Xie *et al. BMC Plant Biology* (2026) 26:313
https://doi.org/10.1186/s12870-026-08101-z

BMC Plant Biology

RESEARCH Open Access

Morphological and phylogenetic analysis of *Schisandra* and *Kadsura*: distribution, trait variation, and hybridization potential

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Abstract
To enhance the research and evaluation of *Schisandra* and *Kadsura* germplasm, we investigate their geographical distribution, morphological traits, and phylogenetic relationships. We found that both genera co-occur across a broad latitudinal range (23°–50°N), with Schisandra exhibiting a wider altitudinal range (0–4500 m) than *Kadsura* (0–1500 m). Morphological analysis of 20 traits across 41 species (24 from *Schisandra* and 17 from *Kadsura*) revealed significant overlaps alongside key distinguishing characteristics. Principal component and orthogonal projections to latent structures discriminant analyses identified flower sexuality, gynoecium morphology, and fruit attributes as primary sources of variation, with some of the *Schisandra* species (e.g., *S. plena*, *S. propinqua*) clustering morphologically with *Kadsura*. Phylogenetic reconstructions based on ITS and matK sequences confirmed a close evolutionary relationship between the genera and suggested potential intergenus hybridization, particularly involving *S. bicolor*, *S. propinqua*, *S. plena*, and *K. scandens*. Our findings provide a foundational framework for understanding the biogeography, trait evolution, and complex phylogeny of these genera, highlighting specific species as prime candidates for future research on hybridization and conservation.

Keywords Schisandra, Kadsura, Morphological traits, Hybridization, Germplasm resources

Introduction

The domestication of new fruit crops from wild resources remains a critical endeavor for agricultural diversification [1–3]. While the 20th century saw the successful introduction of crops like kiwifruit (*Actinidia* L.), blueberry (*Vaccinium* L.), avocado (*Persea* Mill.), and macadamia (*Macadamia* F. Muell.), the pool of potential candidates for the 21st century is vast [4–8]. The *Schisandraceae* plants, including the *Schisandra* and *Kadsura* genera, are widespread, rich in germplasm resources, and possess significant medicinal and edible value.Globally, there are about 58 species of *Schisandraceae* plants belonging to two genera, *Schisandra* and *Kadsura*, predominantly distributed in a disjunctive range from East Asia to North America, with East Asia serving as the core [9–11]. They

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serve as one of the prime materials for large-scale introduction and domestication, as well as for developing new small berry crops in the 21st century.

Many species within the *Schisandra* genus possess significant medicinal and nutritional value. For instance, *S. chinensis* and *S. sphenanthera* are well-known for their medicinal properties, such as antioxidant, anti-inflammatory, and anticancer activities [12–14]. The *Kadsura* genus, also rich in medicinal value, comprises over ten species distributed from tropical to subtropical Asia, with main production occurring in South and Southwest China [15]. *Kadsura coccinea*, also known as "black tiger" or "cool rice ball," *K. heteroclita*, called "seaside wind vine" or "blood-opening," and *K. ananosma*, referred to as "bleeding vine," highlight the diverse names and uses of this genus [16–18]. These plants are traditionally used in medicine to improve blood circulation, reduce blood stasis, relieve pain, and expel wind, cold, and dampness. The *Kadsura* genus contains over 200 types of compounds, primarily lignans and triterpenes [19, 20]. Modern pharmacological research has also demonstrated anti-inflammatory, antioxidant, hepatitis B virus inhibitory and anticancer effects [21–23]. Moreover, the fruit of *K. coccinea* is rich in 20 + amino acids and vitamin C [24], surpassing popular tropical fruits like longans and lychees in nutritional content.

Despite their significant medicinal and economic value, the world's *Schisandraceae* genetic resources remain poorly understood. Consequently, only *Schisandra chinensis* and *Schisandra sphenanthera* are commonly used in medicine (Pharmacopoeia of the People's Republic of China 2020 Edition) [25–27], while the remainder of the genus is scarcely investigated or utilized. Due to the family's climbing nature, rigorous deforestation has destroyed the ecological habitats of these plants, leading to their loss of associated forest and subsequent difficulty in survival. Furthermore, prolonged exploitation has caused the depletion of wild *Schisandraceae* resources [13, 28]. While enhancing the precise identification, classification, collection, and conservation of the genetic resources of the *Schisandraceae* family, the implementation of extensive artificial cultivation is the fundamental solution for addressing the shortage of raw materials. However, the taxonomic delineation of the *Schisandra* and *Kadsura* has been contentious. Traditionally, *Kadsura* species have been characterized by their evergreen woody vines with female floral receptacles not elongating during fruit development, resulting in spherical aggregate fruits. In contrast, *Schisandra* species, which are also evergreen woody vines, exhibit elongated floral receptacles during fruit development, forming elongated spike-like aggregate fruits. However, recent pollen morphological studies have revealed that only *Schisandra grandiflora* display a three-grooved pollen type, while all other *Schisandra* species and all *Kadsura* species exhibit a six-grooved pollen type [29–31]. Consequently, pollen morphological features are unable to distinctly differentiate between the two genera.

The past decade or so has seen a surge in research using molecular sequences and phylogenetic methods to reconstruct taxonomic relationships in plant systematics [32–36]. Studies have been conducted on the inter-genus relationships within the *Schisandraceae* family. Saunders (1998) selected 26 morphological traits and used *S. grandiflora* as an outgroup to conduct phylogenetic analysis of the *Kadsura* [37]. In 2000, Saunders selected 25 morphological traits and used *Illicium dunnianum* as an outgroup to perform a phylogenetic analysis of the *Schisandra* [38]. Hao (2001) conducted a comprehensive analysis of the ITS sequences and morphological traits of *Schisandra* using two species of *Illicium* as outgroups [32]. Shi (2024) evaluated the genetic diversity and population structure of *Schisandraceae* using 122 accessions from various Chinese regions, identifying 78 polymorphic bands with 38 EST-SSR markers, and found that 95.6% of the genetic variation was within five subgroups, reflecting substantial gene flow and regional collection focus [28]. However, these studies had limitations, including incomplete taxon representation, insufficiently refined trait statistics, inaccuracies in the status of some taxonomic groups, low support rates for certain branches and the inability to interpretextensive branches. As such, the conclusions drawn from these studies lack considerable persuasiveness.

This study aims to investigate the distribution patterns of *Schisandra* and *Kadsura* species with respect to latitude and altitude, analyze and compare their morphological traits (including leaves, flowers, and fruits) to understand ecological and phenotypic diversity, and assess the phylogenetic relationships between species using molecular markers from the chloroplast genome. Additionally, the research will develop a novel Orthogonal Projections to Latent Structures-Discriminant Analysis (OPLS-DA) morphological clustering model to categorize species based on their morphological characteristics, offering new insights into interspecific relationships. The hypotheses posited are: (1) the distribution of *Schisandra* and *Kadsura* species is significantly influenced by ecological factors such as latitude, altitude, and local climate conditions; (2) morphological traits, particularly those related to reproductive organs, will show distinct variations between the two genera, reflecting their genetic divergence and ecological adaptations; and (3) phylogenetic analysis will provide clearer insights into intergeneric relationships and evolutionary trends within the Schisandraceae family, including potential hybridization zones. The study will combine geographical, morphological, and molecular data to refine the taxonomic framework and inform future conservation and domestication strategies for these species.

Materials and methods

Sequence acquisition and processing

All sequences, including ITS and matK, were downloaded from NCBI GenBank. BioEditor was used for initial sequence editing and preparation, and Clustal W was then employed for the multiple sequence alignment. Sequences with more than 5% missing or erroneous bases were considered low-quality and discarded. Gaps were treated as missing data. All haplotypes within the same species were retained for further phylogenetic analysis. Sequences' start and end positions were trimmed to ensure proper connection to the assigned species in the taxonomic classification. Only haplotypes with a sequence similarity greater than 99% within the same species were retained for further analysis. Subsequently, as shown in Supplementary Table 2.1 and 2.2, 58 ITS sequences and 43 matK sequences, each with a minimum length of 629 bp and 689 bp, respectively, were selected for further processing. The complete range of ITS and matK sequences, including GenBank accession numbers and sequence lengths, is provided in Supplementary Tables 1 and 2. Finally, the molecular matrix was constructed using Geneious 11 software [39].

