Selection of high-quality tree peony varieties suitable for the south Yangtze River area

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Abstract: To select tree peony varieties with high ornamental value suitable for the hot and humid environment of the south Yangtze River area, 74 tree peony varieties from the Chenshan Botanical Garden in Shanghai were selected as experimental materials. The experiment involved initial selection for leaf humidity and heat tolerance, assessing the ornamental value during the flowering period of the following year and measuring a series of indicators such as the relative chlorophyll content of the leaves. Methods including principal component analysis, cluster analysis, and comprehensive membership function were employed. The results indicated that among the varieties assessed for humidity and heat tolerance, 43 obtained a composite score of 3.75 or above. Upon further assessment of the flowering period for these 43 varieties in the subsequent year, 14 varieties clustered in the top tier based on their scoring for ornamental value. Then, during the summer season, physiological indicators were measured for the previously selected 14 tree peony varieties. Combining these data with the comprehensive membership function, the humidity and heat tolerance of each variety were quantified. The synthesis of scores, combined with cluster analysis, revealed that varieties including 'Yinhong Qiaodui,' Shengge Jin,' Linghua Zhanlu,' Baixue Gongzhu,' 'Di Guan,' and 'Cunsong Ying' exhibit both high ornamental value and tolerance to humidity and heat, making them suitable for cultivation in the south Yangtze River area.

Keywords: cluster analysis; ornamental evaluation; plant heat and humidity tolerance; principal component analysis; tree peony

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Tree peony (Paeonia section Moutan DC) is a traditional flower that is unique to China. Praised as the "king of flowers" by Chinese people, the tree peony is revered for its exceptional ornamental beauty and cultural symbolism (Li et al. 2011). All wild species of section Moutan are native to China (Yang et al. 2020). Tree peony has a cultivation history of over 2000 years in China, with four large cultivar groups having been formed, including Zhongyuan, northwest, southwest, and Jiangnan (Hong 2010; Hong 2011). In addition, there are several smaller cultivar groups, such as the Yan and Bao kang groups (Li et al. 2011). The tree peony cultivars in the Jiangnan group originated in the Tang and Song Dynasties and flourished in the Ming and Qing Dynasties, thereby possessing a long cultural history (Hu, Han 2018). The cultivars from this group originated from the Zhongyuan group, which has unique ornamental value and excellent heat and humidity tolerance as a result of long-term human-driven and natural selection. However, there are only about 30 species in the Jiangnan group (Hu et al. 2018). Traditional Jiangnan tree peony varieties such as 'Fengdan Fen' and 'Xiang Dan' exhibit remarkable adaptability to the high temperature and humid heat of the south Yangtze River area in summer, but their flower petal quality is poor, and they possess only a single colour and shape, resulting in overall low ornamental quality (Wang et al. 2007). The Jiangnan peony varieties are few and have low genetic diversity. The above factors greatly limit the promotion and application of tree peonies south of the Yangtze River.

Relatively limited research has focused on the selection of tree peony varieties for heat and humidity tolerance. The mainstream approach involves assessing various leaf physiological indicators during periods of high summer temperatures. Common methods for assessing heat and humidity tolerance include measurements of malondialdehyde levels, electrical conductivity, and peroxidase enzyme activity. These assessments, combined with techniques such as principal component analysis (PCA), can establish a comprehensive evaluation of heat and humidity tolerance traits in tree peony varieties (Li et al. 2023). To date, Wang et al. (2023a) and Yao et al. (2022) have found that high temperatures and humidity significantly impact various physiological aspects of tree peony, including photosynthetic electron transport, plant morphology, bio-membrane fluidity, permeability, as well as the activity of defensive enzymes and the expression of related genes (Wang et al. 2022), resulting in inhibited growth and development and subsequent weakened vigour and growth. The aim of this study was to use the natural conditions of high temperature and humidity in the south Yangtze River area as screening factors to select excellent tree peony varieties with good resistance to humidity and high ornamental value in order to identify high-quality tree peony varieties for cultivation in the region. The present study will not only provide fundamental support for the development of the peony industry but also offer valuable insights for expanding cultivation areas of certain flower varieties that are constrained by geographical and climatic conditions.

MATERIAL AND METHODS

The tree peony varieties used as test materials were all eight-year-old plants from the Peony Garden area of Shanghai Chenshan Botanical Garden (31°4'52" North longitude, 121°10'14" East latitude). These varieties were initially purchased from Luoyang Shenzhou Peony Garden in 2014 and have been grown under the same environmental and cultivation conditions since then.

Between August 4th and 5th, 2022, an assessment of leaf humidity and heat tolerance was conducted on 74 tree peony varieties [Figure S1 in electronic supplementary material (ESM)] within the garden area. This assessment served as an initial selection for tree peony varieties resilient to humidity and heat. Following this, during the tree peony flowering period in 2023, the retained varieties from the initial selection were subjected to ornamental evaluation. For each variety, three plants with equivalent growth potential were selected as replicates. When assessing the heat and humidity tolerance of leaves and the ornamental value of flowers, the same indicator was evaluated by a single evaluator in triplicate.

Based on this evaluation, rankings were established, and further selection was conducted. Subsequently, the remaining varieties underwent assessments for humidity and heat tolerance indicators. During sampling and assessments, efforts were made to avoid sampling individual plants grown under shade or plants with pest damage.

