

The origin, germplasm resources, and breeding of *Anthurium andraeanum*: an overview

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Abstract

Anthurium (Anthurium andraeanum) is a popular tropical ornamental plant traded globally as cut-flowers, flowering potted plants, and landscape plants. Despite a cultivation history of less than a century, it boasts over 2,000 documented varieties. However, comprehensive information on anthurium breeding remains fragmented. This article aims to fill this gap by exploring the origins of modern anthurium, systematically organizing anthurium germplasm resources, summarizing molecular breeding resources (including transcriptomics and functional genes), detailing breeding methods, and addressing anticipated challenges and opportunities in anthurium breeding.

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Introduction

Anthurium, a genus within the Araceae family, comprises perennial evergreen herbaceous plants encompassing terrestrial, rupicolous, epiphytic, and hemiepiphytic herbs. It is comprised of 1,326 accepted species and over 1,000 estimated species, naturally distributed from Mexico to tropical America, and later introduced to Florida^[1]. The genus is categorized into 18 sections based on plant morphology and flower shape. The section Calomystrium is notable for its distinctive features, including cordate leaves, persistent cataphylls, and glossy spadices with spathes ranging from white to deep red^[2]. Other sections with higher ornamental value include Porphyochitonium, Cardiolonchium, Urospadix, and Pachyneurium. Among these, Porphyochitonium and Cardiolonchium species can hybridize with Calomystrium, producing viable offspring. While Pachyneurium can also undergo interspecific hybridization, it does not successfully cross with Calomystrium. Hybridization within Urospadix is rare. Sections such as Belolonchium and Semaephyllium also can successfully hybridize with Calomystrium, though there are fewer records. Other sections, such as Tetraspermium, Gymnopodium, Leptanthurium, and Dactylophyllium, face difficulties with both intraspecific and interspecific hybridization. Some sections, including Polyphyllium, Oxycarpium, Chamaerepium, and Schizoplacium, have few or no hybridization records, while others, such as Belolonchium and Semaephyllium, can not successfully hybridize with Calomystrium. Modern anthurium, commonly known as *Anthurium andraeanum* Hort., is a collective name that are actually interspecific hybrids between *A. andraeanum* Linden ex. André and other species in the Calomystrium section^[3]. Initially, cultivated anthurium originally referred to hybrids between *A. andraeanum* and species from the Calomystrium and Porphyochitonium sections. Over time, this scope has expanded to include hybrids between *A. andraeanum* and other sections capable of hybridizing with it.

Cultivated anthurium is globally renowned for its distinctive and attractive inflorescence, characterized by a spadix and spathe.

Nowadays, it is globally traded as cut-flowers, flowering potted plants, and landscape plants. *Anthurium* ranks as the second largest tropical flower commodity worldwide, just after orchids^[4–6]. The increasing demand for anthurium has prompted many countries to import numerous new cultivars from the Netherlands or Hawaii for commercial cultivation^[7]. Presently, Holland, Hawaii, Mauritius, and Jamaica are leading global producers of anthurium, with additional contributions from smaller producers in tropical regions such as the Philippines, Brazil, Malaysia, Martinique, and Thailand^[8,9]. Given the rapid turnover of varieties in the flower industry, continuous development of new anthurium cultivars tailored to market demands is crucial for the sustainable progress of the anthurium sector. Despite the relatively short cultivation and breeding history of anthurium, its notable success in interspecific hybridization has resulted in the creation of hundreds of exceptional varieties within a few decades. However, challenges persist in anthurium breeding, including difficulties in accessing native resources, limited understanding of germplasm resources, incomplete breeding information, and so on.

Published research on anthurium has focused on crucial aspects such as breeding methods, cultivation techniques, and tissue culture. Researchers have actively tackled challenges such as susceptibility to low temperatures, bacterial, and viral diseases, and enhancing anthurium's resilience to these biotic and abiotic stresses. Moreover, genetic engineering has emerged as a promising approach to augment the ornamental qualities of anthurium, attracting considerable attention in the scientific community. The identification of key genes regulating the ornamental traits of anthurium represents a significant advancement, providing valuable insights that could potentially be utilized to address challenges and drive innovation within the anthurium industry.

This study provides a comprehensive review of recent literature on *A. andraeanum*, encompassing germplasm resources, molecular breeding resources, and the main breeding methodologies. By synthesizing current knowledge and identifying existing gaps in anthurium germplasm and breeding strategies, this research aims to

inspire breeders and scientific researchers, offering fresh perspectives and stimulating further exploration in the field.