Quantitative phenotype

A quantitative summary and analysis of all taxonomic descriptions were conducted based on references such as "Flora of China" (FOC) (Editorial Committee of Flora of China, 2018), "Higher Plants of China," and "Illustrations of Higher Plants of China." For the morphological analysis, a set of 20 traits was selected, including characteristics related to the life form, leaf morphology, flower and fruit features, and seed attributes. Each trait was assigned a numerical code to facilitate statistical analysis. The life form of species was categorized as deciduous liana (1), evergreen woody liana (0), or evergreen shrub (2). Leaf shape was coded as oval, lanceolate, or narrow (1), while leaf texture was classified as hard papery (0) or thin paper-like (1). Leaf pubescence was coded as glabrous (0) or coated (1), and leaf margin was noted as entire (0) or toothed (1). Flower unisexuality was coded as unisexual (1) or both sexes (0), and the dioecious or monoecious nature was classified using a scale from 1 to 5 based on the species' sexual differentiation. Fruit traits, such as shape, color, and peduncle elongation, were also coded with numerical values corresponding to specific forms, colors, and structural characteristics. Seed characteristics, including shape, surface texture, and hilum shape, were categorized similarly. A thorough investigation of 41 *Schisandra* and *Kadsura* species was conducted using high-resolution specimen images available online. Specimens from the same species sourced from at least six different regions were used to extract and quantify morphological trait information. SPSS 22 software was employed for data standardization [40].

Sequence divergence and phylogenetic analysis

All DNA sequences, including ITS and matK, were initially aligned using MEGA-X software (iGEM, France). As several sequences exhibited a small number of missing bases (typically represented as "nnnnn."), SeqScape version 2.5 (Applied Biosystems, United States) was used to assemble the shared sequences, which were visually inspected for quality. Maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference methods were utilized for phylogenetic reconstruction to determine the interspecific and intergeneric relationships. For the ITS and matK sequences, 1,000 bootstrap replicates of MP or ML analyses were performed using MEGA-X software (iGEM, France) [41]. The ML tree was constructed using the best-fit model recommended by MEGA-X, which was either the Hasegawa-Kishino-Yano + Gamma distribution (G) model or the Kimura 2-parameter (K_2P) model, determined by the Find Best DNA/Protein Models calculation in MEGA-X [42].

Orthogonal projections to latent structures discriminant analysis (OPLS-DA) model construction

An OPLS-DA model was constructed based on normalized data of the 20 morphological traits of 41 species (24 from *Schisandra* and 17 from *Kadsura*), according to the phylogenetic grouping. To analyze phenetic relationships, a cluster analysis was performed. A pairwise dissimilarity matrix was constructed using Gower's distance, which is suitable for datasets with mixed data types. Hierarchical clustering was then carried out using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm. The robustness of the resulting dendrogram was assessed using the cophenetic correlation coefficient. All analyses were performed in R (version 4.3.2) using the cluster and ape packages. Principal component analysis (PCA) was conducted without grouping settings to compare and support the advantages of the OPLS-DA approach. The receiver operating characteristic (ROC) curve which evaluates the effectiveness of grouping boundaries was used to measure the overall performance of diagnostic tests via the area under the curve (AUC), with its 95% confidence interval (CI). If the lower limit of the 95% CI of the AUC for a test is greater than 0.5, it is considered statistically better. Variable importance in projection (VIP) was used to summarize the importance of the variables and ranked to display the larger VIP on the left side. The first eight quantitative traits influencing the clustering model were further analyzed using F-tests and t-tests.

Statistical analysis

Excel was used as a basic tool for data recording, editing, and file format conversion. GraphPad Prism 10.2.2 software (GraphPad Software Inc., San Diego, CA, United States) was used for data analysis. All values are presented as mean ± SD. Statistical analyses such as t-tests, F-tests, mean comparisons, and Kruskal-Wallis tests were performed using R, with the following open-source R packages: stats, dplyr, and ggplot2. Statistical significance of differences was determined by paired t-tests with a p-value < 0.05 or 0.01.

Results

Geographical distribution and altitudinal range of *Schisandra* and *Kadsura*

To identify the optimal ex situ conservation area for the *Schisandra* and *Kadsura*, this study analyzed the global distribution of *Schisandra*, including its longitude, latitude, and altitude. Based on this analysis, we propose the most suitable range of longitude, latitude, and altitude for conservation efforts. Based on information from the Flora of China (FOC) (http://www.iplant.cn/) and the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org) regarding *Schisandra* and *Kadsura* species, it was determined that there are 24 species in the *Schisandra* genus (Fig. 1A-B), with 13 species being mainly distributed within China (3°51′N-53°33′N, 73°33′E-135°05′E) (*S. arisanensis*, *S. bicolor*, *S. glaucescens*, *S. henryi*, *S. incarnata*, *S. lancifolia*, *S. longipes*, *S. macrocarpa*, *S. micrantha*, *S. parapropinqua*, *S. pubescens*, *S. pubinervis*, *S. tomentella*). There are 10 species distributed across China and other regions (*S. chinensis*, *S. elongata*, *S. grandiflora*, *S. neglecta*, *S. perulata*, *S. plena*, *S. propinqua*, *S. repanda*, *S. rubriflora*, *S. sphenanthera*), and only one species endemic to the United States (*S. glabra*). Among all species in the *Schisandra*, except for *S. bicolor*, *S. longipes*, *S. perulata*, and *S. glabra* which are mainly distributed below 1000 m in elevation, the remaining species have a wide altitudinal distribution, ranging from approximately 2000 m. Some *Schisandra* species (e.g., *S. elongata*, *S. grandiflora*) can be found across a range of 0–4500 m, indicating a strong ecological adaptability (Fig. 2). All *Schisandra* species are distributed in the subtropical regions. Among the 13 *Schisandra* species exclusively distributed within China, their latitude distribution primarily falls between 23°-31° North latitude. For the 10 species distributed both domestically and internationally, six species (*S. elongata*, *S. grandiflora*, *S. neglecta*, *S. plena*, *S. propinqua*, *S. rubriflora*) have a latitude distribution range between 23°-31° North latitude. The latitude distribution range of *S. chinensis* is the widest, covering 23°-63° North latitude. The maximum latitude distribution of *S. perulata*, *S. repanda*, and *S. sphenanthera* can reach up to 50°. The exclusively internationally distributed species *S. glabra* is predominantly found between 30°-35° North latitude.

In the *Kadsura* genus, there are 17 species (Fig. 1A-B), with six species exclusively distributed within China (*K. angustifolia*, *K. induta*, *K. longepedunculata*, *K. matsudae*, *K. oblongifolia*, *K. renchangiana*). Five species are distributed both domestically and internationally (*K. coccinea*, *K. heteroclita*, *K. japonica*, *K. philippinensis*, *K. verrucosa*), and six species have an exclusively international distribution (*K. acsmithii*, *K. borneensis*, *K. celebica*, *K. lanceolata*, *K. marmorata*, *K. scandens*). Among all *Kadsura* species, except for *K. longepedunculata* and *K. philippinensis*, which are mainly distributed below 1000 m in elevation (*K. philippinensis* only occurring below 500 m), the remaining species exhibit a wide altitudinal distribution, typically ranging from approximately 1500 to 3000 m. Some *Kadsura* species (e.g., *K. verrucosa*, *K. lanceolata*, *K. marmorata*, *K. scandens*) can be found across a range of 0–3500 m in elevation, indicating a strong ecological adaptability (Fig. 2). Among the six *Kadsura* species exclusively distributed within China, *K. angustifolia*, *K. induta*, *K. matsudae*, and *K. renchangiana* exhibit similar latitude distribution patterns, primarily ranging from 23°-29° North latitude. The latitude distribution range of *K. longepedunculata* mainly falls between 28°-31° North latitude, while *K. oblongifolia* ranges from 11°-28° North latitude. Among the five *Kadsura* species distributed both domestically and internationally (*K. verrucosa*), *K. coccinea* and *K. heteroclita* are densely distributed between 23°-31° North latitude, with *K. heteroclita* having sporadic distribution between – 5°-15° North latitude. *K. japonica* is densely distributed between 23°-38° North latitude. *K. philippinensis* is primarily distributed between 23°-24° North latitude, with sporadic distribution between 3°-15° North latitude. Among the six species with an exclusively international distribution, *K. acsmithii* and *K. celebica* are mainly distributed between 0°-5° North latitude, *K. borneensis* primarily occurs at 6° North latitude, while *K. lanceolata*, *K. marmorata*, and *K. scandens* are widely distributed between – 10° to 10° North latitude. In summary, the optimal ex situ conservation area for *Schisandra* and *Kadsura* should be situated in subtropical regions, covering latitudes from 23° to 50° North, and include a diverse altitudinal range from 0 to 4500 m.