Initial selection for leaf humidity and heat tolerance. From August 4th to 5th, 2022, during peak temperatures between 37 °C and 40 °C, an assessment was conducted from 9 a.m. to 12 p.m., focusing on above-

ground humidity and heat traits. This evaluation targeted characteristics such as leaf curling, leaf yellowing, leaf wilting, and above-ground withering across 74 tree peony varieties within the garden, including 'Di Guan,' 'Baixue Gongzhu,' 'Wujin Yaohui,' among others, as part of the initial assessment for humidity and heat tolerance (Chen et al. 2022) (Table 1). Scores were assigned based on the plant's condition, rated on a five-point scale from high to low. To minimise fluctuations in measurements and subjective assessments, both the measurements and evaluations were carried out by the same individual.

Evaluation of the flowers. Based on the ornamental features outlined in Li's monograph on chinese tree peony (Li et al. 2011), and various literature on ornamental evaluations, the assessment of ornamental value included criteria such as petal density, petal texture, flower quantity, flower diameter, flowering period, and the position of the flowers on the plant (Ma 2023) (Table 2). The weights of each indicator and the composite evaluation scores of the tested varieties were calculated. Cluster analysis was then performed based on the composite scores, and physiological indicator measurements were conducted during the summer for

the varieties ranked in the top tier of the composite scores.

Humidity and heat tolerance determination and comprehensive membership function evaluation. Sampling took place from 9 a.m. to 12 p.m. on July 24th and July 25th in Shanghai under consistent weather conditions. The average temperature for the week prior to sampling ranged from 27 °C to 34 °C, with a relative humidity between 88% and 91%. Healthy tree peony leaves were selected, and measurements were taken for soil and plant analyser development content (SPAD), relative electrical conductivity (REC), soluble sugar content (SS), malondialdehyde content (MDA), catalase activity (CAT), and superoxide dismutase activity (SOD). Harvest the third or fourth leaf from the apex to the base on a single branch of each plant and replicate this procedure thrice. Transport them to the laboratory for quantification of physiological and biochemical indices. Each measurement for every plant should be replicated three times, and subsequently, an average value should be computed. The determination of the indicators was carried out according to the method described by Li (2000). The data of the measured indexes were analysed using the comprehensive af-

Table 1. Evaluation indicators and scores of tree peony leaves

Score	5	4	3	2	1
Leaf curling	no visible leaf curl	some leaves show slight curling of edges	leaf edges distinctly curled	leaf curled inward	leaf curled into a tube
Leaf yellowing	dense green leaf	slight greening of leaf	leaf shows some yellow spots	leaf yellow range up to half	individual leaves all yellowed
Leaf wilting	no leaf wilt	scorched spots on some leaves	increased scorching at the center of spots	wilt spots all over the leaves	most of the leaves wilted
Above-ground withering	above-ground parts are growing well	little wilting above the ground	partial scorching of branches above the ground	scorching of branches above the ground is nearly half	whole plant wilted above ground

Table 2. Evaluation indicators and scores of tree peony ornamental value

Score	5	4	3	2	1
Position of flowers	all above the leaf	partially above leaf level	level with the leaf	below but partly level with leaf	basically all below leaf
Petal density	9–10 layers	7–8 layers	5–6 layers	3–4 layers	1–2 layers
Flower quantity	20-15 flowers	15–12 flowers	12-8 flowers	5–8 flowers	0–5 flowers
Flower diameter	150 mm	130-150 mm	110-130 mm	90-110 mm	70-90 mm
Flowering period	12 days	10 days	7 days	5 days	3 days
Petal texture	petals stiff and well-layered	petals slightly soft and well-layered	petals soft and layered	petals soft, loosely layered	petals slightly wilted and loosely layered

filiation function method, and the indexes negatively correlated with resistance to moisture and heat (such as REC and MDA) were processed positively (Chen et al. 2020).

For positively correlated humidity and heat-resistant indicators, the membership function calculation formula was as follows:

$$U_{ij} = (X_{ij} - X_{j\min}) / (X_{j\max} - X_{j\min})$$
 (1)

For negatively correlated humidity and heat tolerance indicators, the membership function calculation formula was as follows:

$$U_{ij} = 1 - (X_{ij} - X_{j\min}) / (X_{j\max} - X_{j\min})$$
 (2)

where: Uij – humidity and heat resistance membership function value of the $i^{\rm th}$ category for the $j^{\rm th}$ indicator; X_{ij} – measured value of the $j^{\rm th}$ indicator for the $i^{\rm th}$ category; $X_{j\min}$ – minimum value of all categories for the $j^{\rm th}$ indicator; $X_{j\max}$ – maximum value of all categories for the $j^{\rm th}$ indicator; i – specific variety; j – particular indicator.

The aforementioned formula was used to calculate the membership values encompassing indicators for each variety.

Statistical analysis. The PCA, cluster analysis and variance analysis were performed using SPSS version 26.0 software (IBM Corp., Armonk, NY, USA). Excel 2016 (Microsoft Corp., Redmond, WA, USA) was used for comprehensive membership function calculation and graphical representation. The statistical significance of differences between three experimental groups was assessed by using a two-tailed Student's t-test. Differences between the two datasets were considered significant at P < 0.05.

