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The China orchid industry: past and future perspectives

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Abstract

There are nearly 30,000 species of orchids globally, of which over 1,700 species are found in China. Orchids share a profound and intimate connection with Chinese society. With the rapid development of science and technology, China's orchid industry has flourished with many scientific and technological achievements. Here, we summarize the developmental history, current situation, latest research achievements, and industrialization technology of the orchid industry in China, and present a discussion and outlook on the future development direction of orchid research in China. This review unveils new prospects for the high-quality advancement of China's orchid industry.

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Introduction

China is one of the pioneers in the cultivation of orchids and currently holds the largest orchid planting area in the world. Aromatic terrestrial orchids, often referred to as traditional Chinese orchids, display unique attributes, such as fragrance, purity, elegance, and harmony. Since the 1980s, following China's economic reforms, tropical orchids, including *Phalaenopsis* and *Dendrobium*, are introduced in abundance over time. These orchids become integral components of the floriculture industry in China. Simultaneously thriving, the native Chinese orchids and their tropical counterparts have propelled China to the forefront of orchid cultivation.

Over the past two decades, the global orchid market has seen robust growth, but there has been a shift in production trends. Potted orchids now dominate over cut orchid flowers in both production and demand. Countries like China, the Netherlands, and the USA have now overtaken Japan and Korea as primary potted orchid producers. China has now emerged as a key player in cut orchid flower production, whereas countries such as the USA and Japan have faced a decline in their production.

The evolution of the orchid industry sector is closely associated with the technological advancements. Through dedicated efforts of orchid researchers, China's orchid resources have been extensively investigated, and a rigorous orchid conservation system has been put in place. Significant strides have also been made in orchid breeding. New testing guidelines for DUS characteristics of varieties like *Oncidium* and *Cattleya* are now available. As of March 2022, there have been 1,212 applications for new orchid plant varieties, with 372 receiving approvals. Over 21 orchid species have their high-quality genomes mapped, and substantial research advancements have been achieved in cytology, physiology, genetics, reproduction, and cultivation of orchids.

Development history of the orchid industry

China has fostered a unique orchid culture, embodying attributes like fragrance, purity, elegance, and harmony. The foundational era of this culture can be traced back to the Spring and Autumn Period (770 BC−221 BC). Notable figures like Confucius (551 BC−479 BC) has lauded orchids as the 'king of fragrance'. Goujian (496 BC−464 BC) has showcased his resilience by planting orchids, while Qu Yuan (340 BC−278 BC) has wore them as a symbol of his integrity. Post the Tang Dynasty (618−907), these plants have gained immense popularity among researchers, rulers, and military leaders.

Unlike Western preferences, China holds a special reverence for particular fragrant flowers within the *Cymbidium* genus, commonly referred to as Chinese orchids. This includes species such as *Cymbidium goeringii*, *Cymbidium faberi*, *Cymbidium sinense*, *Cymbidium ensifolium*, *Cymbidium tortisepalum*, *Cymbidium tortisepalum* var. longibracteatum, *Cymbidium serratum*, *Cymbidium kanran* and *Cymbidium szechuanicum*. During the Song Dynasty, Huang Tingjian (1045−1105) was the first to classify *Cymbidium goeringii* and *Cymbidium faberi*, noting the difference based on the number of flowers in their inflorescence. Zhao Shigeng's (1233) renowned work, Jinzhang Lanpu, stands as the earliest global record of orchids, documenting various cultivars. Chunlan Tu, the artwork of Zhao Mengjian (1199−1264), is considered the oldest renowned orchid depiction. In the Ming Dynasty, Zhang Yu (1323−1385) extolled the beauty of *Cymbidium* foliage in his writings, emphasizing their value over the flowers, and detailed the graceful shape of *Cymbidium* leaves (Fig. 1a–e). In his poetry, he mentions that 'Leaves are more valuable than flowers', and expressed his deep appreciation for leaf color and shape variegation. The Qing Dynasty witnesses Bao Yiyun (1708−1778) introducing varied petal types of Chinese orchids in his literary work Yi Lan Zha Ji (Fig. 1f–o). This classification was subsequently expanded upon by several researchers (Table 1).

Fig. 1 (a)–(e) Natural mutant of leaf colours and (f)–(o) natural mutant (varieties) of flower types in Chinese orchid, Bar = 1 cm.

Table 1. The number of Chinese orchid (*Cymbidium*) cultivars documented in the references.

Year	*Cymbidium goeringii*	*Cymbidium faberi*	*Cymbidium sinense*	*Cymbidium ensifolium*	*Cymbidium tortisepalum*	*Cymbidium tortisepalum* var. *longibracteatum*	*Cymbidium kanlan*	*Cymbidium serratum*	Total	Authors/ publications
1233			18	21					39	Zhao Shigeng, *Jin Zhang Lan Pu*
1865	25	31							56	Xu Jilou, *Lanhui Tongxinlu*
1900	2		21	100					123	Ou Jinche, *Linghai Lanyan*
1923	66	40							141	Wu Enyua, *Lanhui Xiaoshi*
1993	132	70	144	61	7	4	11		429	Wu Yingxiang, *Chinese Cymbidium*
2010	183	145	234	156	141	168	111	119	1,257	Chen Xinqi, *Complete Book of Chinese Cymbidium* and its varieties

In modern times, coinciding with China's economic reforms, the 1980s marked a revival in the orchid industry. In 1987, the China Orchid Association was founded in Guangdong. This association inaugurated the first China Orchid Expo in 1988 in Guangzhou. Since then, this event has been held 30 times. The appreciation of orchids has evolved over time, with a shift from traditional petal shapes to a more diverse range, including various flower types and leaf color forms. This evolution has significantly boosted China's orchid industry.

Since the 1980s, tropical orchids including *Phalaenopsis*, hybrid *Cymbidium* and *Cattleya* (commonly known as foreign orchids) have been introduced in large numbers, which have gained significant importance in China's flower industry (Tables 2 & 3). Domestic orchids and foreign orchids are developing hand in hand. The orchid planting scale of China ranks No.1 in the world. According to the Ministry of Agriculture's national flower statistics, in 2017, the country's orchid category expanded over an area of 11,664 hectares, accounting for 9.8% of the country's potted flower planting area. The potted flowers received a sale of 9.02 billion yuan, accounting for 23.6% of the country's potted flower sales.

Orchid resources and protection

China stands out as one of the global leaders in orchid diversity. As documented in the Flora Republicae Popularis Sinicae (1999), China boasts 171 genera and 1,247 orchid species[1]. In 2018, the National Forestry and Grassland Bureau initiated a comprehensive survey of wild Orchidaceae resources. This survey covered key orchid-rich provinces of Yunnan and Guizhou, and extended to regions of Tibet and Fujian[2]. By 2021, surveys span to provinces of Zhejiang and Shaanxi, with

Table 2. Hybrid *Cymbidium* and *Phalaenopsis* planting area in China from 2012 to 2020.

Year	Hybrid *Cymbidium* (ha)	*Phalaenopsis* (ha)	Total (ha)
2012	1,721	509	2,230
2013	1,294	672	1,966
2014	753	506	1,259
2015	712	544	1,256
2016	1,767	610	2,377
2017	1,706	571	2,277
2018	1,888	789	2,677
2019	1,867	727	2,594
2020	1,904	852	2,756

Table 3. *Oncidiums* and pot orchids planting area in Taiwan, China from 2009 to 2019.

Year	*Oncidiums* (ha)	Pot orchids (ha)	Total (ha)
2009	213	608	821
2010	207	645	852
2011	217	726	943
2012	243	662	905
2013	249	677	926
2014	261	691	952
2015	261	707	968
2016	266	745	1,011
2017	249	751	1,000
2018	247	750	997
2019	237	761	998

the project set to conclude in 2023. Current data reveal investigations of 78,776 quadrats, recording approximately 132,000 orchids from 1,258 species[2]. Notably, around 800 native orchid species are conserved *ex-situ* in botanical gardens, with a significant percentage protected within national or provincial nature reserves[2]. During these botanical explorations, 31 new species and a new genus, *Microtatorchis*, are identified (Table 4). Presently, China recognizes 181 genera and 1,708 orchid species, with five new genera and 365 new species described during the last 21 years[7].

Stringent conservation measures have been implemented to recognize the significance of Orchidaceae in China. In 2018, key protection initiatives are introduced, with nearly 300 species across 23 genera receiving protection, including 41 primary and 256 secondary protected species (Table 5)[8]. Wild orchids under state protection constitute a significant portion of China's wild plants. As of June 2021, national nature reserves safeguarded around 1,100 species, with provincial reserves and botanical gardens conserving additional species[7].