Comparative analysis of morphological and floral traits in *Kadsura* and *Schisandra*

This study investigates the trait recorded in the "Flora of China" (FOC)", "Higher Plants of China", and "Illustrations of Higher Plants of China" requirements for the *Kadsura* genus and *Schisandra* genus plants in the emerging small berry industry and conducts a comparative analysis of their comprehensive traits. Table 1 presents a

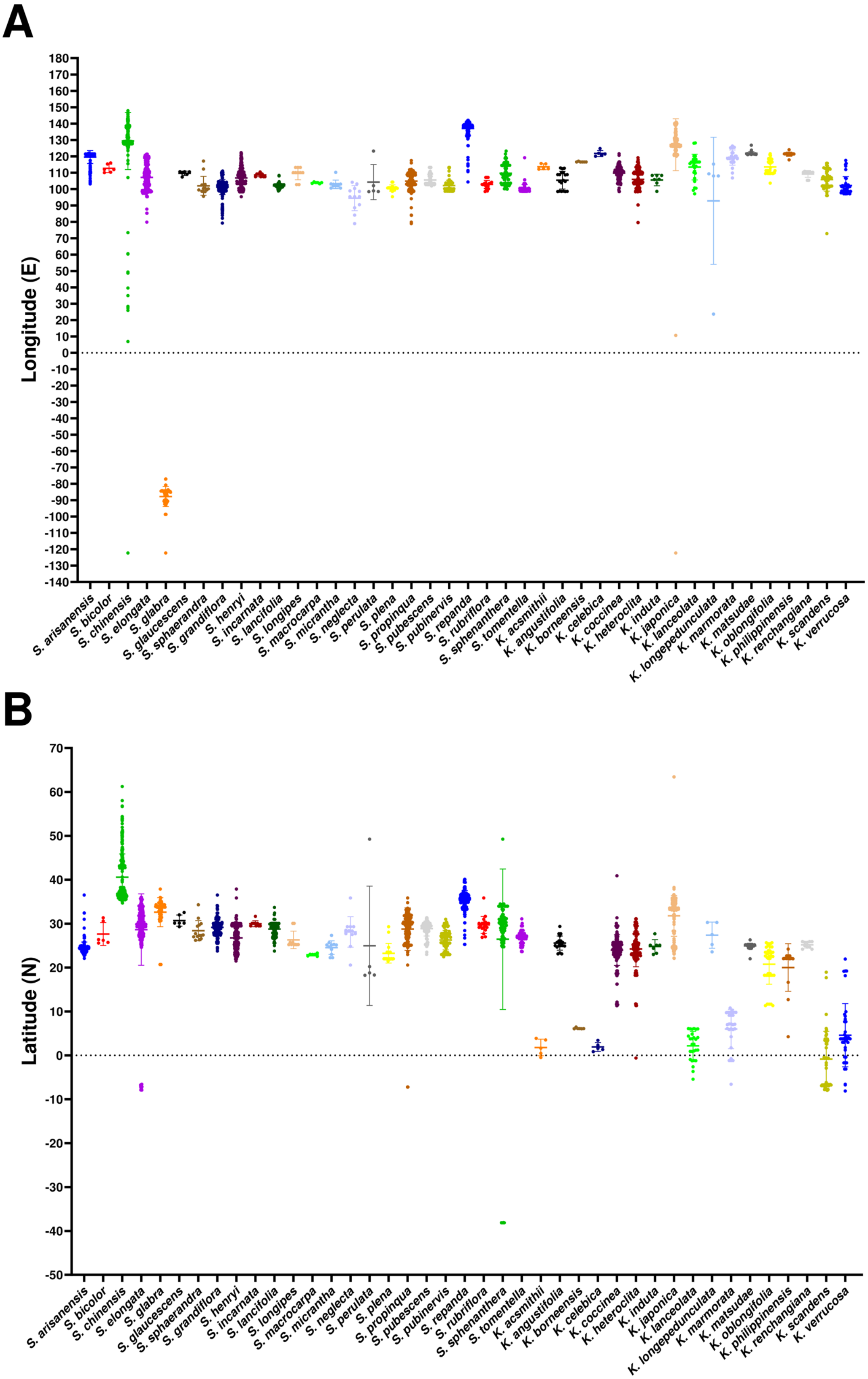

Fig. 1 Dimensional and altitudinal distribution of *Schisandra* genus and *Kadsura* genus globally. (**A**) Global longitude distribution of the *Schisandra* and *Kadsura* genus. (**B**) Global latitude distribution of the *Schisandra* and *Kadsura* genus

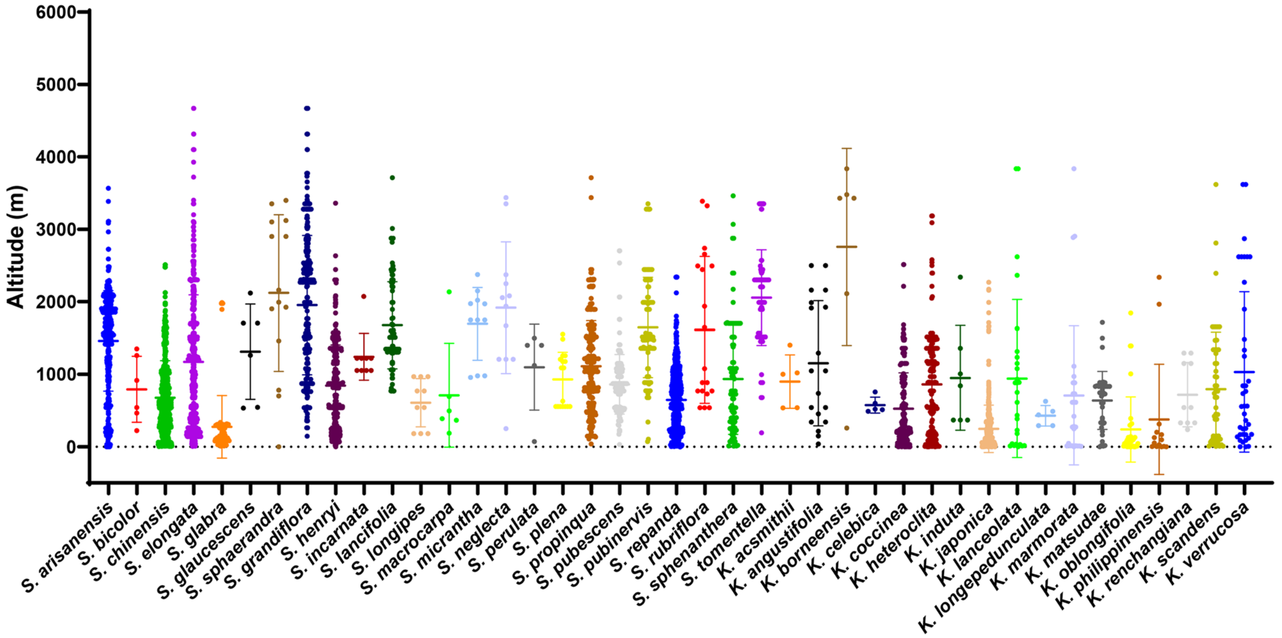

Fig. 2 The global distribution of the genera *Schisandra* and *Kadsura* across altitudinal ranges

comprehensive comparison of morphological characteristics between the *Kadsura* genus and *Schisandra* genus. Notable differences can be observed in various aspects. Firstly, in terms of habit, all species within the *Kadsura* genus are evergreen. Within the *Schisandra* genus, all species are deciduous, except for the *S. propinqua*, the *S. plena* and the *S. macrocarpa*, which exhibit evergreen traits (Supplementary Table 1.1). This distinction in leaf shedding patterns indicates distinct adaptations to varying environmental conditions. When examining the stems, *Kadsura* possesses 1 to 7 transverse septa, while *Schisandra* has 2 to 40 transverse septa. Additionally, the vessel density in *Schisandra* is higher, with an average of 107 vessels/mm^2, compared to *Kadsura*'s average of 78 vessels/mm^2. The fibrothermal cell length also differs, with *Kadsura* having cells up to 1.7 mm and *Schisandra* having cells less than 1 mm. Furthermore, *Schisandra* lacks sheath cells in its stem, which is present in *Kadsura*. It is evident that the stem characteristics are of certain value in the species classification of *Schisandraceae*.