RESULTS

Initial assessment of humidity and heat tolerance in the leaves of various tree peony varieties.

Through the initial selection of leaf phenotypes, tree peony varieties with final scores above 3.75 were considered as the good standard from a pool of 74 varieties (Table S1 in ESM). Some varieties showed poor performance, such as 'Zhao Fen, Zhi Yu', and 'Dazong Zi', which scored only between 2.5 and 1 (Table S1, ESM). Among the evaluated varieties, a final selection of 43 tree peony varieties, in-

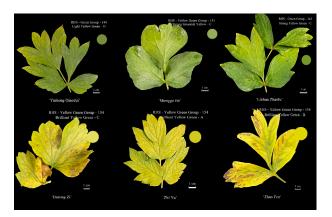


Figure 1. Photos of some tree peony leaves
Upper part – varieties with good leaf conditions under hot
and humid conditions; lower part – varieties with extremely
poor leaf conditions under hot and humid conditions
RHS – the Royal Horticultural Society colour chart (specific
colour codes)

cluding 'Di Guan,' 'Baixue Gongzhu' and 'Wujin Yaohui,' showed excellent leaf performance under high temperature and high humidity conditions (Figure 1). These were further selected as candidates for the following year's flowering period based on their ornamental value. The aforementioned varieties then underwent an evaluation for their ornamental value during the following year's flowering period.

Ornamental evaluation of the tree peony varieties. According to the ornamental evaluation criteria, various indicators for the 43 tree peony varieties were assessed and scored after the initial selection (Table 3), and PCA was performed on six indicators: petal density, petal texture, flower quantity, flower diameter, flowering period, and position of the flowers on the plant. Three principal components were then extracted through variance decomposition. The contribution rates of variance for the first three principal components reached 26.3%, 20.3%, and 19.9%, with a cumulative variance contribution rate of 66.5%. Subsequently, based on the results of the PCA, weights for each indicator were calculated.

The composite score was computed by combining these scores using the following formula:

$$Y = 0.20057425X_1 + 0.15157101X_2 + 0.14728445X_3 + 0.15641859X_4 + 0.17281922X_5 + 017133249X_6$$
 (3)

where: Y – composite score of the variety; X_1 – X_6 – evaluation scores of the variety's indicators (petal density, petal texture, flower quantity, flower diameter, flowering period and position of the flowers on the plant).

Table 3. Score of flower ornamental indexes for 43 tree peony varieties

Varieties	X_1	X_2	X_3	X_4	X_5	X_6	Varieties	X_1	X_2	X_3	X_4	X_5	X_6
'Di Guan'	5	5	2	5	3	5	'Xueying Taohua'	5	1	4	3	2	5
'Baixue Gongzhu'	5	5	4	5	3	4	'Yuegong Zhuguang'	5	5	5	5	2	4
'Wujin Yaohui'	5	5	3	4	4	4	'Wulong Pengsheng'	5	5	1	2	1	4
'Tianxiang Xiancai'	4	3	3	3	3	3	'Fenzhong Guan'	1	5	1	4	3	3
'Hong Yu'	4	5	4	4	4	4	'Fen Lian'	5	4	4	4	4	5
'Juanye Hong'	5	3	3	5	2	4	'Hong Tu'	5	4	2	5	3	3
'Shengge Jin'	5	4	3	5	3	4	'Linghua Zhanlu'	5	4	4	4	3	4
'Yumian Taohua'	5	4	5	5	3	4	'Morun Juelun'	4	4	4	5	2	3
'Hu Hong'	5	3	3	4	2	3	'Moyu Zhenghui'	4	4	2	3	2	4
'Yinhong Qiaodui'	5	4	2	5	4	5	'Lvmu Yinyue'	5	4	2	3	4	3
'Shouan Hong'	5	3	2	2	4	4	'Ying Hong'	5	1	1	4	2	5
'Zhuguang Morun'	4	5	3	5	4	4	'Dao Jin'	5	2	5	4	5	5
'Yu Hong'	5	3	3	4	2	3	'Shanhu Tai'	5	3	5	4	3	5
'Nihong Huancia'	3	4	2	2	2	3	'Tong Yun'	4	3	4	4	2	4
'Xiang Yu'	2	5	2	3	2	4	'Moyu Jinhui'	5	3	1	4	3	4
'Baiyuan Hongxia'	2	4	1	3	4	3	'Huang Guan'	4	5	3	4	3	4
'Cusong Ying'	4	5	2	5	3	5	'Hongshi Zi'	5	4	2	5	2	4
'Tai Yang'	4	3	3	4	3	4	'Luoyang Hong'	5	5	2	2	2	3
'Riyue Jin'	5	4	2	2	2	3	'Xu Gang'	5	2	4	4	2	5
'Yuhou Fengguang'	5	3	2	3	2	4	'Fang Ji'	3	3	2	3	3	4
'Ri Mu'	4	3	2	3	4	4	'Cai Hui'	2	1	2	5	2	3
'Fen Dan'	2	3	3	5	5	3							

 X_1 – X_6 – petal density, petal texture, flower quantity, flower diameter, flowering period, position of the flowers

Cluster analysis was conducted based on the composite scores, categorising each variety into four different grading levels (Table 4).