Botanical description

A. andraeanum, a perennial herbaceous plant of the family Araceae, typically grows between 30–100 cm tall. Its optimal growth temperature ranges from 15 °C to 35 °C, with growth being inhibited at temperatures below 14 °C^[10]. Prolonged exposure to temperatures above 35 °C, particularly under intense light conditions, can lead to leaf scorching, flower bud abortion, or malformation^[11]. *A. andraeanum* features short stems and alternate, leathery, glossy leaves that are mostly 10–30 cm long and 10–20 cm wide, with blunt to gradually pointed tips, and deeply cordate bases. The terminal flowers are borne on slender peduncles. The commercial 'flower' comprises a spathe, spadix, and peduncle (flower stalk). The spathe, a modified bract, measures typically 5–30 cm long and 2–18 cm wide, showcasing a variety of colors and a bright waxy sheen^[12]. The spadix is cylindrical and erect, 3–15 cm long, densely spirally arranged with minute hermaphroditic florets that are protogynous^[13]. Each floret contains a pistil and four staminate structures positioned around it (Fig. 1). Approximately six months after fertilization, the ovary enlarges to form a single berry containing one to two seeds, which eventually detach from the spadix upon maturity^[14]. Anthurium undergoes a distinct juvenile phase characterized by monopodial growth, where nutrient buds appear in leaf axils without flower production. Upon entering the reproductive phase, it transitions to sympodial growth, with floral buds emerging from leaf axils, resulting in an alternating leaf-flower growth pattern^[14].

Origin germplasm resources of anthurium

Anthurium andraeanum Linden ex. André is widely accepted as the progenitor of modern anthurium cultivars. This vine-like epiphyte features an orange-red, heart-shaped spathe with a blistered texture, reaching up to 14 cm long and 9 cm wide, on a long peduncle where basal lobes slightly overlap or fuse at the base.

Native to the wet forests at elevations of approximately 400 to 1,200 m in Northern Ecuador and Southern Colombia, it was first discovered in 1876 in the tropical rainforests of southwestern Colombia. French botanist Eduard André introduced it to Jean Linden's nursery in Belgium, sparking cultivation and breeding efforts. By 1935, various mutant species had been cultivated, leading to the development of several varieties like album (white spathe), garneri (bright red spathe), lawrencae (large white spathe), rbodocbilum (rose-colored with light green lobes), roseaum (shiny rose-pink), salmoneama (orange-red), and sangauineau (deep red). Subsequently, breeding programs in Hawaii, the Netherlands, and other locations were launched, driving the advancement and diversification of modern anthurium varieties *A. andraeanum* Linden ex. André, through hybridization with other species in the Calomystrium section, has led to the development of today's cut-flower varieties of anthurium^[15].

Many other original species of distinct sections (not only Calomystrium and Porphyrochitonium) were also used as parental germplasm resources of modern anthurium cultivars, such as *A. scherzerianum* Schott, *A. antioqueense*, *A. amnicola*, *A. antioquiense*, *A. ornatum*, *A. standleyi*, and so on (Fig. 2). *A. andraeanum* Linden ex André, through hybridization with other species in the Calomystrium section, has led to the development of today's cut-flower varieties of anthurium^[2]. *A. antioqueense* and *A. amnicola*, known for their compact size and prolific flowering, were used as parental plants in breeding programs that resulted in numerous potted anthurium cultivars^[16–18]. Moreover, these species were crossed with various cut-flower anthurium varieties to create hybrids showcasing a diverse array of colors^[18]. Aromatic anthurium germplasm resources like *A. armenianse*, *A. fragrantissimum*, *A. lindenianum*, *A. ochrantum*, and *A. roseospadix* were also hybridized with *A. andraeanum*, resulting in the production of many aromatic anthurium varieties now available in the market^[19]. The original *A. andraeanum* features a heart-shaped spathe, whereas cultivated anthurium varieties exhibit diverse spathe forms. For instance, tulip-shaped varieties may trace their origins to other species within the Calomystrium section or arise from species that are known hybrids between other sections (Cardiolonchium and Porphyrochitonium) and *A. andraeanum*^[20].