Moving on to leaves, the texture varies from leathery or firm in *Kadsura* to papery, firm, or leathery in *Schisandra*. The leaf margin is mostly entire in *Kadsura* and often serrated in *Schisandra*. Both genera exhibit anastomosing crenate pinnate or concurrent with true pinnate venation. Regarding floral characteristics, *Kadsura* flowers typically have 7 to 24 petals, while *Schisandra* flowers range from 5 to 20 petals. Stamens are separated in both genera but differ in number, with *Kadsura* having 13–80 and *Schisandra* having 5–60. Pistil numbers range from 17 to 300 in *Kadsura* and 12–120 in *Schisandra* (Table 1 and Supplementary Table 1.1). Notably, female flowers in *Kadsura* do not elongate during fruit setting, whereas those in *Schisandra* do. Additionally, the receptacle of the female flower in *Kadsura* does not thicken during fruit setting, whereas in *Schisandra*, it does. The male flower development type is columnar in both genera but can also be flat or ball-shaped in *Schisandra*. Finally, in terms of fruit and seed characteristics, *Kadsura* fruits are spherical or ellipsoid aggregate berries, while *Schisandra* fruits are elongated spike-like aggregate berries. The number of seeds varies from 2 to 5 or more in *Kadsura* to 1–2 (-3) in *Schisandra*. The seed coat ornamentation is reticulate in both genera but can also be verrucose in *Schisandra*. Pollen furrows are either 3 or 6 in both genera. These differences in leaf margins, floral development, and fruit characteristics underscore each genus's adaptation strategies and ecological roles, providing key insights for breeders seeking to optimize yield and suitability in different environments.

UPGMA cluster and PCA analysis reveal morphological distinctions and overlaps between *Schisandra* and *Kadsura*

Although we have identified significant differences in *Kadsura* and *Schisandra* based on morphological features, a comprehensive understanding of their morphological relationships necessitates the use of more sophisticated statistical and analytical tools. We conducted a UPGMA (Unweighted Pair Group Method with Arithmetic Mean) cluster analysis using 20 morphological traits to investigate the systematic relationships within and between the *Kadsura* and *Schisandra* (Supplementary Table 1.1). Utilizing PCA (principal component analysis) models, we performed cluster analysis on the

Table 1 Morphological comparison of genera *Kadsura* and *Schisandra*

No	Characteristic	Kadsura	Schisandra
1	Habit	Evergreen	Deciduous or Evergreen
2	Stem (vessels)	1 to 7 transverse septa	2 to 40 transverse septa
3	Stem (vessels density)	Average78 vessels/mm^2	Average 107 vessels/mm^2
4	Stem (fibrothermal cells)	Up to 1.7 mm	Less than 1 mm
5	Stem (rays)	With sheath cells	Without sheath cells
6	Leaf (texture)	Leathery or firm	Papery, firm or leathery
7	Leaf (margin)	Mostly entire	Often serrated
8	Leaf (veins)	Anastomosing crenate pinnate or concurrent with true pinnate	Anastomosing crenate pinnate
9	Flower (petals)	7 to 24	5 to 20
10	Flower (stamens)	Separated	Separated or united
11	Flower (stamens number)	13–80	5–60
12	Flower (pistil number)	17–300	12–120
13	Flower (female flower stem)	Does not elate during fruit setting	Elongates during fruit setting
14	Flower (female flower receptacle)	Does not thicken during fruit setting	Thickens during fruit setting
15	Flower (male flower development type)	Column type	Column type, Flat type, and Ball type
16	Fruit (shape)	Spherical or ellipsoid aggregate berries	Elongated spike-like aggregate berries
17	Seed (number)	2–5 or more	1–2 (-3)
18	Seed (coat ornamentation)	Reticulate	Verrucose or reticulate
19	Pollen (furrows)	6	3 or 6
20	Hilum shape	Not marked or bar	V-shaped or U-shaped

collected morphological data of *Kadsura* and *Schisandra* (Supplementary Table 1.2). The morphological traits of the 41 species in the *Schisandra* and *Kadsura* were clustered into two distinct groups, with *Schisandra* species exhibiting more concentrated clustering and *Kadsura* species displaying a broader range of trait variation (Fig. 3A). This suggests that *Schisandra* species may share more similar morphological characteristics compared to *Kadsura*, whose traits are more variable. The PCA results further support this observation. The loading plot (Fig. 3B) shows that several key traits, including flower unisexuality, gynoecium morphology, flowering characteristics and fruit traits are strongly associated with the first principal component. This indicates that these traits contribute significantly to the variation among species. The scree plot (Fig. 3C) suggests retaining the first three principal components as they capture a substantial portion of the 58.45%variance in total. Specifically, PC1 accounts for 31.15%, PC2 for 16.60%, and PC3 for 10.71% of the variation (Fig. 3D). Overall, these findings demonstrate that the morphological traits in the *Schisandra* genus are more consistent, whereas the *Kadsura* genus exhibits more diversity and the PCA effectively captures and distinguishes these variations.

Building on the insights from PCA and the observed differences in trait distribution between genera, the clustering analysis further confirms the morphological distinctiveness of the *Schisandra* and *Kadsura*. The analysis reveals that the majority of *Schisandra* species—*S. longipes*, *S. pubescens*, *S. pubinervis*, *S. rubriflora*, *S. sphaerandra*, *S. grandiflora*, *S. elongata*, *S. chinensis*, *S. lancifolia*, *S. micrantha*, *S. rependa*, *S. neglecta*, *S. glaucescens*, *S. viridis*, *S. henryi*, and *S. sphenanthera*—cluster into a single branch (Fig. 4A). Similarly, most *Kadsura* species—*K. borneensis*, *K. verrucosa*, *K. acsmithii*, *K. coccinea*, *K. induta*, *K. marmorata*, *K. heteroclita*, *K. interior*, *K. angustifolia*, *K. renchangiana*, *K. scandens*, *K. japonica*, and *K. longipedunculata*—form a distinct cluster. However, a few *Schisandra* species (*S. plena*, *S. propinqua*, and *S. glabra*) and *Kadsura* species (*K. celebica* and *K. oblongifolia*) do not fit neatly into these primary clusters, suggesting some overlap or shared traits between these genera. The formation of a separate cluster by species like *K. lanceolata* and various *Schisandra* species indicates that morphological similarities exist between certain members of both genera, challenging the clear-cut distinction and highlighting the complexity of their morphological relationships.

Refinement of morphological clustering and differentiation between *Schisandra* and *Kadsura* using OPLS-DA

While UPGMA and PCA provided valuable insights into the general clustering of morphological traits, they were insufficient for achieving precise differentiation between the genera. Consequently, we introduced Orthogonal Projections to Latent Structures-Discriminant Analysis (OPLS-DA) to refine our clustering approach and further elucidate the distinct morphological characteristics of the two genera. The results indicate that all 41 species cluster together into three groups, with G1 belonging to *Schisandra* (Fig. 4B). G2 (*K. angustifolia*, *K. coccinea*, *K. heteroclita*, *K. induta*, *K. japonica*, *K. oblongifolia*, *K. longipedunculata*, *K. renchangiana*, *K. interior*) and G3 (*K. lanceolata*, *K. marmorata*, *K. scandens*, *K. verrucosa*, *K. ananosma*, *K. acsmithii*, *K. celebica*, *K. borneensis*) belong to *Kadsura* (Fig. 4C). The ROC curve (with SVM, Decision Tree, Random Forest and Logistic Regression) shows an AUC value above 90%, indicating the effectiveness of the OPLS-DA model in analyzing morphological