Genetic diversity of orchid resources

Genetic diversity and relationships among Orchidaceae have been extensively researched using various molecular markers. Studies have delved into the genetic diversity of species like *Cymbidium*[9,10] and *Dendrobium*[11]. With the advent of high-throughput sequencing, numerous SNP markers have been identified in orchids. These markers have been instrumental in studying the origin, evolution, and genetic diversity of species such as *Dendrobium*[12] and *Phalaenopsis*[13].

Cytological insights

Chromosomal studies have revealed a rich diversity in orchid species. The chromosome number has been observed to be x = 11, 13, 18, 19, 20, 27, and so on. For example, most *Paphiopedilum* species have 2n = 26 chromosomes (x = 13). However, the chromosome number of different species in the *Paphiopedilum* subgenus *Paphiopedilum* section *Barbata* varied, with 2n = 32 for *Paphiopedilum callosum*, 2n = 38 for *Paphiopedilum microchilum*, *Paphiopedilum appletonianum* and *Paphiopedilum hainanensis*[14–16]. There are diploids, triploids and tetraploids in the cultivated cultivars of *Phalaenopsis*, and many aneuploids are produced in the process of cross breeding[17]. Zhu et al.[18] identified the chromosome ploidy of 57 introduced Japanese *Dendrobium* cultivars and 20 native species by flow cytometry and chromosome compression method. The results have showed that the coincidence rate of the two methods is 86.4%. Among the spring *Dendrobium* hybrids introduced from Japan, tetraploid cultivars account for 64.9%, triploid cultivars account for 28.1%, the diploid and hexaploid cultivars account for 3.5% respectively, indicating that most of the cultivated hybrid species of *Dendrobium* were polyploid (96.5%). In the study of

Table 4. List of orchids newly discovered during the botanical investigation.

Genera	Species	Type of discovery	References
Herminium	*Herminium lijiangense*	New species	[3]
Peristylus	*Peristylus fasciculatus*	New species	[3]
	Peristylus tenuicallus	New recorded species	[3]
Platanthera	*Platanthera milinensis*	New species	[3]
Ponerorchis	*Ponerorchis gongshanensis*	New species	[3]
Cheirostylis	*Cheirostylis chuxiongensis*	New species	[4]
	Cheirostylis yei	New species	[4]
Myrmechis	*Myrmechis lingulata*	New species	[4]
	Myrmechis longii	New species	[4]
Bulbophyllum	*Bulbophyllum ximaense*	New species	[4]
	Bulbophyllum xizangense	New species	[4]
	Bulbophyllum retusum	New species	[4]
	Bulbophyllum pulcherissimum	New species	[4]
	Bulbophyllum frostii	New recorded species	[4]
	Bulbophyllum raskotii	New recorded species	[4]
	Bulbophyllum nematocaulon	New recorded species	[4]
Gastrochilus	*Gastrochilus yei*	New species	[5]
	Gastrochilus minimus	New species	[5]
Luisia	*Luisia simaoensis*	New species	[5]
	Luisia inconspicua	New recorded species	[5]
Taeniophyllum	*Taeniophyllum xizangense*	New species	[5]
Tuberolabium	*Tuberolabium subulatum*	New species	[5]
Cleisostoma	*Cleisostoma tricornutum*	New recorded species	[5]
Liparis	*Liparis aureolabella*	New species	[6]
	Liparis mengziensis	New species	[6]
	Liparis bingzhongluoensis	New species	[6]

chromosomes of several genera of Subtrib. *Aeridinae* Pfitz. their chromosome bases are all x = 19. Among these, *Renanthera coccinea* is diploid and hexaploid, *Vanda concolor* is diploid and tetraploid, *Vanda pumila* is tetraploid and the rest are diploid[19–21]. Most of the *Cymbidium* species exhibit a chromosome number of 2n = 40, except for *Cymbidium lancifolium* (2n = 38) and *Cymbidium serratum* (2n = 41, 43, 60 and 80)[22]. Additionally, the formation of natural 2n gametes in orchids like *Phalaenopsis*[23] and *Cymbidium hybridum*[24] has been explored, paving the way for future polyploid breeding endeavors.

Table 5. Wild orchids under special state protection in China.

Genera	I Protected species	II Protected species
Aerides		*Aerides odorata*
Anoectochilus		All species
Bletilla		*Bletilla striata*
Bulbophyllum		*Bulbophyllum rothschildianum*
Calanthe	*Calanthe striata* var. *sieboldiier*	*Calanthe dulongensis*
Changnienia		*Changnienia amoena*
Corybas		*Corybas taliensis*
Cremastra		*Cremastra appendiculata*
Cymbidium	*Cymbidium insigne* and *Cymbidium wenshanense*	All species except *Cymbidium lancifolium*
Cypripedium	*Cypripedium subtropicum*	All species except *Cypripedium plectrochilum*
Danxiaorchis		All species
Dendrobium	*Dendrobium flexicaule* and *Dendrobium huoshanense*	All species
Gastrodia		*Gastrodia elata* and *Gastrodia angusta*
Gymnadenia		*Gymnadenia conopsea* and *Gymnadenia orchidis*
Ludisia		*Ludisia discolor*
Paphiopedilum	All species	*Paphiopedilum hirsutissimum* and *Paphiopedilum micranthum*
Phaius		*Phaius hainanensis* and *Phaius wenshanensis*
Phalaenopsis	*Phalaenopsis zhejiangensis*	*Phalaenopsis lobbii*, *Phalaenopsis wilsonii* and *Phalaenopsis malipoensis*
Pleione		All species
Renanthera		All species
Rhynchostylis		*Rhynchostylis retusa*
Vanda		*Vanda coerulea*
Vanilla		*Vanilla shenzhenica*

Assessment of resources —— multiomics and exploration of key genes

Orchid genome analysis

Leveraging the swift advancements in high-throughput sequencing technology, genomic data of 26 orchids have been disclosed, and notably, Chinese researchers have made significant contributions to 20 of these datasets (Table 6). These research studies indicate that a distinct Whole Genome Duplication (WGD) event takes place in the Orchidaceae lineage around the Cretaceous/Paleogene transition. Subsequently, within a short timeframe, differentiation into five subfamilies transpired, namely Apostasioideae, Cypripedioideae, Vanilloideae, Orchidoideae, and Epidendroideae. Notably, the subfamily Apostasioideae exhibits the highest gene loss, while the subfamily Vanilloideae has the least. *Phalaenopsis equestris* is the first orchid to be sequenced[25]. Three years after the publication of the *Phalaenopsis equestris* genome in 2015, researchers in Taiwan sequenced and assembled the *Phalaenopsis aphrodite* genome, which becomes the first orchid genome to be integrated with SNP-based gene-linkage mapping and validated through physical mapping[26]. In 2017, the publication of the *Apostasia shenzhenica* genome by Chinese researchers in the journal *Nature* triggered a new era of discussion about Darwin's conjecture in the scientific community. The successful assembly of *Apostasia shenzhenica* genome reconstructed the 'genetic toolkit' of ancestral orchids[27], and revealed the species-specific adaptive evolution of orchids, including the epiphytic adaptation, floral differentiation and reversion, and pollen aggregation into pollinia[28].

Table 6. Orchid genome published by Chinese scientists.

Species	Genome size (Gb)	Chromosome number	Contig N50	Scaffold N50	Protein-coding genes	References
Apostasia shenzhenic	0.35	2N = 2X = 68	0.08	3.03	21,841	[27]
Apostasia ramifera	0.37	–	0.03	0.29	22,841	[28]
Bletilla striata	5.06	2N = 2X = 32	2.37	1.65	146.39	[40]
Cymbidium sinense	3.52	2N = 2X = 40	1.11	–	29 638	[42]
Cymbidium goeringii	4.1	2N = 2X = 40	1.04	209.04	29,272	[44]
Cymbidium goeringii	3.99	2N = 2X = 40	0.38	178.2	29,556	[45]
Cymbidium ensifolium	3.62	2N = 2X = 40	1.21	154.88	29,073	[43]
Dendrobium officinale	1.35	2N = 2X = 38	0.001	0.04	35,567	[29]
Dendrobium catenatum	1.01	2N = 2X = 38	0.03	0.39	28,910	[31]
Dendrobium huoshanense	1.285	2N = 2X = 38	0.6	71.79	21,070	[32]
Dendrobium chrysotoxum	1.37	2N = 2X = 38	1.54	67.8	30,044	[33]
Dendrobium officinale	1.23	2N = 2X = 38	1.14	63.07	25,894	[30]
Dendrobium nobile	1.19	2N = 2X = 38	1.62	64.46	29,476	[34]
Gastrodia elata	1.12	–	0.07	4.9	18,969	[37]
Gastrodia elata	1.043	2N = 2X = 36	21.33	–	21,115	[38]
Gastrodia menghaiensis	0.987	2N = 2X = 36	2.37	6.82	14,233	[39]
Phalaenopsis equestris	1.086	–	0.02	0.36	29,431	[25]
Phalaenopsis aphrodite	1.025	2N = 2X = 38	0.02	0.95	28,902	[26]
Platanthera guangdongensis	4.19	2N = 2X = 42	1.77	192.35	24,513	[47]
Platanthera zijinensis	4.2		1.57	193.14	22,559	