The top tier consisted of 'Dao Jin', 'Fen Lian', 'Baixue Gongzhu', 'Yumian Taohua', 'Yuegong Zhuguang', 'Yinhong Qiaodui', 'Di Guan', 'Wujin Yaohui', 'Shanhu Tai', 'Zhuguang Morun', 'Hong Yu', 'Shengge Jin', 'Linghua Zhanlu', and 'Cunsong Ying'. These 14 varieties scored the highest in composite ornamental value (Figure 2).

Effect of high humidity and heat tolerance performance of the physiological indicators of 14 tree peony varieties with high ornamental value. The performance of the aforementioned 14 varieties was evaluated in terms of summer humidity tolerance. Measurements were taken for the indicators of SPAD, REC, CAT, SOD, MDA, and SS. The SPAD value of the leaves quantitatively reflects the chlorophyll content and thereby indicates the extent of damage caused by high humidity and heat. All tree peony varieties assessed exhibited SPAD values above 45 mg/g, with 'Shengge Jin' showing the highest SPAD value among all tested varieties, reaching

65 mg/g. This variety showed a significant advantage compared to the other varieties. Additionally, most varieties, such as 'Di Guan', 'Linghua Zhanlu', 'Hong Yu,' 'Yinhong Qiaodui,' 'Cunsong Ying,' and 'Yumian Taohua', exhibited relatively good SPAD content indicators, exceeding 50 mg/g. Although 'Fen Lian' and 'Baixue Gongzhu' showed slight leaf discolouration, their SPAD values were still 12.1% and 14.2% higher, respectively, than that of 'Dao Jin' at 45 mg/g (Figure 3A). The REC is associated with the relative permeability of plant cell membranes. The higher the membrane permeability, the greater the degree of stress the plant experiences. 'Shengge Jin' and 'Fen Lian' both exhibited REC values within 10%, indicating minimal damage to their cell membranes. Meanwhile, 'Yuegong Zhuguang', 'Linghua Zhanlu, 'Cunsong Ying' and 'Baixue Gongzhu' showed REC values between 10.8% and 11.7%, also exhibiting relatively good performance (Figure 3B). The REC values among the 14 varieties were significantly different. Among them, 'Zhguang Morun' recorded the highest relative conductivity at 18.15%, approximately 30% higher than that of 'Wujin Yao-

Table 4. Composite score and ranking of the ornamental value of 43 tree peony varieties

Varieties	Composite score	Rank	Varieties	Composite score	Rank
'Dao Jin'	4.39	Rank I	'Tong Yun'	3.5	Rank II
'Fen Lian'	4.37	Rank I	'Fen Dan'	3.46	Rank II
'Baixue Gongzhu'	4.34	Rank I	'Shouan Hong'	3.44	Rank II
'Yumian Taohua'	4.33	Rank I	'Moyu Jinhui'	3.43	Rank II
'Yugong Zhuguang'	4.31	Rank I	'Xueying Taohua'	3.42	Rank II
'Yinhong Qiaodui'	4.23	Rank I	'Ri Mu'	3.4	Rank II
'Di Guan'	4.21	Rank I	'Hu Hong'	3.38	Rank II
'Wujin Yaohui'	4.2	Rank I	'Yu Hong'	3.38	Rank II
'Shanhu Tai'	4.19	Rank I	'Yuhou Fengguang'	3.25	Rank III
'Zhuguang Morun'	4.16	Rank I	'Luoyang Hong'	3.23	Rank III
'Hong Yu'	4.15	Rank I	'Moyu Zhenghui'	3.2	Rank III
'Shengge Jin'	4.04	Rank I	'Tianxiang Xiancai'	3.2	Rank III
'Linghua Zhanlu'	4.03	Rank I	'Ying Hong'	3.13	Rank III
'Cunsong Ying'	4.01	Rank I	'Wulong Pengsheng'	3.08	Rank III
'Huang Guan'	3.83	Rank II	'Riyue Jin'	3.08	Rank III
'Xu Guang'	3.72	Rank II	'Fang Ji'	3.02	Rank III
'Hong Tu'	3.72	Rank II	'Xiang Yu'	2.95	Rank III
'Hongshi Zi'	3.72	Rank II	'Baiyuan Hongxia'	2.83	Rank IV
'Juanye Hong'	3.71	Rank II	'Fenzhong Guan'	2.76	Rank IV
'Morun Juelun'	3.64	Rank II	'Nihong Huancai'	2.68	Rank IV
'Lvmu Yinyu'	3.58	Rank II	'Cai Hui'	2.49	Rank IV
'Tai Yang'	3.53	Rank II		_	

hui. This suggests that under the same conditions, 'Zhuguang Morun' experiences a higher degree of stress compared to the other varieties.