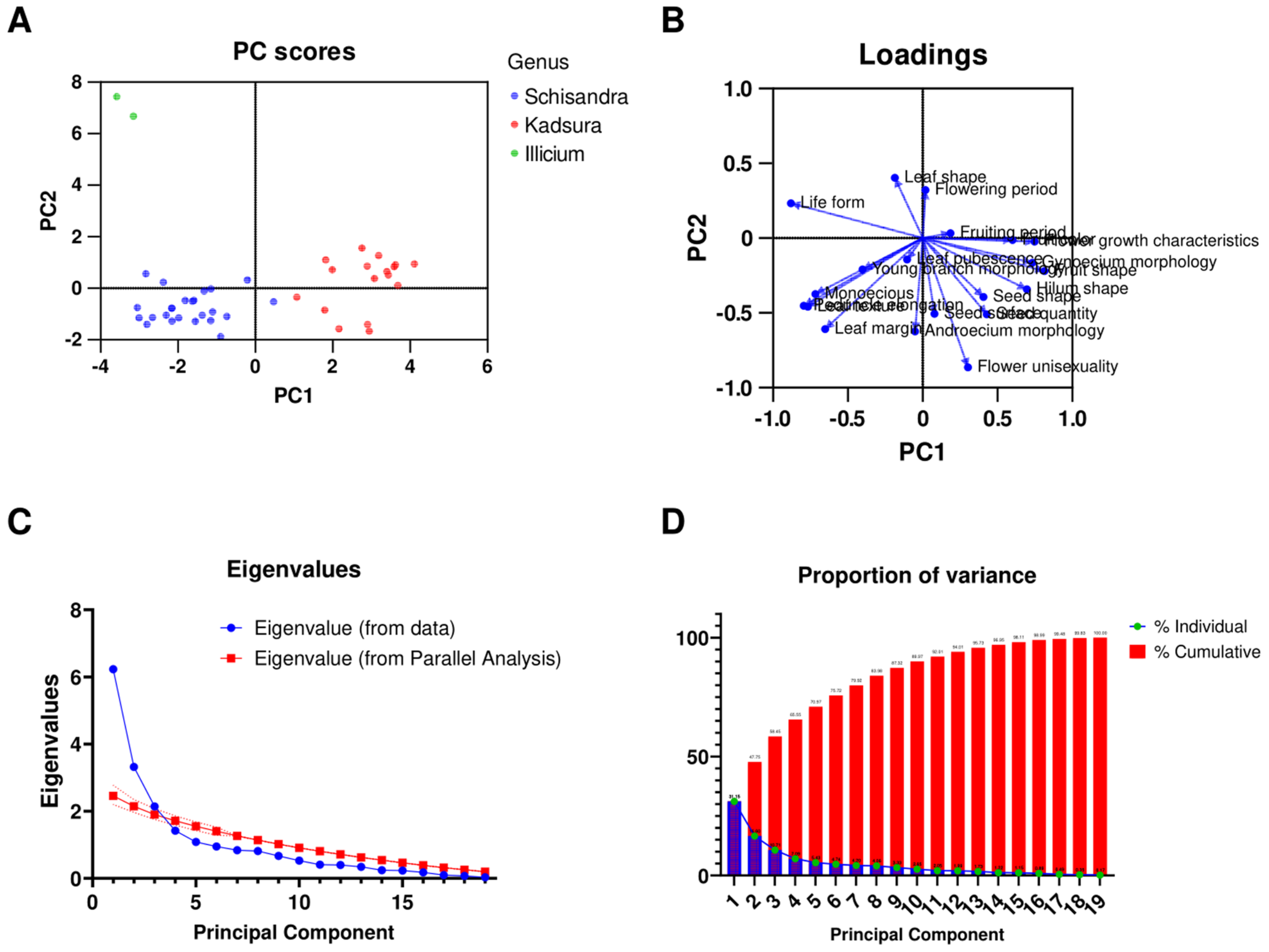

Fig. 3 Application of Principal Component Analysis (PCA) in multi trait clustering of *Kadsura* and *Schisandra*. (**A**) Principal component scores of *Kadsura* and *Schisandra*. Pure principal component analysis performed by using morphological traits were extracted and quantified according to the records of the Flora of China. (**B**) Loadings plot of *Kadsura* and *Schisandra*. Loadings are the correlations (or covariances) between the data column and the principal components. (**C**) Gravel plot of *Kadsura* and *Schisandra*. It is used to confirm the main component quantity to be included during PCA. (**D**) Variance proportion plot of *Kadsura* and *Schisandra*. Used to plot the proportion of variance explained by each principal component. The variance proportion is equal to the eigenvalue of the principal component divided by the sum of the eigenvalues of all principal components (reported as a percentage)

grouping. Moreover, the top seven morphological traits (with VIP > 1, where VIP stands for Variable Importance in Projection) that influence the current clustering model, as shown in Fig. 4D, are leaf margin, peduncle elongation, fruit shape, leaf texture, life form, monoecious, flower growth characteristics, gynoecium morphology and fruit color. The top 9 morphological traits that influence clustering are critical for understanding the differentiation between the genera. These traits are crucial for differentiating between the genera and may be pivotal in identifying and classifying species within them.

The normalization of the top nine morphological trait data substantiates the findings from the OPLS-DA analysis. As illustrated in Fig. 5 and Supplementary Table 1.3–1.11, apart from the leaf margin trait, eight out of the nine morphological traits demonstrated significant differences among the three groups. Specifically, the G1 group was distinctly separable from the G2 and G3 groups based on these traits (Fig. 5B-I). These traits include peduncle elongation, fruit shape, leaf texture, life form, monoecious nature, flower growth characteristics, gynoecium morphology and fruit color. They are crucial in the morphological clustering of *Kadsura* and *Schisandra*. In contrast, when comparing Groups G2 and G3, only the trait of fruit color effectively distinguished G2 from G3. Notably, there was no significant difference in fruit color between Group 1 and G2. However, the fruit color of Group 3 was significantly darker than that of Group 1 and 2 (Fig. 5I). Given that deeper fruit color is often associated with enhanced market value due to its superior appearance and potentially higher medicinal quality, the significantly darker fruit color of Group 3 suggests a potential market advantage. Consequently, Group 3 (comprising *K. lanceolata*, *K. marmorata*, *K. scandens*, *K. verrucosa*, *K. ananosma*, *K. acsmithii*, *K. celebica*, and *K. borneensis*) may hold greater value in terms of both