In China, orchids are been revered for millennia for their medicinal properties. They have garnered significant attention, especially those with therapeutic and nutritional benefits. Seven *Dendrobium* species have undergone whole genome sequencing, includes *Dendrobium officinale*[29, 30], *Dendrobium catenatum*[31], *Dendrobium huoshanense*[32], *Dendrobium chrysotoxum*[33], *Dendrobium nobile*[34] and *Dendrobium* × *sp.*[35]. Successful assembly of *Dendrobium* genomes provides an analytical basis for in-depth understanding of the formation mechanism of *Dendrobium* medicinal components and the regulation of *Dendrobium* polysaccharide synthesis. *Gastrodia elata* is a common traditional Chinese medicine used to treat neurological headaches, numbness and convulsions. As a fully mycoheterotrophic orchid, the mechanism of interactions between *Gastrodia elata* and fungi has been a hot research topic[36–38]. Genomic analysis of *Gastrodia menghaiensis* suggests that the proteome of *Gastrodia menghaiensis* is the smallest proteome thus far among angiosperms[39]. The Chinese herbal medicine *Bletilla striata* has the effects of astringency, blood coagulation, subduing swelling and promoting muscle growth. By assembling and analyzing the *Bletilla striata* genome, transcription factor *BsMYB2* was found to regulate the biosynthesis of BSPs[40]. *Cremastra appendiculata* has the medicinal effects of relieving heat and removing toxins, resolving phlegm and dispersing knots. Based on its genomic information, the researchers have identified 35 key genes in the colchicine biosynthesis pathway, and systematically elucidated the phylogenetic relationship of O-methyltransferase[41].

Cymbidium species hold the most cultural significance in China. Genomic sequencing has been completed for *Cymbidium sinense*[42], *Cymbidium ensifolium*[43], and *Cymbidium goeringii*[44, 45]. The *Cymbidium sinense* genome reveals the molecular regulatory mechanisms of important horticultural traits such as flowering time, floral morphology, color and fragrance[42]. Both *Cymbidium ensifolium*[43] and *Cymbidium goeringii* genomes shed light on the genetic basis of floral diversity[45]. In 2023, the *Cymbidium mannii* genome is reported[46], combined with other multi-omics data, the mechanisms of CAM photosynthesis in epiphytic plants has been revealed in this work.

Floral patterning

Floral pattern is a distinctive feature of orchids, and understanding its formation has been a focal point of research. There are two main directions for research on orchid floral patterns, one direction is to study the flower development mechanism, and the other direction is to study the specific formation mechanism of flower organs. The transcriptome sequencing of *Cymbidium ensifolium* was conducted to analyze gene expression during the four stages of flower development in order to understand molecular mechanisms during floral organ development. These sequences provide valuable information on the molecular mechanisms of floral development and flowering as the first major genomic resource for the genus *Cymbidium*[48]. In *Cymbidium faberi*, 12 *TCP* transcription factors and 34 *MADS-box* genes were selected for transcriptome analysis by using vegetative and flower buds[49]. In addition to genus *Cymbidium*, there is also a report on floral patterning research in genus *Dendrobium*. In *Dendrobium officinale*, joint analysis of transcriptome and metabolome found that MIKC-type MADS-box proteins and ARFs, endogenous hormones IAA and ABA are potentially involved in the development of flower organs[50]. Current research on the formation mechanisms of specific floral organs of orchid plants are concentrated in the genus *Cymbidium*. In *Cymbidium goeringii*, the transcriptome combined with microRNA analysis was used to screen out two transcription factor/microRNA-based genetic pathways that may be involved in the formation of the multi-petal trait[51], and by using proteome profiling, three transcription factors *bHLH13*, *WRKY33* and *VIP1* were identified as candidate regulators related to specific floral organ development[52]. Analysis of the *Cymbidium sinense* transcriptome shows that interactions between *MADS* factors play a crucial role in orchid floral zygomorphy and that mutations in these factors may be maintained during artificial selection[53].

Timing of flowering

To regulate the orchid flowering time, it is essential to grasp their flowering traits. Chinese scholars have investigated flowering physiology of *Cymbidium*, *Dendrobium*, *Oncidium*, and *Phalaenopsis*, identifying the molecular controls of flowering in these orchids. Based on multi omics data analysis and gene screening, flowering promoter such as *SOC1*, *CO/COL*, *AGL24*, *AP1*, *FTIP1* from *Dendrobium*, *MADS2*, *MADS4*, *SEP3*, *OAGL6-1*, *AP1*, *MADS11* of *Oncidium* and *FD*, *MADS7*, *SEP3* from *Phalaenopsis* have been identified, heterologous overexpression in model plants have resulted in early-flowering, while overexpression of *SVP*-like genes from *Cymbidium* and *Phalaenopsis*, *TFL1*-like genes in *Dendrobium* and *Oncidium*, *COL* genes of *Cymbidium* and *Doritaenopsis DhEFL2*,*3*,*4* in different heterologous systems resulting in delayed-flowering. Those results indicate that most homologs of the flowering-relevant genes play evolutionarily conserved roles in orchid compared with model plants such as *Arabidopsis* and *Nicotiana benthamiana*.

There also exist many species-specific regulatory patterns. For example, a group of tandem repeats of *DAM* (Dormancy Associated *MADS-box*) transcription factors, has been identified in the genomes of woody trees as a potential marker of dormancy[54]. However, the whole genome sequencing of orchids does not find any *DAM* orthologs, suggesting that orchids work independently of the networks regulated by *SVP*/*StMADS11* in other perennial species, such as kiwifruit, *Populus trichocarpa*, and Rosaceae species[55,56,57].

Flower and leaf color

The color of orchids is mainly composed of three pigments: chlorophyll, flavonoids and carotenoids. The expression of structural genes of the pigment synthesis pathway can affect the synthesis and accumulation of pigment, thereby affecting the color phenotype of orchid plant tissues[58]. The structural genes for anthocyanin synthesis that have been cloned in orchids include *CHS*, *CHI*, *F3H*, *F3'5'H*, *F3'H*, *DFR*, *UFGT* and *ANS*[59]. Several structural genes involved in carotenoid synthesis have been cloned in orchids, including *PSY*, *PDS*, *ISO*, *NCED*, *HYB*, *ZEP*, *CCD1*, *and CRTISO*[59]. There are some reports on structural genes related to chlorophyll synthesis in genus *Cymbidium*, involving all known structural genes in the process of chlorophyll synthesis and metabolism. There are some reports on structural genes related to chlorophyll synthesis in orchids, among which *PORB* and *CLH* have been cloned[60,61]. Transcription factors affect orchid color changes by regulating the

expression of structural genes. Among the transcription factors involved in regulating the anthocyanin biosynthesis pathway, the most studied ones are *MYB*[62], *bHLH*[63], *WRKY*, *MADS* and *ZIP*[59]. These transcription factors affect the presentation of orchid flower color by activating or inhibiting the expression levels of structural genes[59]. Compared with structural genes, there are fewer studies on transcription factors in the carotenoid synthesis pathway. Currently, only the *R2R3-MYB* transcription factor gene *RcRCP1* that regulates CBP structural genes has been found in *Cattleya*[62]. For the chlorophyll metabolite pathway, *CsERF2* transcript factor triggers structural changes in chloroplasts by regulating sugar signals, thereby promoting the degradation of chlorophyll[63]. Multi-omics analysis methods can also be used to analyze the formation mechanism of color in orchids. In terms of the mechanism of orchid flower color formation, most of the research ideas adopted are to select petals of different flower color varieties and use transcriptome combined with metabolome to explore key metabolic pathways. The important role of *CeMYB104* in the regulation of flower color in *Cymbidium ensifolium* was identified by joint analysis of transcriptome and metabolome[64]. In *Pleione limprichtii*, transcriptomic methods were used to analyze the coloring mechanisms of petals of three different colors and found that *PlFLS* plays a decisive role in whether the petals appear white, *PlANS* and *PlUFGT* are related to the accumulation of anthocyanins. And an important candidate transcription factor PlMYB10 was predicted to form an MBW protein complex (MYB, bHLH, and WDR), regulate *PlFLS* expression[65].