Under identical temperature and humidity conditions, we assessed the SOD enzyme activity and CAT enzyme activity in the leaves of the 14 tree peony

varieties. The results indicated that varieties such as 'Yinhong Qiaodui,' 'Di Guan,' 'Yumian Taohua,' 'Fen Lian,' and 'Wujin Yaohui' exhibited higher levels of SOD activity (Figure 4A). Among them, 'Yinhong Qiaodui' exhibited the highest SOD activity at 437.6 U/g, which was significantly higher



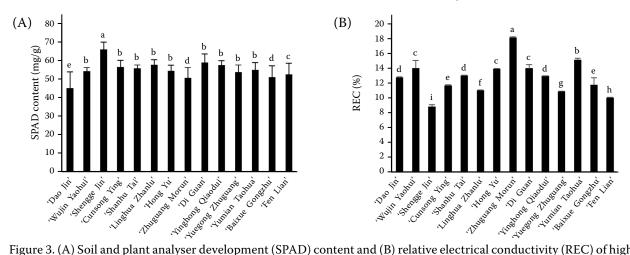


Figure 3. (A) Soil and plant analyser development (SPAD) content and (B) relative electrical conductivity (REC) of high ornamental tree peony cultivars leaves

 $^{^{}a-i}$ the same lowercase letters above the columns indicate significant differences between the treatments (P < 0.05)

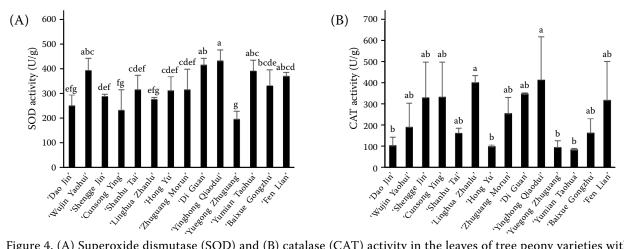


Figure 4. (A) Superoxide dismutase (SOD) and (B) catalase (CAT) activity in the leaves of tree peony varieties with high ornamental value

 $^{^{}a-g}$ the same lowercase letters above the columns indicate significant differences between the treatments (P < 0.05)

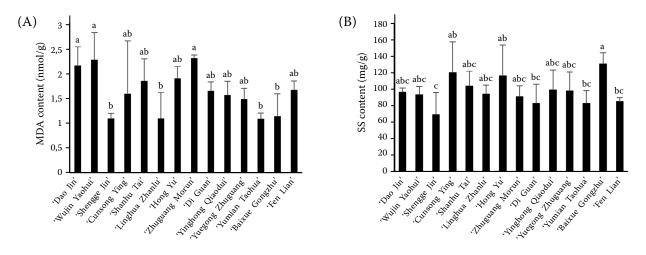


Figure 5. (A) Malondialdehyde (MDA) and (B) plant soluble sugar (SS) content in the leaves of tree peony varieties with high ornamental value

 $^{^{}m a-c}$ the same lowercase letters above the columns indicate significant differences between the treatments (P < 0.05)

than that of the majority of varieties (ranging from 300 U/g to 350 U/g). However, a few varieties, such as 'Yuegong Zhuguang', 'Cunsong Ying', and 'Dao Jin', showed lower SOD enzyme activity, maintaining levels between 200 U/g and 253 U/g. These findings indicate that the varieties exhibiting lower activity were significantly affected by high-temperature and high-humidity climates, experiencing substantial impediments in SOD synthesis. It also indicates that these varieties have inferior tolerance of humidity and heat. The CAT activity varied significantly among the 14 tree peony varieties, with 'Linghua Zhanlu' and 'Yinhong Qiaodui' showing the highest CAT activity at 419 U/g and 406 U/g, respectively. Other varieties, including 'Di Guan', 'Shengge Jin', 'Cunsong Ying,' and 'Fen Lian,' also exhibited activity within the range of 200–350 U/g. The relatively high CAT activity in these tree peony varieties indicates their heightened capability to eliminate peroxides, safeguarding cells from damage caused by oxidative stress under high temperatures and high humidity. The varieties with lower SOD activity, such as 'Dao Jin' and 'Yuegong Zhuguang', showed similar CAT activity, with values of only 84 U/g and 95 U/g, respectively (Figure 4B). This indicates that these varieties have weaker peroxide elimination capabilities under high-temperature and high-humidity stress conditions, resulting in potential cell damage.

We assessed the MDA and SS content in the leaves of the 14 tree peony varieties. Varieties such as 'Yumian Taohua', 'Linghua Zhanlu', 'Shengge Jin', and 'Baixue Gongzhu' exhibited lower MDA content compared to other varieties, with an average MDA content of only 1.09 nmol/g. This suggests that these varieties experienced minimal damage to their cell membrane structure under high temperatures and high humidity. However, some varieties, including 'Zhuguang Morun,' 'Wujin Yaohui,' and 'Dao Jin,' showed relatively higher MDA content, significantly surpassing the lower content observed in the aforementioned four tree peony varieties, with MDA contents of 2.29 nmol/g, 2.26 nmol/g and 2.15 nmol/g, respectively. The elevated MDA levels in these varieties suggest their lower tolerance to high temperature and high humidity, weaker antioxidative capability, and damage to cell membrane structure, leading to an accumulation of more peroxides within the cells (Figure 5A).

The SS content among the 14 varieties differed only slightly. Varieties such as 'Baixue Gongzhu', 'Cunsong Ying', and 'Hong Yu' exhibited higher SS contents, reaching 130 mg/g, 120 mg/g and 115 mg/g, respectively (Figure 5B). These results indicate that based solely on the SS content, these initially selected varieties exhibited relatively minimal damage after experiencing high temperature and high humidity stress. By enhancing respiration to consume their own sugars, they maintained their cell membrane integrity, demonstrating robust tolerance to wet heat stress.