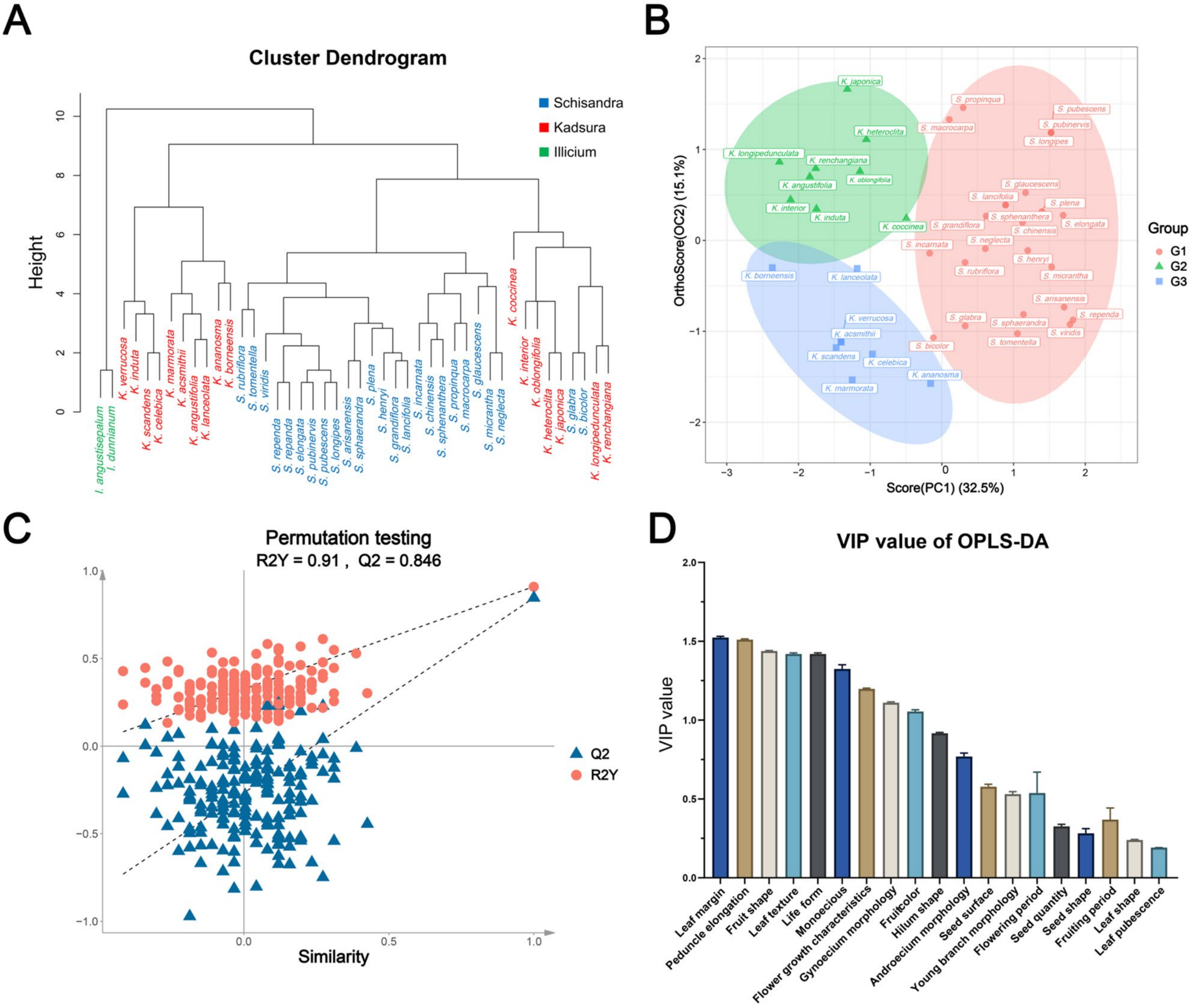

Fig. 4 Application of OPLS-DA model based on latent structure in multi trait clustering of *Kadsura* and *Schisandra*. (**A**) UPGMA clustering dendrogram based on Gower's distance of 20 morphological traits, showing the phenetic relationships among *Kadsura* and *Schisandra*. (**B**) With the orthogonal partial least squares discriminant analysis (OPLS-DA) based on the morphological traits, 41 species were well clustered into 3 groups, which were marked with G1, G2, and G3. (**C**) OPLS-DA permutation testing plot. R2 and Q2 represent the explanatory variables and predictability of the model, which can distinguish the advantages and disadvantages of the model. Generally, R2 and Q2 higher than 0.5 are better, and higher than 0.4 is acceptable. The abscissa of the graph represents the similarity with the model. If the ordinates are R2Y and Q2, the intercept of R2 on the Y axis is less than 0.4, and the intercept of Q2 on the Y axis is less than 0.05, the model is considered to have not been fitted. (**D**) The variable importance for the projection (VIP) summarizing the importance of the variables, and this plot is sorted to display larger VIPs to the left

aesthetic appeal and marketability, positioning it as a prime candidate for future evaluations.

Phylogenetic relationships and hybridization potential between *Schisandra* and *Kadsura*

Although the plants of the *Schisandra* and *Kadsura* can be well distinguished, there are many overlaps in terms of latitude and longitude (Fig. 1), altitude distribution (Fig. 2), and comprehensive traits (Figs. 3 and 4). Is there a possibility of distant hybridization between the plants of the *Schisandra* genus and *Kadsura* genus, which may lead to many overlapping traits and geographical distributions? To facilitate comparative analysis with traditional plant taxonomy, we collected publicly available sequences of plants in the genus *Schisandra* and conducted phylogenetic analysis. This study used matK sequences from 26 species and ITS sequences from 29 species to construct a matrix and perform molecular phylogenetic analysis (Supplementary Table 2.1). There are 58 parsimony characters in ITS matrix and 43 parsimony characters in matK matrix (Supplementary Table 2.2). Using *llicium micranthum* as an outgroup, a strict consensus tree was constructed using ITS-based MP and ITS and matK-based ML (maximum likelihood).

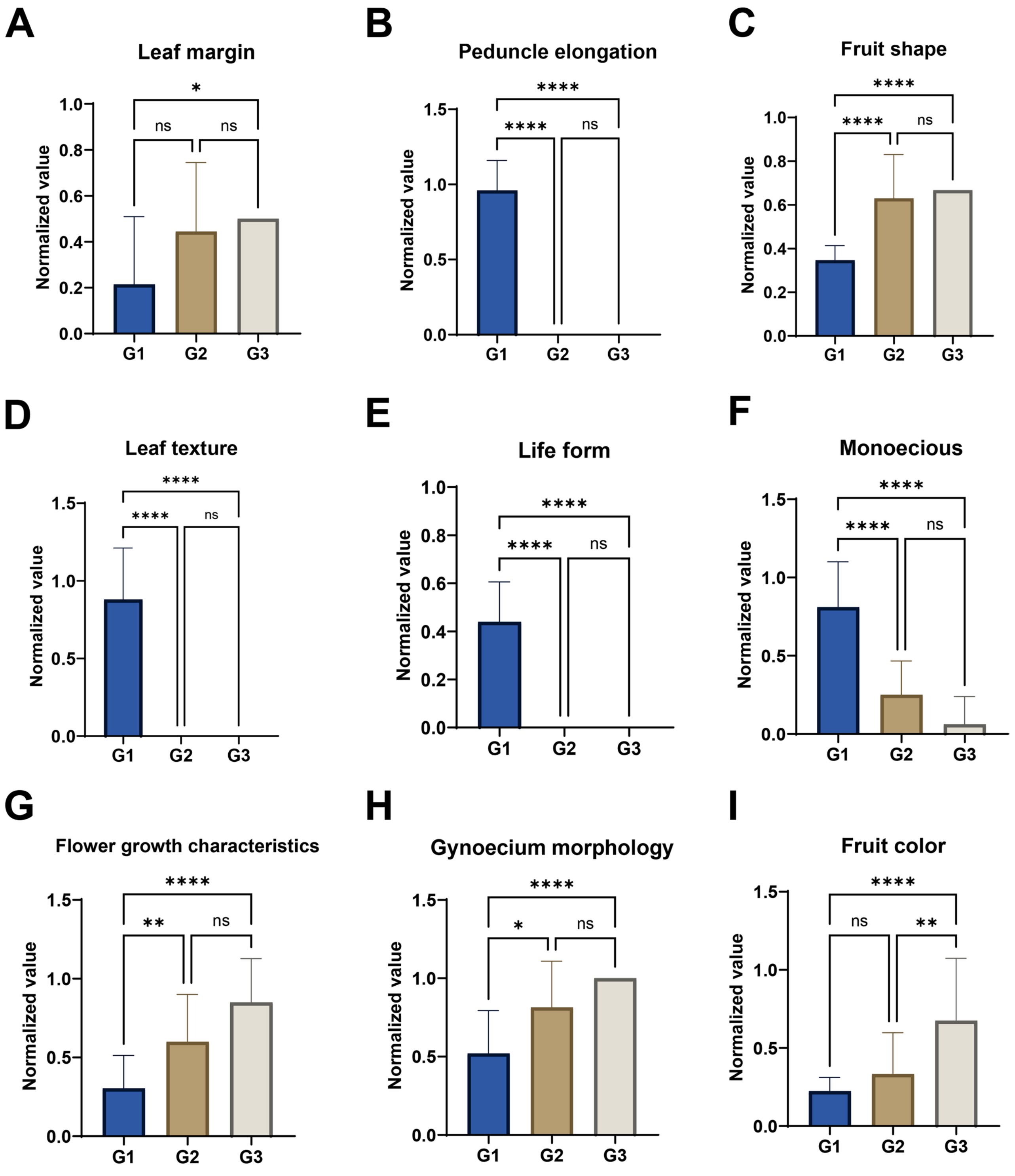

Fig. 5 Analysis of differences in morphological traits among different groups of *Schisandra* and *Kadsura*. (**A**) Leaf margin; (**B**) Peduncle elongation; (**C**) Fruit shape; (**D**) Leaf texture; (**E**) Life form; (**F**) Monoecious; (**G**) Flower growth characteristics; (**H**) Gynoecium morphology (**I**) the Fruit color. ($N > 8$; Tukey's multiple comparisons test, **** $p < 0.0001$; *** $p < 0.001$; ** $p < 0.01$; and * $p < 0.05$; ns: no significantly different)

A Bayesian molecular clock analysis based on the ITS sequences of the *Schisandra* and *Kadsura* (Supplementary Table 2.3) revealed that each genus divides into two major branches, indicating evolutionary divergence in two distinct directions (Fig. 6). In addition, *S. propinqua* and *S. plena* are clearly identified, clustered on the same branch as *K. scandens* (Fig. 6). The biparental inheritance of the ITS region means its phylogenetic signal can be