Fragrance

Currently, research on molecular regulation of orchid fragrance is mainly focused on the terpene metabolism pathway. In *Oncidium*, five key *TPS* genes were screened based on transcriptome data, and the key *TPS* genes are different in varieties with different aromas[66,67]. Through expression level analysis combined with exogenous application of methyl jasmonate, *DoTPS10* and *DoGES* are involved in the synthesis of linalool and geraniol respectively in *Dendrobium officinale*[68, 69]. *PbGDPS* may play an important regulatory role in the synthesis of monoterpenes in *Phalaenopsis*[70]. In *Cymbidium sinense*, a key enzyme *SjHMGR* gene in the MVA pathway of terpenoid biosynthesis, may be closely related to the formation of floral fragrance[71]. In addition, a comparison of transcriptome information from different Phalaenopsis fragrant types reveals that *PbbHLH4* is crucial in controlling the biosynthesis of floral monoterpenes in orchids[72]. In *Cymbidium, CsMYB1* is involved in regulating the synthesis of phenylpropanoid/benzene compounds in the *Cymbidium* cultivar 'Seal Bit'[73]. Methyl jasmonate is one of the main aroma components of *Cymbidium faberi*. The promoters of the *CfAOC* gene and *CfJMT* gene are related to the synthesis of methyl jasmonate which is activated by heterologously overexpression of four *CfMYB* genes, and the content of methyl jasmonate is increased, indicating that *CfMYB* can regulate the synthesis of methyl jasmonate[74].

Resistance

Resistance is also a very important issue in orchid growth and development. Both abiotic and biotic stresses can have significant adverse effects on the growth and yield of orchids or even cause death. Chinese researchers have extensively studied orchid stress resistance using multi-omics joint analysis, gene function identification, and gene family systematic analysis. Orchids native to the tropics are sensitive to low temperatures, especially during the reproductive growth stage. In the typical tropical orchid *Phalaenopsis*, researchers not only analyzed the expression patterns of the classic cold-resistant transcription factors *CBF* and *ICE1*[75], but also used transcriptome, sRNA combined with degradome to screen out the key cold-resistant genes *digalactosyldiacylglycerol synthase 2* (*DGD2*) and its specific natural antisense transcripts (NATs)[76].

When considering drought resistance, the integrated data from the transcriptome and metabolome in *Dendrobium* suggest multiple pathways related to purine metabolism and phenylpropanoid biosynthesis[77]. These pathways along with networks connected to nucleotide processes and stress responses[78], are pivotal to drought adaptation by *Dendrobium* orchids. Terrestrial and epiphytic orchids employ different drought survival strategies. Proteome analyses indicate that epiphytic orchids are more drought-resistant than their terrestrial counterparts. Epiphytic orchids are superior in sustaining carbon equilibrium and responding to ABA[79].

Cymbidium mosaic virus (CymMV) and Odontoglossum ringspot virus (ORSV) are global threats to orchid economic stability, intensifying the focus on disease resistance within the industry. Studies in China show that genes such as *NPR1*[80,81] and plant A20/AN1 proteins[82] boost orchid defenses against CymMV and ORSV. Investigations also suggest that custom-engineered microRNAs (miRNAs) enhance orchid disease specificity[83].

Beyond identifying key resistance genes in various stress scenarios, exploring gene families comprehensively is critical for understanding the role of stress-resistant gene clusters and future applications. To date, published gene family analyses in orchids encompass families like *AGO*[84], *GRAS*[85], *LEA*[86], prenyl-synthase-terpene synthase[87], *R2R3-MYB* transcription factors[88], *SOD*[89], and *WRKY*[90]. These studies typically involve gene family structure analysis, stress-conditioned gene expression analysis, and essential gene functionality identification.

Orchid breeding

The Royal Horticultural Society (RHS) established a global orchid hybrid registry in 1854, with *Calanthe Dominyi* (*Calanthe furcata* × *Calanthe masuca*) being the inaugural registration[91]. With the development of aseptic seeding technology of orchids, the number of new hybrids of orchids has shown an explosive growth, and there are currently more than 170,000 registered orchid hybrids. Among them, we have registered 109 novel hybrids.

In the agriculture and forestry sectors of China, protection for new orchid varieties has expanded to nine genera, including *Paphiopedilum*, *Pleione*, *Phalaenopsis*, *Cattleya*, *Cymbidium*, *Cypripedium*, *Dendrobium*, *Gastrodia* and *Vanda* (Table 7). As of October 6, 2023, national authorization for new plant variety rights has been granted to 536 orchid varieties. Notably, varieties of *Phalaenopsis* represent 79.48% of these (sources: www.nybkjfzzx.cn/p_pzbh/sub_gg.aspx?n=21, http://lygc.lknet.ac.cn/s/sqpzsjk.html). Regarding medicinal orchids, of the 30 *Dendrobium* newcomers, nearly 50% are *Dendrobium officinale*, while new variety authorizations for medicinal *Gastrodia* remain absent. Within *Cymbidium*, selection breeding from 1993 to 2020 resulted in 621 natural variants (data from Orchid Branch of China Flower Association, not yet published).

Table 7. Number of orchids granted new plant variety rights in China.

Genus	Number of varieties	Percentage (%)
Paphiopedilum	0	0
Pleione	0	0
Phalaenopsis	426	79.48
Cattleya	2	0.37
Cymbidium	78	14.55
Dendrobium	30	5.60
Cypripedium	0	0
Gastrodia	0	0
Vanda	0	0
Total	536	100

Ploidy breeding

Polyploid orchids typically exhibit enhanced organ dimensions and augmented resilience to stress, and polyploidization is useful for restoring the fertility of some excellent germplasm resources with low or no fertility[92]. Researchers have identified endopolyploids (spontaneous polyploid occurrences) within diverse cells, tissues, and organs across multiple genera, including *Phalaenopsis*, *Cymbidium*, and *Cattleya*[92]. As orchid tissue culture techniques have reached to advanced levels, there is a growing trend in studies focusing on polyploid stimulation in conjunction with these methods. Over the last two decades in China, orchid polyploid breeding was extended to 13 different genera, with *Phalaenopsis*, *Dendrobium*, and *Cymbidium* receiving more attention (Table 8). The primary approach to inducing polyploidy in orchids involves the use of chemicals such as colchicine, oryzalin, and pendimethalin on various orchid parts, including seeds, protocorms, protocorm-like bodies, cluster buds, rhizomes, and stem explants. By using these chemicals, the rates of polyploid induction ranges from 6.32% to 72.7%. A study shows that the formation rates of 2n male gametes (unreduced gametes) fluctuate between 0.15% and 4.03%, and by utilizing 2n gametes for sexual crossbreeding also presents a potent strategy for procuring polyploid orchids[93].

Mutation breeding

Mutation breeding is the use of various methods to induce plants to produce new traits. It has a unique role in the improvement of ornamental plant varieties, and it can induce acquisition of new genes or new germplasm. Compared with traditional hybridization, mutation breeding has the advantages of higher mutation frequency and rich mutation types within a short time. Mutation breeding in China began in the 1950s, and there are many reports on orchids at present. Except natural variation and artificially induced polyploids, ^{60}Co-γ physical radiation is the most reported method, and it has been used in several species of orchids such as *Phalaenopsis spp*., *Epidendreae spp*., *Paphiopedilum delenatii*, *Paphiopedilum callosum*, *Cymbidium goeringii*, *Cymbidium faberi*, *Dendrobium crumenatum*, *Dendrobium Officinale* and *Dendrobium Sonia*'166'[103,104]. The radiation dose ranged from 5 to 40 Gy. Heavy ion radiation and space mutation are also alternative methods to create mutants. The rhizoids of four *Cymbidium hybridum* were irradiated by $^{12}C^{6+}$ heavy ions, and SSR molecular marker detection revealed new polymorphic bands of '17-33' at a dose of 20 Gy[104]. A new *Phalaenopsis* cutivar 'Hangdie No.2' was selected from space mutation, and it formed a series of excellent characteristics over the original varieties[105].