The composite scores of the 14 tree peony varieties under heat and humidity stress. The membership values of each tested indicator for every variety were calculated using the abovementioned formula. The membership values of each indicator were summed to obtain the comprehensive membership value for the variety, representing its tolerance to wet and hot conditions (Table 5).

Then, systematic clustering was conducted based on the obtained composite scores to rank the 14 highly ornamental tree peony varieties according to their tolerance to wet and hot conditions (Figure 6).

When the Euclidean distance was set at 5, the tree peony varieties were divided into three gradients. The best-performing varieties included 'Yinhong Qiaodui,' 'Shengge Jin,' 'Ling Hua Zhan Lu,' 'Baixue Gongzhu,' 'Di Guan,' 'Cunsong Ying,' and 'Fen Lian.' Those with average performance included 'Yumian Taohua,' 'Shanhu Tai,' 'Hong Yu,' 'Wujin Yaohui,' and 'Yuegong Zhuguang.' The poor performers included 'Zhuguang Morun' and 'Dao Jin.'

Table 5. Membership function of high ornamental tree peony varieties

Varieties	Rank	Composite score
'Yinhong Qiaodui'	Rank I	0.71
'Shengge Jin'	Rank I	0.69
'Linghua Zhanlu'	Rank I	0.68
'Baixue Gongzhu'	Rank I	0.62
'Di Guan'	Rank I	0.60
'Cunsong Ying'	Rank I	0.59
'Fen Lian'	Rank I	0.57
'Yumian Taohua'	Rank II	0.48
'Shanhu Tai'	Rank II	0.46
'Hong Yu'	Rank II	0.42
'Wujin Yaohui'	Rank II	0.41
'Yuegong Zhuguang'	Rank II	0.40
'Zhuguang Morun'	Rank III	0.27
'Dao Jin'	Rank III	0.23

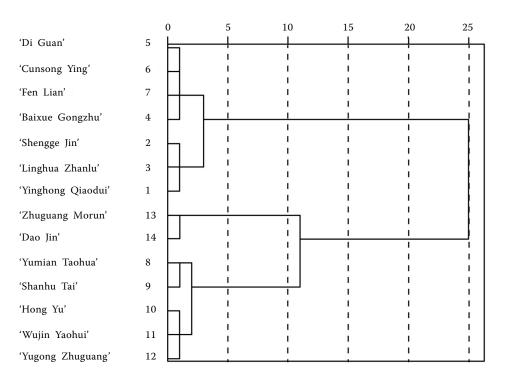


Figure 6. Cluster genealogy of composite scores for the heat and humidity tolerance of tree peony varieties with high ornamental value

DISCUSSION

Plants employ various responses to sustain normal growth under conditions of high humidity and heat stress (Wang et al. 2023b). Photosynthesis is sensitive to high-temperature and high-humidity environments, and chlorophyll content directly reflects the photosynthetic capacity of a plant. Hence, chlorophyll content is often used as an indicator to assess plant suitability (Liao et al. 2017). In this study, the selected tree peony varieties with better adaptability, such as 'Yinhong Qiaodui,' 'Shengge Jin,' 'Linghua Zhanlu,' and 'Baixue Gongzhu', exhibited relatively stable SPAD values under high-temperature and highhumidity conditions. This was reflected in the overall leaf condition, with minimal yellowing, curling, and leaf death. By contrast, varieties with lower SPAD values, including 'Zhuguang Morun' and 'Dao Jin', experienced a more significant degradation in chlorophyll content due to high temperatures. This resulted in noticeable leaf yellowing and curling compared to the better-performing varieties. The observed leaf phenotypes were closely correlated with the SPAD values, confirming SPAD as a reliable indicator for measuring plant tolerance to humidity and heat.

When plants encounter environmental stress, they generate reactive oxygen species (ROS), leading

to the production of peroxides (Li et al. 2022). If the ROS cannot be promptly eliminated, plants may suffer irreversible damage (Wei et al. 2020). The plants exhibit an excessive production of ROS in response to drought stress, leading to cellular membrane damage and subsequent protein denaturation and inactivation (Gill, Tuteja 2010; Uzilday et al. 2012). The study showed that the crucial protective enzymes SOD and CAT typically work together to remove peroxides, serving as a defence mechanism against adverse conditions (Liang et al. 2023; Liao et al. 2023). Among the seven well-adapted varieties identified in this study, "Yinhong Qiaodui, 'Yumian Taohua,' and 'Fen Lian' maintained relatively high activity of these protective enzymes under adverse conditions. This indirectly indicates their strong adaptability to high-temperature and high-humidity environments. Conversely, 'Dao Jin', as a Japanese tree peony variety, exhibited lower SOD and CAT enzyme activities, aligning with findings from other studies (Li et al. 2023).

Plants accumulate MDA under stressful conditions, which, as a peroxidation product, exerts strong toxicity on cells (Zhao et al. 2021). The quantity of MDA produced in hot and humid environments exhibits a negative correlation with plant tolerance. Typically, MDA content is used inversely to represent a plant antioxidant capacity (Zheng et al. 2021).