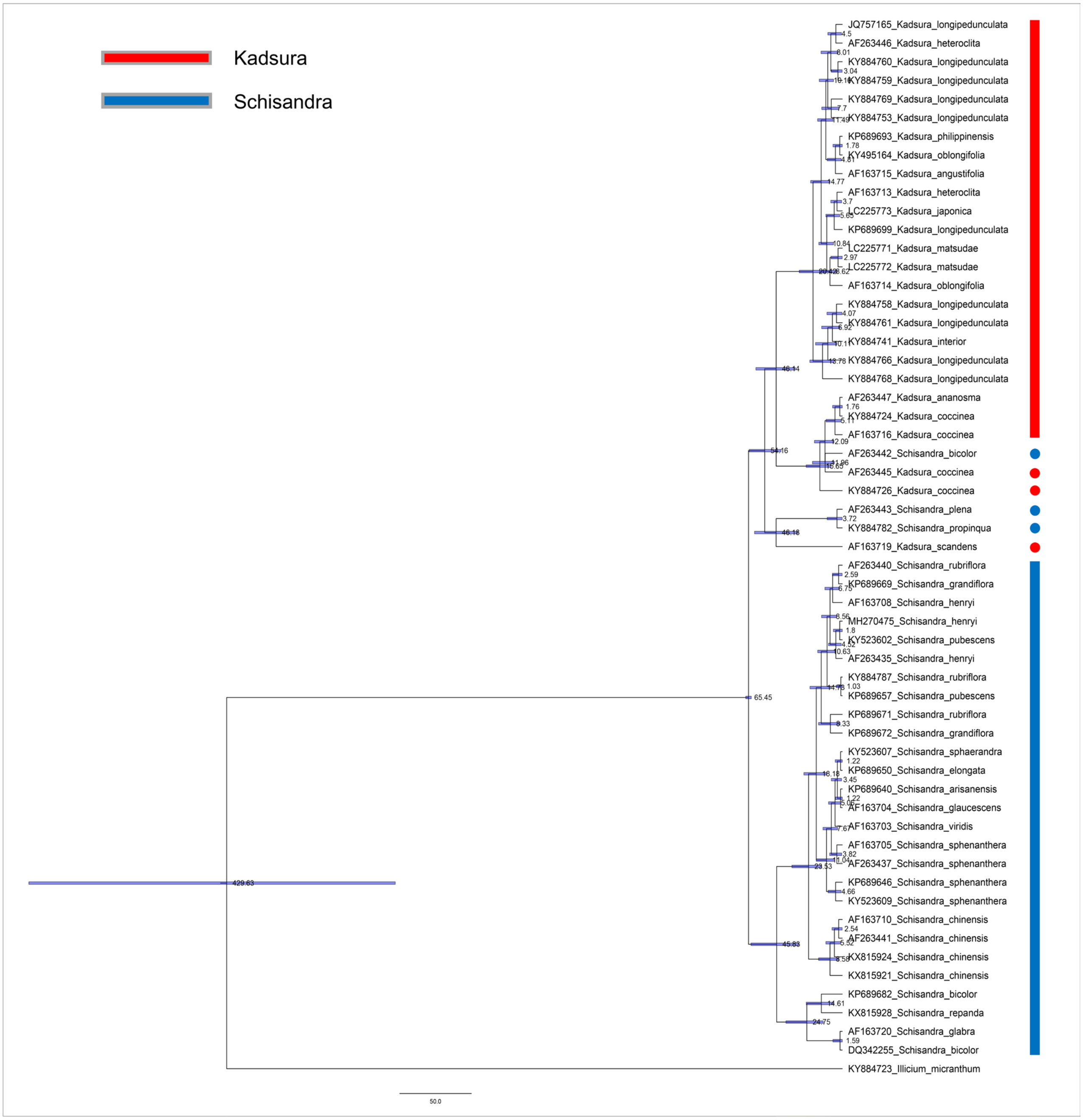

Fig. 6 Bayesian molecular clock of *Schisandra* genus and *Kadsura* genus based on ITS sequences

influenced by hybridization and introgression, unlike the strictly maternally inherited matK. The placement of *S. bicolor* within the *Kadsura* clade in the ITS tree (Fig. 6), which is congruent with our morphological clustering (Fig. 4A), could be interpreted as evidence of historical hybridization or introgression between the ancestors of this species and the *Kadsura* lineage. However, we acknowledge that alternative explanations, such as incomplete lineage sorting or the presence of undetected paralogs, could also produce this pattern. Therefore, this result should be viewed as a compelling hypothesis for future testing with genome-scale data.

As special species within the *Schisandra* genus, *S. propinqua*, *S. bicolor*, *K. scandens* and *S. plena* may have the potential for intergenus hybridization and grafting. Therefore, these four species have the potential to become the foundation species or precious wild resources for future crossbreeding. In contrast to the ITS tree, the matK tree (Supplementary Fig. 1), being maternally inherited, is not expected to reflect hybrid ancestry in the same way and primarily tracks the evolutionary history of the plastid genome. The matK tree, which is largely consistent with traditional taxonomy, provides a robust estimate of maternal lineage history. The discordance between the species relationships inferred from the biparentally-inherited ITS and the maternally-inherited matK (specifically regarding the placement of *S. bicolor*, *S. propinqua*, and *S. plena*) further reinforces the possibility of complex evolutionary histories, such as hybridization or deep coalescence, in these specific lineages. Our integrated analysis reveals that despite being distinguishable, *Schisandra* and *Kadsura* exhibit significant overlap in distribution and morphological traits. The phylogenetic discordance between nuclear and plastid markers, particularly for specific species like *S. bicolor*, *S. propinqua*, and *S. plena*, provides tentative molecular support for the hypothesis of past intergenus gene flow.

Discussion

Because key physiological and ecological characteristics influencing yield are often challenging to measure directly through agronomic traits, breeders typically rely on morphological indicators, such as plant height, leaf size, leaf color, leaf thickness, and plant type, as practical selection criteria for breeding [43–45]. In this context, the analysis of distribution patterns and genetic diversity of plant germplasm resources plays a crucial role in supporting species conservation and guiding the sustainable development and utilization of these resources [46–48]. In recent years, research on *Schisandra* and *Kadsura* has primarily concentrated on its chemical constituents and pharmacological activities, with comparatively less focus on its foundational biology and germplasm resources [14, 49–51]. To ensure the most effective ex situ conservation of the *Schisandra* and *Kadsura*, it is crucial to focus on several key factors. Prioritize regions within the subtropical zones, particularly those spanning latitudes from 23° to 50° North (Fig. 1A and B), which cover the areas where most *Schisandra* species thrive. Conservation efforts should also target elevations up to 4500 m to accommodate the diverse altitudinal ranges of these species (Fig. 2). Additionally, include both lowland and highland environments to cater to the broad ecological adaptability of *Schisandra*. For species confined to China, such as *S. arisanensis* and *S. glaucescens*, concentrate on subtropical regions between 23° and 31° North, while for more widely distributed species like *S. chinensis*, extend efforts to regions up to 63° North. The *Kadsura* genus, encompassing 17 species, demonstrates varied distribution patterns with distinct altitudinal and latitudinal preferences. Chinese species exhibit a concentration in latitudes from 11° to 31° North, with altitudinal ranges largely below 1500 m. International species show broader latitudinal and altitudinal variability, with some, like *K. verrucosa*, thriving between 0 and 3500 m. Notably, species like *K. coccinea* and *K. heteroclita* are more latitude-specific, while others, such as *K. lanceolata* and *K. scandens*, display substantial ecological adaptability. This comprehensive approach will help meet the varied ecological needs of both endemic and broadly distributed *Schisandra* and *Kadsura* species.

The morphological characteristics of the *Kadsura* and *Schisandra*, as detailed in Table 1, provide valuable insights into the evolutionary adaptations and ecological strategies of these species. The contrast in habit between the two genera, with *Kadsura* being predominantly evergreen and *Schisandra* showing either deciduous or evergreen habits, suggests adaptation to different seasonal conditions. Evergreen habits may provide *Kadsura* with a competitive advantage in stable, year-round climates, whereas the deciduous nature of *Schisandra* could be an adaptation to seasonal changes, potentially enhancing the survival of young plants during harsh winters. The structural differences in stems, including vessel number, density, and the presence of fibrothermal cells, indicate varying strategies for resource acquisition and growth in the two genera. The higher vessel density and larger fibrothermal cells in *Schisandra* suggest a more robust hydraulic system, potentially supporting higher water and nutrient transport rates. This may be an adaptation to environments with variable water availability, such as seasonally dry areas. The distinct leaf characteristics, such as texture, margin, and venation pattern, likely reflect different strategies for minimizing water loss and maximizing light interception. The diverse flower structures, including petal number, stamen arrangement and pistil number, suggest different pollination syndromes and reproductive strategies. The morphological changes in the female flower stem and receptacle during fruit setting in *Schisandra*, compared to *Kadsura*, indicate contrasting reproductive behaviors and seed dispersal strategies. The divergence in fruit and seed characteristics further highlights the distinct ecological roles of the two genera. The elongated spike-like aggregate berries of *Schisandra* may enhance seed dispersal through wind or animals, while the spherical or ellipsoid aggregate berries of *Kadsura* may rely more on gravity and animal dispersal. The variation in seed number and coat ornamentation also suggests different strategies for seed survival and dispersal. However, despite considerable differences in traits among plants of the *Schisandra* and *Kadsura*, the growth patterns of all species within each genus are remarkably similar (Table 1 and Supplementary Table 1.1), aligning with previously reported findings [30, 52].