In addition, mutants are also easily produced through callus or protocorm propagation during tissue culture. Most of the reported mutant characters are leaf color variation in *Cymbidium* and *Dendrobium*, and mutation with flower pattern, flower color and spots found in *Phalaenopsis*[106]. *Phalaenopsis* exhibited notable genetic variability, with the occurrence of somaclonal variants spanning from 5.6% to 47.9%[107]. Some red flower *Phalaenopsis* varieties with *Phalaenopsis equestris* or *Phalaenopsis pulcherrima* lineages, such as *Phalaenopsis* Formosa Rose, *Phalaenopsis* King Shiang's Beauty, *Phalaenopsis* King Shiang's Rose, are easy to produce three-lip flower type variation in tissue culture. Waxy flower varieties with spotted, yellow or red flowers are also prone to variation, but large white flower varieties are less susceptible to variation[91]. Therefore, somaclonal variation is one of the effective ways to breed new varieties of *Phalaenopsis*. In the process of tissue culture of *Phalaenopsis* Sogo Vivien, we also found some leaf color variation types, and selected a new cultivar 'Jingxiang' with large gold edges on the leaves.

Crossbreeding

Crossbreeding is a widely employed and highly effective method for breeding orchids. Achieving successful interspecies and even inter-genus hybridization is feasible, although orchid seeds pose unique challenges due to lack of endosperm and immature embryos. To overcome these obstacles, they rely on symbiotic fungi for germination in limited rates[91]. The success of orchid hybridization hinges on several crucial factors, including pollen viability, stigma acceptability and ploidy, making the selection of hybrid parents a pivotal task. In the case of *Phalaenopsis*, we have seen the creation of various intergeneric hybrid combinations, such as those between *Phalaenopsis* and other genera like *Sedirea*, *Neofinetia*, *Renanthera*, *Rhynchonopsis* and *Vanda*, aiming to yield new varieties with delightful fragrances or vibrant hues. The success rate of these crosses ranges from 2.78% to 12.50%[108]. Overcoming incompatibility between genera is possible through techniques like expanding the range of parental hybridization, repeated pollination, cross-pollination, and embryo rescue[108].

In the realm of *Cymbidium* orchids, the breeding of *Cymbidium hybridium* stands out as a prominent achievement in domestic orchid breeding. After years of interspecific hybridization, a diverse array of varieties has emerged. Enhancements in flower color, flower type, fragrance, flowering time, leaf color, and plant shape have been achieved by crossing *Cymbidium hybridium* with native species of florets in *Cymbidium*, such as *Cymbidium goeringii*, *Cymbidium kanran*, *Cymbidium sinense* and other indigenous Chinese species[109]. Notably, hybrid combinations with *Cymbidium hybridium* as the female parent have exhibited very low seed setting rates or no seed at all, while the same hybrids with *Cymbidium hybridium* as the male parent have displayed varying degrees of seed setting[109]. Meanwhile, the fruit setting rate is as high as 100.0% when the *Cattleya* hybrid 'KTL4' is the female parent. However, it is only 10.0%. when it is a male parent[110]. These findings underscore that the compatibility of the same orchid species differs when it serves as a male or female parent.

Molecular marker-assisted breeding

Molecular marker-assisted breeding serves as an effective means to expedite plant breeding efforts. Several molecular markers, including SRAP, AFLP, ISSR, SSR, and EST-SSR, are

Table 8. Polyploidy induction of orchids.

Genera	Species	Type of explant	Optimal treatment	Assessment method	Induction rate	References
Cymbidium	*Cymbidium hydridum*	PLBs	Colchicine 0.1% for 3 d	A, C	27.6%	[94]
	Cymbidium hybridium 'Sunrise'	PLBs	Colchicine 0.05% for 5 d	A, D	23.7%	[95]
	Cymbidium hybridium 'Hongpubu'	Cluster buds	Colchicine 0.05% for 24 h	A, B, D	28.2%	[95]
	Cymbidium sinense	Rhizomes	Colchicine 0.01% for 3 d	A, B	11.1%	[96]
	Five *Cymbidium sinense* cultivars and four hybrids	2n gametes	Interspecific hybridization to produce sexual polyploids	A, B, C	seven pairs of crosses produced five triploid and two tetraploid hybrids	[93]
	Cymbidium Ruby Shower 'Murasakin Okimi'	Protocorms	Colchicine 300 mg/L for 15 d	A, B	30.0%	[95]
	Cymbidium Golden Elf 'Sundust'	Rhizomes	Oryzalin 0. 002% for 48 h, and then EMS 50 mg /L for 1 month	A, B, D	40%	[95]
	Cymbidium sinense 'Lvmosu' × *Cymbidium hybridum* 'Shijieheping' F1 generation	Protocorms	Colchicine 0.03% for 72 h	A, C, D	36%	[95]
	Cymbidium lowianum	Cluster buds	Colchicine 0.04% for 72 h	A, B, D	60%	[95]
	Interspecific hybrids	Rhizomes	Colchicine 0.1% for 48 h	A, B	36%	[95]
	Cultivar 'Suxinhuang'	Protocorms	Colchicine 0.005% for 3 d	A, B	16.7%	[95]
	Cymbidium faberi	Cluster buds	Colchicine 0.5% for 48 h	A, B, D	13.3%	[95]
	Cymbidium iridioides	Cluster buds	Colchicine 0.05% for 72 h	A, B, D	74%	[97]
Dendrobium	*Dendrobium officinale*	Protocorms	Oryzalin 14.4 μM for 24 h	A, B, C	37.4%	[98]
	Dendrobium officinale	PLBs and cluster buds	Colchicine 0.09% for 24 h	A, B, D	48%	[95]
	Dendrobium officinale	Protocorms	Colchicine 0.1% for 15 d	A, B, C	57.69%	[95]
	Dendrobium officinale	Seeds and PLBS	Colchicine 50 mg/L	A, B, C	50%	[95]
	Dendrobium officinale	Protocorms	Colchicine 0.6 mg/L for 30 min	A, B, C, D	16.7%	[95]
	Dendrobium officinale	Protocorms	Colchicine 2.0 mg/L for 36 h	A, B, C, D	20%	[95]
	Dendrobium cariniferum	Protocorms	Colchicine 0.05% for 24 h	A,B, C, D	33.0%	[99]
	Dendrobium devonianum	Cluster buds	Colchicine 0.03% for 24 h	A, B	60.0%	[95]
	Hybrids of *Dendrobium* snow flake 'Red star' and *Dendrobium* white rabbit 'Sakurahine'	Cluster buds	Colchicine 0.06% for 12 h	A, B, D	69.1%	[95]
	Dendrobium wardianum	Protocorms	Colchicine 0.1% for 12 h	A, B, D	26%	[95]
	Dendrobium sinese	Protocorms	Oryzalin 20 mg/L for 4 d	A, B, C, D	35%	[95]
	Dendrobium hybrida 'Sonia'	Protocorms	Colchicine 0.01% + Oryzalin 5 mg/L for 8–10d	A, B	Above 90%	[95]
	Dendrobium ochreatum	Protocorms	Colchicine 0.05%–0.1% for 2–3 d	A, B, C, D		[95]
	Hybrids of *Dendrobium* utopia 'Messenger' × *Dendrobium* Whiterabbit 'Sakurahime'	Tube seedlings	Colchicine 0.6 mg/L for 24 h	C, D	62.2%	[95]
Phalaenopsis	H-03	Seeds	Colchicine 0.05% for 15d	A, B, C, D	50.0%	[100]
	Phalaenopsis Tailin 'Red Angle'	leaves and adventitious buds	Colchicine 0.01% for 30 d	A, B, D	33.3%	[100]
	Phalaenopsis 'TsueiFoa Lady'	Protocormsand PLBs	Colchicine 0.1% for 7 d	A, B, D	30%	[100]
	Phalaenopsis amabilis *Phalaenopsis aphrodite*	Protocorms	Endopolyploid. in vitro regeneration	A, C	A large number of stable polyploid plants were obtained in a short time	[100]
	Phalaenopsis aphrodite	Protocorms	Endopolyploid, Horizontal cutting		Polyploid plants can be produced in large numbers	[100]
	Phalaenopsis zhejiangensis	Seeds	Colchicine 0.2% for 1 d	A, C, D	27.75%	[100]
	Hybrids	Cluster buds	Colchicine 0.05% for 24 h	A, B, D	20%	[100]
Ionopsis	*Ionopsis utricularioides*	Leaves and embryoids	Colchicine 200 mg/L for 24 h	A, C, D	8.53%	[100]
Arundina	*Arundina graminifoli*	Protocorms	0.1% colchicine for 12 h	A, B, C, D	23.33%	[100]
Cremastra	*Cremastra appendiculata*	Protocorms	Colchicine 0.05% for 1 d	A, B	20%	[101]
Phaius	*Phaius tankervilleae*	Protocorms	Colchicine 0.02% for 6 d	A, B	22.5%	[100]
Pleione	*Pleione maculaata*	Protocorms	Colchicine 0.2% for 60 h	A, B	25.64%	[100]
Nervilia	*Nervilia fordii*	Rhizomes	Colchicine 300 mg/L + DMSO 10 ml/L + 2.0 mg/LKT for 28 d	A, B, D	50%	[102]