Research on tree peony, Sassafras (Sassafras tzumu Hemsl.) and Magnolia (Magnolia denudate Desr.) suggest that these plants accumulate a significant amount of MDA under conditions of drought and waterlogging stress. The higher the content of MDA, the greater the damage inflicted upon plants, indicating a diminished resistance to stress (Wang et al. 2020). The tree peony varieties, including 'Dao Jin', 'Zhuguang Morun', and 'Wujin Yaohui', exhibited suboptimal performance in terms of SPAD, SOD, and CAT indicators, as well as MDA indicator results. This implies that MDA serves as a reliable indicator for evaluating the robustness or vulnerability of a plant stress tolerance. Osmoregulation is a pivotal process employed to alleviate stress and safeguard plants against drought-induced damage (Zhang et al. 2017). Soluble sugars within the plant play a critical role in osmotic regulation, wherein higher intracellular soluble sugar content signifies reduced impairment to biological membranes (Liu 2020). Among the 14 tree peony varieties examined in this study, 'Baixue Gongzhu', 'Cunsong Ying, 'Hong Yu,' and 'Yuegong Zhuguang' exhibited elevated levels of SS. This observation suggests that these particular varieties exhibit higher SS contents under hot and humid conditions. In conjunction with the previously obtained results for MDA and REC, these varieties demonstrate exceptional performance across various indicators of heat and humidity resistance, indicating excellent membrane permeability. Moreover, these varieties promptly regulate intracellular osmotic pressure in response to environmental stress.

In previous studies, most researchers only relied on the measurement of physiological and biochemical indicators to screen out tree peony varieties with stress resistance (Zhu et al. 2020). Through this approach, the screened varieties exhibited favourable stress tolerance. However, their ornamental value might be limited, thereby reducing their practical application potential. The drawback of the disconnection between tolerance and ornamental value was particularly evident in the screening of peony varieties. For instance, the traditional variety Fengdan from the southern Yangtze River region demonstrated excellent tolerance to high temperature and humidity but possessed single white petals that lacked aesthetic appeal. Herein, we aimed to select tree peony varieties based on a combination of high ornamental value and strong adaptability in the south Yangtze River area. Therefore, we initially began by assessing the leaf phenotype of the 74 tree peony varieties, resulting in the selection of 43 varieties with promising characteristics. Considering the flowering period of the remaining varieties, we then used PCA and cluster analysis to narrow the selection down to 14 tree peony varieties with high ornamental value. Based on this result, we conducted assessments of resistance to heat and humidity, effectively combining ornamental characteristics with resistance to heat and humidity. We then obtained high-quality tree peony varieties suitable for the south Yangtze River area. Among them, varieties with both high ornamental value and strong adaptability included 'Yinhong Qiaodui', 'Shengge Jin', 'Linghua Zhanlu', 'Baixue Gongzhu', 'Di Guan', and 'Cunsong Ying'. Varieties with moderate performance included 'Yumian Taohua,' 'Shanhu Tai,' 'Hong Yu,' 'Wujin Yaohui,' and 'Yuegong Zhuguang'. Varieties with poor performance included 'Zhuguang Morun' and 'Dao Jin'. The varieties 'Yinhong Qiaodui, 'Shengge Jin, 'Linghua Zhanlu,' 'Baixue Gongzhu, 'Di Guan,' and 'Cunsong Ying' not only possessed strong resistance to humidity and heat but also exhibited exceptional ornamental characteristics, making them suitable for cultivation in the south Yangtze River area. The seven tree peony varieties obtained through rigorous selection in this study exhibit a harmonious combination of aesthetic appeal and environmental resilience, marking the first instance where both aspects have been integrated into variety screening. This achievement elevates the practical value of such research by enhancing its applicability. Tree peony cultivars possessing these dual advantages not only prove more suitable for cultivation in the southern Yangtze River region, thereby generating greater economic benefits but also serve as a foundation for future breeding programs targeting heat and humidity tolerance, as well as investigations into molecular mechanisms and related studies.

REFERENCES

Chen X.P., He M.M., Wang W., Li X.W., Zheng Y.X., Zhang J.F., Dai S.P. (2020): Effects of high-temperature stress on physiological and biochemical indexes of leaves of two species of tulip orchids. Chinese Agricultural Science Bulletin, 36: 72–77. (in Chinese)

Chen Y., Zhou X.Y., Xiao H.W., Zhu J.J., Huang W.C., Peng D.H. (2022): Heat and humidity tolerance of five