The UPGMA analysis (Fig. 4A), based on 20 morphological traits, supports the hypothesis that there are significant morphological differences between *Schisandra* and *Kadsura*. This is consistent with our PCA findings

(Fig. 3), where the morphological traits of the 41 species from both genera generally clustered into two main groups. *Schisandra* species exhibit a more concentrated clustering, suggesting that they possess a relatively homogeneous set of morphological characteristics compared to *Kadsura*, which displays a broader spectrum of traits and hence a more dispersed clustering pattern. This differentiation indicates that *Schisandra* species are more morphologically similar to each other while *Kadsura* species are more diverse in their morphological traits. The loading plot reveals that key traits such as flower unisexuality, gynoecium morphology, flowering characteristics, and fruit traits are prominently associated with the first principal component. These traits, therefore, play a critical role in defining the morphological variation observed among species. The scree plot supports retaining the first three principal components, which together account for a substantial 58.45% of the total variance. This suggests that while the first principal component captures the major variation, the additional components contribute valuable insights into the differentiation among species. The clustering reveals that most Schisandra species group into a single branch, highlighting their morphological consistency. Conversely, *Kadsura* species form a separate cluster, reflecting their greater morphological diversity. However, the presence of some *Schisandra* species, such as *S. plena*, *S. propinqua*, and *S. glabra*, and *Kadsura* species, including *K. celebica* and *K. oblongifolia*, that do not neatly fit into these primary clusters, indicates a degree of overlap between the genera. This overlap is further exemplified by species like *K. lanceolata* and certain *Schisandra* species, which form a separate cluster, suggesting that some members of both genera share morphological similarities. This finding challenges the notion of a clear-cut distinction between *Schisandra* and *Kadsura*, highlighting the complexity and fluidity in their morphological relationships.

The application of OPLS-DA (Fig. 4) has provided a refined perspective on the morphological differentiation between the *Schisandra* and *Kadsura*, surpassing the insights offered by traditional UPGMA and PCA [32, 53]. The clustering results, which segregate the 41 species into three distinct groups, underscore the effectiveness of OPLS-DA in enhancing the precision of morphological trait differentiation. The clear separation of Group 1 (*Schisandra*) from Groups 2 and 3 (*Kadsura*) based on various morphological traits confirms the model's robustness. Traits such as peduncle elongation, fruit shape, leaf texture, and fruit color exhibit significant variation among the groups (Fig. 5), which aligns with the morphological characteristics traditionally used to differentiate these genera. The notable exception of the leaf margin trait highlights a potential area for further investigation, as its consistent values across groups may suggest a less discriminative role in this context. The distinction between Groups 2 and 3 primarily through fruit color emphasizes its importance in marketability and aesthetic value. Group 3's darker fruit color, often associated with higher quality and market appeal, suggests a potential economic advantage and underscores the need for further exploration into the commercial applications of these morphological traits.

In this study, phylogenetic analyses demonstrate that while *Schisandra* and *Kadsura* can be morphologically and geographically distinct, there are notable overlaps in their traits and distributions. This overlap, observed in Figs. 1, 2, 3 and 4, suggests that there might be underlying evolutionary connections between these genera. Our Bayesian molecular clock analysis, based on ITS sequences, reveals that both genera diverge into two major branches, pointing to distinct evolutionary paths. This divergence is crucial as it highlights how *Schisandra* and *Kadsura* have evolved in parallel from a common ancestor, adapting to different ecological niches over time (Fig. 6). Within the *Schisandra* genus, the clustering of *S. bicolor* with *Kadsura* species in the same branch underscores a close genetic relationship that transcends traditional genus boundaries. This clustering is supported by morphological trait analysis (Fig. 4A) and suggests that *S. bicolor* and *Kadsura* species might share more genetic and evolutionary similarities than previously recognized. Similarly, the grouping of *S. propinqua* and *S. plena* with *K. scandens* indicates that these species, despite their classification in different genera, exhibit substantial phylogenetic affinity. The observed genetic closeness between *Schisandra* and *Kadsura*, particularly in species such as *S. bicolor* and *K. scandens*, suggests a potential for hybridization. However, further research is needed to examine reproductive barriers (e.g., pollen tube inhibition, chromosomal mismatches, sterility) to confirm hybridization potential. The ITS-based molecular phylogenetic analysis provides valuable insights into the genetic relationships of potential hybrids, indicating that these genera may have the ability to interbreed under certain conditions. The clustering of *S. propinqua*, *S. bicolor*, *K. scandens*, and *S. plena* on similar branches suggests that these species might serve as a foundation for future crossbreeding efforts, with implications for both conservation and horticulture.

However, the matK sequences, which predominantly reflect maternal inheritance, offer a different perspective. The matK phylogenetic tree (Supplementary Fig. 1) delineates the *Schisandra* and *Kadsura* into five distinct parts, presenting a more detailed and complex picture of their evolutionary relationships. This complexity, as indicated by the matK data, reinforces the notion that while the genera are closely related, their phylogenetic relationships are intricate and may involve more nuanced genetic interactions than can be captured by traditional taxonomic methods. The potential for hybridization between *Schisandra* and *Kadsura* species opens exciting avenues for future research. The close genetic relationships observed suggest that inter-genus hybridization could be feasible, which may lead to the development of new plant varieties with desirable traits.

Conclusion

The analyses of distribution patterns, genetic diversity and morphological characteristics of *Schisandra* and *Kadsura* provide critical insights into their evolutionary adaptations and conservation needs. The consistent patterns of overlapping morphological traits and the discordance between nuclear and plastid phylogenetic signals generate a compelling hypothesis of possible historical hybridization or introgression between the genera. This hypothesis, however, requires direct testing through future experimental crosses and population genomic studies. If confirmed, this evolutionary relationship would offer promising avenues for research in conservation and horticulture. These findings underscore the importance of integrated morphological and genetic studies for understanding complex evolutionary relationships and for identifying key questions to guide future research on these species.

Abbreviations

PCA	Principal component analysis
OPLS-DA	Orthogonal Projections to Latent Structures Discriminant Analysis
UPGMA	Unweighted Pair Group Method with Arithmetic Mean
ITS	Internal Transcribed Spacer
FOC	Flora of China
GBIF	Global Biodiversity Information Facility
PC	Principal component
ROC	Receiver operating characteristic
AUC	Area under the curve
VIP	Variable Importance in Projection
ML	Maximum likelihood
CA	Cladistics analysis
NCBI GenBank	National Center for Biotechnology Information
CI	Confidence interval

Acknowledgements
Not applicable.

Authors' contributions

ZQ XIE & M GUO: Data curation, Formal analysis, Methodology, Investigation, Validation. MT, K C, HJ X, JX YANG & SQ FAN: Formal analysis, Investigation. Resources. Rafiq M & CS CHENG: Conceptualization, Supervision, Project administration, Methodology, Validation.

Funding
The authors gratefully acknowledge financial support from Jiangxi Province Double Thousand Talent-Leader of Natural Science Project (jxsq2023101038), Jiangxi Province Urgently Overseas Talent Project (2022BCJ25027), and the Key Research and Development Special Project of Jiangxi Province (S2023ZPYFB0294 & 20223BBH80007). This work was also funded by the Science and Technology Innovation Team Project in Key Areas of Jiujiang City Base and Talent Plan (S2022TDJS029), the Natural Science Foundation of Jiangxi Province of China (20242BAB25341) and the Special Project for Lushan Plants (2023ZWZX07).

Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

NA.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 30 April 2025 / Accepted: 2 January 2026

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