(to be continued)

Table 8. (continued)

Genera	Species	Type of explant	Optimal treatment	Assessment method	Induction rate	References
Spathoglottis	*Spathoglottis plicata*	Seeds and transverse thin cell layer	Colchicine 0.3% for 30 d	A, B, D	27.8%	[100]
Oncidium	*Oncidium flexuosum*	PLBs	Colchicine 1,500 mg/L for 54 h	A, B, C, D	26.67 %	[100]
Bletilla	*Bletilla striata*	PLBs	Colchicine 0.2% for 36 h	A, B, C, D	26.7%	[100]
Anoectochilus	*Anoectochilus roxburghii*	Stems	Pendimethalin 90 mg/L for 48 h	A, C	50.0%	[100]
	Anoectochilus roxburghii	Stems	Colchicine 0.1% for 48 h	A, B, D	48%	[100]
	Anoectochilus roxburghii	Stems	Pendimethalin 200 μmol/L for 8 d	A, B, D	44.17%	[100]
	Anoectochilus roxburghii	Stems	Colchicine 700 mg/L for 15 h	A, B, D	53%	[100]
	Anoectochilus roxburghii	Stems	Colchicine 300 mg/L for 13 d	A, B	72.7%	[100]

commonly employed in orchid breeding and have found widespread application in plant identification, fingerprinting, core germplasm establishment, genetic diversity assessment, and phylogenetic analysis[111]. This approach is particularly valuable when working with domestic medicinal and endangered wild orchid resources, such as *Dendrobium loddigesii*[112], *Liparis japonica*[113] and *Cymbidium tortisepalum*[114]. Notably, SSR markers were used to identify the genes associated with flower color, shape and resistance of *Phalaenopsis*, which provided valuable insights for genetic engineering breeding of *Phalaenopsis*[115]. In a separate study, eight pairs of SSR markers were screened to distinguish accurately the pure yellow-green flowers and varietal flowers in hybrid offspring of *Cymbidium hubridum* 'Xiao Feng' and *Cymbidium sinense* 'Wu Zi Cui'[116]. Additionally, specific-locus amplified fragment sequencing and bulked segregant analysis led to the identification of two single-nucleotide polymorphism (SNP) markers linked to flower ground color in *Phalaenopsis*, achieving an impressive accuracy rate of 93.3%[117].

Furthermore, the advent of high-throughput sequencing has facilitated the development of numerous SNP markers through simplified genome sequencing and genotyping by sequencing. The construction of high-density genetic linkage maps using polymorphic SNP markers has emerged as a pivotal method for identifying functional genes or markers closely linked to specific traits[12]. Presently, there are 14 reports on genetic maps for orchids, with a primary focus on four genera: *Paphiopedilum*, *Phalaenopsis*, *Dendrobium* and *Cymbidium* (Table 9). These maps have unveiled QTLs (or eQTLs) and candidate genes associated with flower color, polysaccharide content, as well as traits of leaves and stems. Nevertheless, further refinement and verification of these findings remain necessary.

Transgenic breeding

Transgenic breeding generates desired traits by transferring exogenous genes or changing the expression characteristics of endogenous genes, which is precise, targeted, and time saving compared to traditional breeding methods[121]. As early as 1997, Hsieh reported the method of transforming *Phalaenopsis equestris* protocorms mediated by *Agrobacterium*, successfully introducing the *GUS* (*β-glucuronidase*) reporter gene into *Phalaenopsis equestris*[122]. After that, other reporter genes and functional genes were successively reported in *Dendrobium*[123], *Oncidium*[124], *Cymbidium*[125], *Cattleya*[126], *Doritis*[127], and *Paphiopedilum*[128]. Moreover, there are also genetic transformation studies of interspecific hybrids and intergeneric hybrids. For example, *CLF* gene was introduced into *Cymbidium* × *Dendrobium*[129], and the *GUS* reporter gene was injected into *Arachnis* × *Vanda*[130] and *Dendrobium* × *Phalaenopsis*[131].

To date, more than 70 reports (Table 10) have been presented on the genetic transformation system and transgenic breeding of orchids in China. The molecular breeding for orchids mainly involves the color, flowering period, flower development, disease resistance and cold resistance related research. The explants include protocorms, quasi-protocorms, callus and pollen tube channels. The key transformation techniques included *Agrobacterium*-mediated transformation and the use of gene guns.

Gene editing

In the field of molecular biology, significant strides have been made in the Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/CRISPR-associated (Cas) system, representing a groundbreaking genome editing technique[135]. Recent years have witnessed remarkable breakthroughs in gene editing technologies based on Crispr/Cas, enabling targeted modifications of gene characteristics in plants. These alterations encompass gene knockout, reduction of gene expression, and the augmentation of gene expression by modifying promoters[136–138].

Nevertheless, the application of the CRISPR/Cas9 method for genetic editing of orchids in China has seen limited exploration. Only a handful of studies have reported successful gene editing in orchids, involving the modification of genes related to the lignin synthesis pathway (*C3H*, *C4H*, *4CL*, *CCR*, and *IRX*) in *Dendrobium*[139] and the editing of *MADS44*, *MADS36*, and *MADS8* genes in *Phalaenopsis*[140].

The progress of genome editing in ornamental plants faces constraints, including the absence of specialized transformation systems, inefficiencies in existing transformation methods, and limited comprehension of certain trait-regulatory networks. Thus, it becomes imperative to develop suitable expression systems and target sequence configurations tailored to different ornamental plants. Additionally, adherence to legal regulations and the enhancement of target traits is essential during genome editing. Despite the challenges of low transformation and gene editing efficiencies in orchids, the burgeoning orchid market and increased research endeavors are expected to yield more gene editing studies in orchids and other ornamental plants, ultimately resulting in the establishment of efficient genome editing systems for orchids.

Table 9. Genetic map of orchids.

Genus	Mapping population	Population type	Population size	Marker type	Total distance of map (cM)	Average distance (cM)	Number of markers	QTL or eQTLs	References
Paphiopedilum	*Paphiopedilum concolor* × *Paphiopedilum hirsutissimum*	F1	95	SNP	1,616.18	0.19	8,410	12 QTLs linked to leaf length, leaf width, leaf thickness, and leaf number	[13]
Phalaenopsis	*Phalaenopsis* '462' × *Phalaenopsis* '20'	F1	88	AFLP	Phal '462': 878.3 Phal '20': 820.3	5.0 6.7	175 122		[118]
	Phalaenopsis aphrodite × *Phalaenopsis equestris*	F1	117	SNP	l5l92.05	0.l3	113,517	10 QTLs associated with four color related traits	[119]
Dendrobium	*Dendrobium* Lucky Gal × *Dendrobium* Fantasy	F1	90	RAPD	6,568.7	50.11	121		[118]
	Dendrobium Second Love × *Dendrobium* Sekand Rave	F1	92	SSR	Den. Second Love: 571 Den. Sekand Rave: 566.3	4.6 8.5	124 67		[118]
	Dendrobium officinale × *Dendrobium hercoglossum*	F1	90	RAPD SRAP	Den. officinale: 629.4 Den. ercoglossum: 1,304.6	11.2 11.6	62 112		[118]
	Dendrobium officinale × *Dendrobium moniliforme*	F1	90	EST-SSR, SRAP, ISSR, RAPD	D. moniliforme: 1,332.6 D.officinale: 1,425.9	10.41 10.41	226 220		[118]
	Dendrobium officinale × *Dendrobium aduncum*	F1	140	SRAP SSR	1,580.4	11.89	157		[118]
	Dendrobium nobile × *Dendrobium moniliform*	F1	90	RAPD ISSR	D. nobile: 1,474 D. moniliform: 1,326.5	14.75 14.88	116 117		[118]
	Dendrobium moniliforme × *Dendrobium officinale*	F1	111	SNP	2,737.49	0.32	8,573	5QTL for Polysaccharide content	[120]
	Dendrobium nobile × *Dendrobium wardianum*	F1	100	SNP	3,612.12	0.41	9,645	2 eQTL for stem length and 1 eQTL for stem diameter	[12]
	Dendrobium mangosteen × *Dendrobium* Burana Pink No.2	F1	190	SSR, SRAP, RSAP, ISSR	1,421	9.56	274		[118]
	Dendrobium mangosteen × *Dendrobium* Burana Pink No.2	F1	190	SSR, SRAP, ISSR	1,548.9	9.91	230		[118]
Cymbidium	*Cymbidium hybridum* 'Yunv' × *Cymbidium Sinense* 'Huangyehongmo'	F1	94	SSR	1,608.9	32.15	56		[118]

Orchid reproduction and rapid propagation

Orchid seeds present a unique challenge due to their incomplete embryo development, lacking both endosperm and cotyledons, which hinders natural germination. They predominantly rely on symbiotic fungi and are typically propagated through division, a process characterized by its sluggishness. Orchid rapid propagation initiated in the 1960s when Morel utilized stem-tip tissue from Hybrid *Cymbidium*, cultivating it on a cytokinin-containing medium. This led to the formation of protocorms, which subsequently differentiated into roots and leaves, resulting in the first virus-free orchid plantlets[141]. Today, tissue culture methods have enabled the propagation of over 60 genera and hundreds of orchid species.