- Salvia species. Journal of Northwest Forestry University, 37: 45–50. (in Chinese)
- Gill S.S., Tuteja N. (2010): Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry, 48: 909–930.
- Hong D.Y. (2010): Peonies of the World: Taxonomy and Phytogeography. Richmond, Kew Publishing; St. Louis, Missouri Botanical Garden Press.
- Hong D.Y. (2011): Peonies of the World: Polymorphism and Diversity. Kew, Royal Botanic Gardens Kew Publishing; St. Louis, Missouri Botanical Garden Press.
- Hu Y.H., Han J.G. (2018): Tree Peony, Its Varieties, Cultivation and Use in East China. Beijing, Science Press. (in Chinese)
- Li H.S. (2000): Principles and Techniques of Plant Physiology and Biochemistry Experiments. Beijing, Higher Education Pres:, 57–162. (in Chinese)
- Li J.J., Zhang X.F., Zhao X.Q. (2011): Chinese Tree Peony. Beijing, Encyclopedia of China Publishing House. (in Chinese)
- Li M., Cheng Z.Y., Tao J., Meng J.S. (2023): Heat tolerance analysis of 38 tree peony varieties. Molecular Plant Breeding, 22:5758–5768. (in Chinese)
- Li Y.H., Liu J.H., Mi J.J., Lv P., Pan Y., Zhao B.P., Allen X. (2022): Response of active oxygen scavenging system in oat leaves to humic acid water-soluble fertiliser application under severe drought stress. Acta Botanica Boreali-Occidentalia Sinica, 42: 803–810. (in Chinese)
- Liang J.C., Liao J.Y., Cao S.J., Xu K., Wu L.S. (2023): Effects of high temperature stress on the growth and physiology of three species of rhododendrons. Northern Horticulture, 18: 54–62. (in Chinese)
- Liao D., Chen J., Liu Q., Cheng Y., Wu J.Y., Chen M.G., Wu Z., Yan, J.X. (2017): Response of water-logging stress on cholorophyll content and anti-oxydant enzyme of Cyclobalanopsis glauca seedling provenances clone. Journal of Central South University of Forestry & Technology, 37: 1–6. (in Chinese)
- Liao Z.F., Liu H., Shen Y.Y., Xie G.Y., Wei G.L., Qin. S.S., Mou J.H., Wei K.H. (2023): Response of antioxidant enzyme system during adversity stress in medicinal plants. Molecular Plant Breeding, (early access), 1–18. (in Chinese)
- Liu K.Q. (2020): Effects of water stress on growth and yield components of oat. [Masters Thesis.] Xining: Qinghai University. (in Chinese)
- Ma Y.Y. (2023): Comprehensive evaluation of tree peony ornamental value based on hierarchical analysis method. Modern Horticultural, 46: 114–116. (in Chinese)
- Uzilday B., Turkan I., Sekmen A.H., Ozgur R., Karakaya H.C. (2012): Comparison of ROS formation and antioxidant enzymes in *Cleome gynandra* (C4) and *Cleome spinosa* (C3) under drought stress. Plant Science, 182: 59–70.

- Wang J., Hu Y.H., Zhang Q.X. (2007): Research on tree peony varieties in Jiangnan. Northern Horticulture, 160–162. (in Chinese)
- Wang K., Yang S.H., Ding Y.L. (2023a): Advances in uncovering mechanisms of plant responses to heat stress. Plant Physiology Journal, 59: 759–772.
- Wang M.J., Peng J., Qi L.J., Li J.G. (2023b): Research advances on light control of plant responses to abiotic stresses. Plant Physiology Journal, 59: 682–704.
- Wang X.X., Fang Z.W., Zhao D.Q., Tao, J. (2022): Effects of high temperature stress on photosynthetic characteristics and antioxidant enzyme system of *Paeonia ostii*. Phyton (Buenos Aires), 91: 599–615.
- Wang Y.S., Fang W., Wang X.T., Zhao X.T., Liao G.L., Duan J., Ma L.Y. (2020): Effects of waterlogging stress on growth, physiological and piochemistry characteristics of *Magnolia wufengensis*. Journal of Beijing Forestry University, 42: 35–45. (in Chinese)
- Wei Q., Xu C., Li K.X., He H.J., Xu Q.J. (2020): Advances in the study of superoxide dismutase and plant stress tolerance. Plant Physiology Journal, 56: 2571–2584.
- Yang Y., Sun M., Li S.S., Chen Q.H., Silva J.A.T., Wang A.J., Yu X.N., Wang L.S. (2020): Germplasm resources and genetic breeding of *Paeonia*: A systematic review. Horticulture Research, 7: 107.
- Yao Y.P. (2022): Mining of genes in tree peony in response to high temperature stress based on transcriptome sequencing technology. Central South University of Forestry & Technology, 67–70. (in Chinese)
- Zhang M., Wang L.F., Zhang K., Liu F.Z., Wan Y.S. (2017): Drought-induced responses of organic osmolytes and proline metabolism during pre-flowering stage in leaves of peanut (*Arachis hypogaea* L.). Journal of Integrative Agriculture, 16: 2197–2205.
- Zheng S.L., Lin Y., Huang Y., Liu L. (2021): Effect of hightemperature stress on physiological characteristics of two alumina-rooted potted cultivars. Journal of Minnan Normal University, 34: 114–118. (in Chinese)
- Zhao C.Y., Si J.H., Feng Q., Yu T.F., Luo H., Qin J. (2021): Ecophysiological responses to drought stress in *Populus euphratica*. Sciences in Cold and Arid Regions, 13: 326–336.
- Zhu L.Q., Fan L.K., Fu Q. (2020): Evaluation of tree peony ornamental value in Hangzhou West Lake Scenic Spot and the effect of different flower bud pruning on the growth potential of tree peony. Modern Horticultural, 43: 20–22. (in Chinese)

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