeMix were visualised using the ggplot2 (v3.5.1) package in the R language.

Demographic history reconstruction

To estimate historical population sizes of *A. odoratissima* on Hainan Island, we used the pairwise sequentially Markovian coalescent (PSMC) model with parameters: -N25 -t15 -r5 -p "4+25 * 2+4+6" [45]. Although the default parameter – p "4+25 * 2+4+6" was the atomic time interval designed for human analysis, this parameter is also effective for many organisms [46, 47]. According to the reference, we used a mutation rate (μ) of 2.5×10^{-9} [48] per base per generation, and a generation time of 6 years for the PSMC analysis.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06373-5.

Supplementary Material 1: Table S1. List of information for *A. odoratissima* sample collection and sequencing.

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Authors' contributions
ZL and YG conceived and supervised the study. ZL and QJ analyzed and interpreted the genetic diversity and population structure. YY processed and analyzed the sequencing data. YG and MX reviewed the manuscript. All authors read and approved the final version of the manuscript.

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Data availability
Sequence data that support the findings of this study have been deposited in the Genome Sequence Archive repository with the primary accession code CRA019035.

Declarations

Ethics approval and consent to participate
Fresh young leaves were collected from the *Albizia odoratissima* growing in Hainan. The voucher specimens were deposited in the herbarium of Hainan Normal University (voucher numbers: SP20230510, SP20230520, SP20230601, SP20230607, SP20230621, SP20230710, SP20230717) and identified by Yong Yang. This study complies with relevant institutional, national, and international guidelines and legislation.

Competing interests
The authors declare no competing interests.

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