In China, after the 1970s, orchid reproduction and rapid propagation gained prominence, including *Cymbidium ensifolium*[142], *Cymbidium sinense*[143], *Cymbidium goeringii*[144], among others.

Orchid reproduction and rapid propagation primarily involve aseptic seeding and shoot-tip induction pathways, although other explants such as leaves, stems, root tips, flower stalks, and axillary buds can also be induced. Wimber first successfully induced protocorms from leaves of *Cymbidium faberi*, demonstrating the feasibility of obtaining regenerated plants using leaf explants[145]. Churchill et al. used root tips as explants to achieve successful plant regeneration[146]. Furthermore, protocorm-like bodies were successfully induced from flower buds of *Cymbidium sinense*, *Dendrobium* by Zhang & Ou[143]. However,

Table 10. Transgenic research on orchids.

Species	Explants	Genetic transformation	Report gene	References
Phalaenopsis	PLB (PLBs)	*Agrobacterium*	*ACS*	[132]
	PLB (PLBs)	*Agrobacterium*	*LFY*	[132]
	PLB (PLBs)	*Agrobacterium*	*GFP*	[132]
	PLB (PLBs)	*Agrobacterium*	*VwF3'5'H, GUS*	[133]
	PLB (PLBs)	*Agrobacterium*	*GFP, Hpt*	[132]
	PLB (PLBs)	*Agrobacterium*	*CymMV-CP*	[132]
	PLB (PLBs)	*Agrobacterium*	*ICE1*	[133]
	PLB (PLBs)	*Agrobacterium*	*CAMV, GUS, eGFP*	[133]
	PLB (PLBs)	*Agrobacterium*	*GUS*	[133]
	PLB (PLBs)	*Agrobacterium*	*YUCCA6, GUS, Hpt*	[133]
	Callus	*Agrobacterium*	*LTP*	[133]
	Callus	*Agrobacterium*	*GUS, Hpt*	[133]
	Pollen tube	*Agrobacterium*	*Cbf1*	[133]
	Immature embryo	*Agrobacterium*	*LycB*	[133]
	Leaf	*Agrobacterium*	*GAFP-NP1*	[133]
	Ovary	*Agrobacterium*	*GUS, Hpt*	[133]
	PLB (PLBs)	Particle gun	*GUS*	[132]
	PLB (PLBs)	Particle gun	*Hpt, GUS*	[133]
	PLB (PLBs)	Particle gun	*PeUFGT3*	[133]
Dendrobium	PLB (PLBs)	*Agrobacterium*	*DOH1*	[132]
	PLB (PLBs)	*Agrobacterium*	*RTACO*	[133]
	PLB (PLBs)	*Agrobacterium*	*ACS*	[132]
	PLB (PLBs)	*Agrobacterium*	*aiiA-hacD*	[133]
	PLB (PLBs)	*Agrobacterium*	*GUS*	[133]
	PLB (PLBs)	*Agrobacterium*	*GUS, Hpt*	[132]
	PLB (PLBs)	*Agrobacterium*	*PR1, PR10*	[133]
	PLB (PLBs)	*Agrobacterium*	*CHS, F3'5'H*	[133]
	PLB (PLBs)	*Agrobacterium*	*CyMV-CP, ORSV-CP*	[132]
	PLB (PLBs)	*Agrobacterium*	*RTACS*	[133]
	PLB (PLBs)	*Agrobacterium*	*NAC*	[133]
	PLB (PLBs)	*Agrobacterium*	*GUS*	[133]
	Callus	*Agrobacterium*	*DcOSEP1*	[133]
	Callus	*Agrobacterium*	*Hpt*	[133]
	Callus	*Agrobacterium*	*AFP*	[133]
	Ovary	*Agrobacterium*	*GUS, Hpt*	[133]
	PLB (PLBs)	Particle gun	*GUS, Hpt*	[133]
	PLB (PLBs)	Particle gun	*CymMV CP*	[133]
	PLB (PLBs)	Particle gun	*LFY*	[133]
Oncidium	PLB (PLBs)	*Agrobacterium*	*pflp*	[133]
	PLB (PLBs)	*Agrobacterium*	*ACS*	[133]
	PLB (PLBs)	Particle gun	*CBF3*	[133]
	PLB (PLBs)	*Agrobacterium*	*AtTIP5;1*	[133]
	PLB (PLBs)	*Agrobacterium*	*CyMV-CP ORSV-CP*	[133]
	Callus	*Agrobacterium*	*GAFP-NP1*	[133]
	Callus	*Agrobacterium*	*GUS*	[133]
	PLB (PLBs)	*Agrobacterium*	*GUS*	[134]
Cymbidium	PLB (PLBs)	*Agrobacterium*	*ICE1*	[133]
	PLB (PLBs)	*Agrobacterium*	*GAFP*	[133]
	PLB (PLBs)	*Agrobacterium*	*CyMV, ORSV*	[133]
	PLB (PLBs)	*Agrobacterium*	*GUS*	[132]
	Somatic embryo	*Agrobacterium*	*GAFP-NP1*	[133]
	Rhizome	*Agrobacterium*	*GUS*	[133]
	PLB (PLBs)	*Particle gun*	*CiDREB1, PeDREB2, CYMV-CP*	[133]
Doritis	Ovary	*Agrobacterium*	*GUS*	[127]
Cattleya	PLB (PLBs)	*Agrobacterium*	*GUS, ORSV*	[126]
Cymbidium goeringii × *Cymbidium hybridum*	PLB (PLBs)	*Agrobacterium*	*CLF*	[129]
Archnis × *Vanda*	PLB (PLBs)	Particle gun	*GUS*	[130]
Dendrobium × *Phalaenopsis*	PLB (PLBs)	*Agrobacterium*	*GUS*	[131]

floral organs as explants generally yield low induction rates and pose a greater challenge.

The tissue culture-based rapid propagation of orchids necessitates the use of intermediary propagules, primarily rhizomes or PLBs. Orchids like *Cymbidium*, *Dendrobium*, *Oncidium*, *Cattleya*, and *Arundina graminifolia* have PLBs as intermediary propagules, and they are considered easily propagated species. In contrast, *Phalaenopsis*, due to the propensity of PLBs to generate variations, is moderately challenging to propagate. Terrestrial orchids such as *Cymbidium sinense*[147], *Cymbidium ensifolium*[148], and *Cymbidium goeringii*[144] rely on rhizomes as intermediary propagules, which pose challenges for shoot regeneration, categorizing them as difficult-to-propagate species. Zeng et al. successfully established a rapid propagation system for *Paphiopedilum hangianum* and *Paphiopedilum Maudiae* through tissue culture, marking a pioneering achievement on a global scale[149].

Orchid flowering regulation

Cultivation facilities have enabled the manual control of orchid flowering periods, a practice extensively employed in orchid varieties such as *Phalaenopsis* and *Dendrobium*. Orchid flowering regulation research primarily centers around temperature, light, nutrient levels, and hormone signaling.

For many orchids, the induction of flower buds require low-temperature exposure and day/night temperature fluctuations. For instance, *Phalaenopsis*[150] requires low-temperature treatment to initiate flower bud formation. Temperatures below 15 °C reduce flowering rates, while those exceeding 28 °C hinder flowering[151]. In contrast, most *Cymbidium* orchids, including *Cymbidium goeringii*[152], form flower buds at high temperatures, but the subsequent flower bud differentiation requires lower temperatures. While *Oncidium*[153] do not strictly require low temperatures for flower formation, a certain degree of cold exposure enhances flower development.

Light plays a crucial role in orchid flowering. While orchids are not particularly stringent about day-length requirements, adequate light is essential for nutritional accumulation, while insufficient light can lead to growth retardation and delays flowering. A 7-h photoperiod fosters nutrient growth in *Phalaenopsis*, a 5-h photoperiod delays flowering, and a 9-h photoperiod enhances *Phalaenopsis* flower quality[154]. Additional lighting stimulates reproductive growth in *Cymbidium goeringii*[155] , advancing their flowering time.

Nitrogen, phosphorus, and potassium are vital elements for orchid growth and development. Elevated nitrogen levels promote vegetative growth, while increased phosphorus and potassium levels enhance reproductive growth. Treatment with 5 mmol/L KCL solution accelerates *Cymbidium sinense* flower bud emergence by 20 d[156]. Application of 500 mg/L nitrogen fertilizer and 250 mg/L potassium fertilizer increase the number of *Cymbidium* orchid leaf blades, while 500 mg/L nitrogen and 500 mg/L potassium fertilizer enhance the number of *Cymbidium* orchid flower stalks[157].

Exogenous plant hormones are extensively employed to manipulate orchid flowering times. 6-BA stimulates flower bud differentiation, increasing the number of flower stalks and flowers in *Phalaenopsis*[158]. GA_3 promotes flowering in *Paphiopedilum callosum*[159], serving as a substitute for the low-temperature requirement for flowering in certain *Phalaenopsis* varieties, enabling flowering at room temperature[160]. PP_{333} reduces the

height of *Dendrobium nobile*[161], resulting in compact flower arrangements, improved resistance to collapse, and earlier flowering. Combining hormones can synergistically regulate flowering. For instance, combining 6-BA with GA_3 can mitigate blooming deformities caused by high GA_3 concentrations, promoting flowering in *Cymbidium sinense*[162] and *Cymbidium ensifolium*[163].

Orchid pests and diseases

Numerous diseases and pests pose threats to orchids. Therefore, disease identification and technological control are pivotal in orchid care. Common orchid diseases encompass stem rot, white silk disease, brown spot disease, leaf blight, and anthracnose[164,165]. Fungal stem rot and bacterial soft rot, especially, present significant challenges in orchid production. Stem-rot strains of *Cymbidium*[166], *Paphiopedilum*[167], *Phalaenopsis amabilis*[168], and *Cymbidium hybridum*[169] have been identified to be affected by *Fusarium oxysporum* and *Fusarium solani*. Additionally, *Fusarium fujikuroi* is known to cause *P. amabilis* flower stem rot[168]. Bacterial soft rot, primarily affecting orchid leaves, can lead to rapid plant death in high-temperature conditions. Chrysanthemum bacteria (*Erwinia chrysanthemi*) have been identified as the causative agents of soft rot in *Phalaenopsis* in regions such as Zhejiang, Yili, and Taiwan[170]. Pathogenic microbes responsible for other diseases like anthracnose, white silk disease, blight, gray rot disease, include *Colletotrichum gloeosporioides*, *Atheliarolfsii*, *Phytophthora parasitica*, *Phytophthora palmivora*, *Phytophthora cactorum*, and *Sclerotina fucheliana*. Some biocontrol effects on *Fusarium oxysporum* have been observed with *Trichoderma viride*, *Trichoderma harzianum*, and *Trichoderma pseudokoningii*[171].

Orchid viral diseases pose challenges in orchid care, with up to 30 viruses known to infect orchids, including *Cymbidium* mosaic virus (CymMV), cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), *Odontoglossum* ring spot virus (ORSV)[172], impatiens necrotic spot virus (INSV)[173], *Phalaenopsis* chlorosis spot virus (PhCSV)[174], *Capsicum* chlorosis virus (CaCV), *Basella* rugose mosaic virus (BaRMV), *Rhabdovirus*, *Potyvirus*, and *Tospoviruses*. Stem tip culture to breed virus-free seedlings is a primary method for controlling viral diseases.

Endophytic fungi in orchids

Endophytic fungi are vital components of the Orchidaceae plant micro-ecosystem, playing crucial roles in orchid propagation. Orchids require a stable symbiotic relationship with fungi for seedling development, as these fungi provide essential nutrients through mycorrhizal associations, facilitating germination and healthy plant growth. Although China began researching endophytic fungi in Orchidaceae relatively late, approximately 50 orchid species, including *Dendrobium*[175], *Bletilla*[176], *Cymbidium goeringii*[177], and *Anoectochilus roxburghii*[178], have had their endophytic fungi isolated and identified. These fungi play critical roles in germination, growth, and disease resistance in orchids. For instance, symbiosis with three endophytic fungi significantly increased stem and leaf dry weights in the aseptic seedlings of *Cymbidium* sp. compared to mineral nutrient enhancement, improving growth by 173.2% to 250.1% and promoting nutrient absorption[179]. Some endophytic fungi can produce active ingredients found in medicinal plants and stimulate their host plants to produce these ingredients, significantly enhancing growth and polysaccharide synthesis in *Anoectochilus roxburghii (Wall.) Lindl.*[180]. Mycorrhizal fungi isolated from wild *Cymbidium* roots have been shown to significantly enhance respiration rates, cytochrome C oxidase, and peroxidase activity in *Cymbidium sinense* and *Cymbidium ensifolium*, positively affecting plant growth, development, and resistance[181] .

Prospects

Orchids exhibit unique features, including diverse floral structures, vibrant colors, variable plant types, leaf shapes, leaf colors, complex growth habits (epiphytic, overground, and saprophytic), diverse propagation modes (rhizomes, protocorms, clustered buds), different photosynthetic pathways (C3 and CAM pathways), and various flowering characteristics (seasonal flowering, continuous flowering). Numerous challenges and opportunities within the realms of horticulture, biology, genetics, pollination, embryology, microbiology, and molecular biology concerning orchids. These include diverse pseudobulb types (monocotyledonous and compound), non-rigid genus (species) definitions, sexual hybridization polyploidy, underdeveloped embryos (lack of endosperm), dependence on symbiotic bacteria, lengthy juvenile periods, endangered species, medicinal components, and mechanisms of action. Substantial advancements are expected in molecular mechanism analysis and the identification of functional genes related to critical traits.

Orchids are high-value flowers, particularly the commercial orchid varieties such as *Phalaenopsis*, *Cymbidium*, *Dendrobium*, *Cattleya*, *Paphiopedilum*, *Oncidium* and *Vanda*. Breeding objectives and perspectives for these orchids are diversifying, with a focus on delicate fragrance, enhanced leaf and flower characteristics, and energy-efficient and emission-reducing attributes in response to carbon emissions and carbon neutrality requirements. Advancements in breeding technology, including molecular marker-assisted breeding, transgenic techniques, gene editing, and molecular design breeding, are poised to usher orchid breeding from systematic breeding (breeding 1.0) and hybrid breeding (breeding 2.0) to molecular breeding (breeding 3.0) and intelligent design breeding (breeding 4.0). With the progression of digital and information-based agricultural technologies, orchid research on resources, breeding, physiology, cultivation, facilities, equipment, and agricultural economics is expected to become more systematic, further expanding the orchid industry.

Beyond the established commercial orchids, species like *Bulbophyllum* (1,789 species), *Eupatorium* (1,125 species), *Habenaria* (848 species), *Maxillaria* (552 species), *Masdevallia* (507 species), *Liparis* (418 species), *Eria* (404,000 species), *Calanthe* (187 species), *Coelogyne* (182 species), *Dracula* (111 species), *Prosthechea* (93 species), *Cypripedium* (50 species), *Lycaste* (50 species), *Phaius* (48 species), *Cycnoches* (33 species), *Tolumnia* (31 species), *Aerides* (25 species), *Pleione* (20 species), *Renanthera* (17 species), *Erycina* (seven species), *Rhynchostylis* (three species), and *Neofinetia* (two species), which possess great ornamental or medicinal values, remain largely untapped. These orchids represent a rich source for the development of new commercial flowers, promising to diversify and enrich the future flower market.

The Chinese have developed the national orchid and influenced Japan, South Korea and other East Asian countries, which have been increasingly accepted by Western countries in recent years. *Phalaenopsis* is mainly native to tropical and subtropical areas of Asia and Oceania. Currently, three production centers have emerged, including China, Europe and the United States. *Cattleya* native to tropical regions of central and south America, is mainly produced in Thailand and other Southeast Asian countries. China is going to become a major center of research, development, production and consumption of orchids in the future.

Author contributions

The authors confirm contribution to the paper as follows: original manuscript preparation: Yang F, Wong SM, Zhu G; data analysis: Gao J, Li J, Wei Y, Xie Q, Jin J, Lu C, Zhu W. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All data generated or analyzed during this study are included in this published article.

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Conflict of interest

The authors declare that they have no conflict of interest.

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