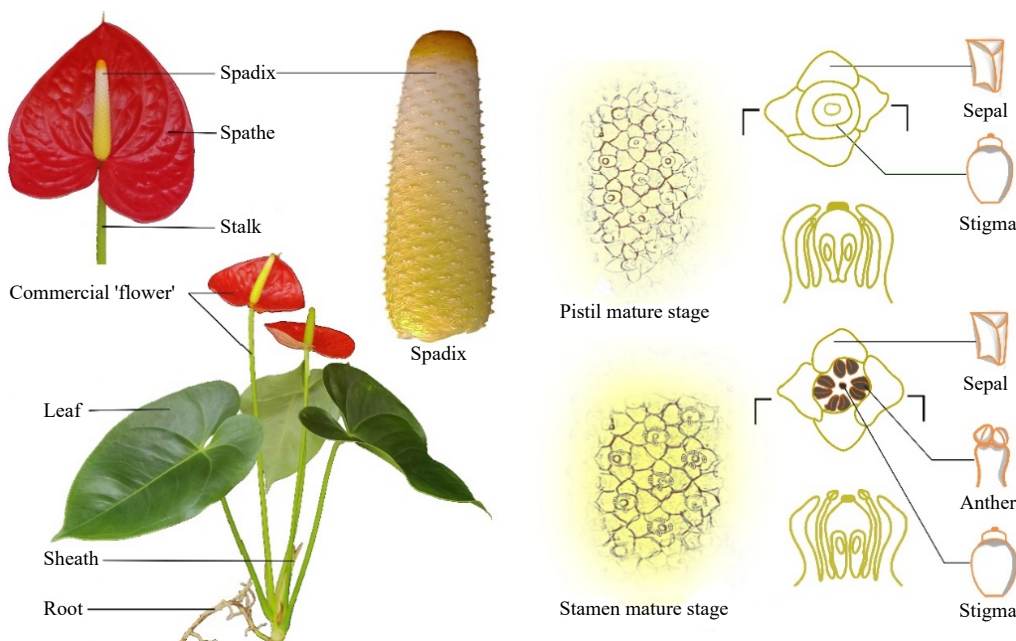


Fig. 1 The biological morphology and organs of *A. andraeanum*.



Fig. 2 Some parent species used for anthurium breeding. The publicly accessible websites for downloading these images are listed in [Supplementary Table S1](#).

Cultivated varieties of anthurium

After decades of selection and cultivation, over 600 anthurium cultivars are now available globally, categorized primarily as potted plants and cut flowers to cater to distinct market demands. Breeders have focused intensively on enhancing anthuriums' ornamental features, particularly emphasizing the characteristics of the spathe, including shape, color, size, and texture. These cultivars are typically grouped into three main types based on spathe characteristics: standard, obake, and tulip varieties^[21,22] (Fig. 3). Standard varieties feature symmetrical heart-shaped spathes with uniform colors such as red, pink, orange, coral, white, green, purple, and brown (Fig. 3a–g). Their spadix is gently angled and shorter than the spathe. Obake types display a bicolor appearance with green lobes and a contrasting center color (Fig. 3h–n), while tulip varieties resemble upright, cupped spathes reminiscent of tulip petals, with straight, erect spadices (Fig. 3o–t). Some cultivars also fall under patterned types, showcasing additional colors and patterns such as stripes or splashes on either heart-shaped or tulip-shaped spathes^[22]. Due to their tropical nature, regional influences play a significant role in the development of new anthurium varieties, with the Netherlands leading in cultivar registrations, followed by Hawaii and Florida, highlighting regional strengths in anthurium breeding and cultivation.

The Netherlands has a rich history of anthurium breeding and is widely recognized as a dominant force in the industry. Many renowned companies, including Anthura, Rijnplant, and AVO, have been actively involved in anthurium research for nearly 80 years. They have developed a series of cut flower and potted flower varieties such as 'Candy', 'Cheers', 'Arena', 'Carisma', 'Grand slam', 'Kaseko', 'Acropolis', 'Tropical', 'Choco', 'Cheers', 'Marysia', 'Fantasia', 'Dakota', 'Alabama', 'Sweet dream', 'Royal pink champion', 'Madural', 'Turenza', and 'Valerie', establishing their dominance in the global anthurium market^[23].

Hawaii also holds prominence cultivating anthurium varieties worldwide, with a history spanning over 80 years. In the late 1930s and 1940s, Hawaii growers made significant advancements by mastering anthurium propagation through seeds. This breakthrough not only expanded cultivation but also enriched the variety of

anthurium plants^[16]. The University of Hawaii played a pivotal role in advancing anthurium breeding, launching a program in the 1950s that involved collecting wild resources from South America for hybrid breeding. Through their efforts, they developed innovative breeding and evaluation technologies, which enabled them to gradually create multiple cut flower varieties such as 'Nitta', 'Midori', 'Marian Seeforth', 'Paradise Pink', 'Kalapana', 'New Era', and 'Tropical Flame', along with some pot varieties, like 'Southern Blush', 'Hokuloa', 'Manoa mist', 'Sundial', and cut dual-use varieties^[23–25].

In Florida, anthurium research started later than in other regions. In the 1980s, researchers from the University of Florida's Horticulture Department and the Oglesby Plant Laboratory initiated efforts to hybridize *A. andraeanum* with compact wild anthurium species. This breeding program led to the cultivation of numerous potted flower varieties, including popular series such as 'Red Hot', 'Tropical Fire', 'Orange Hot', 'Salsa', 'Purple Plum', 'Favorita', 'SmallTalk', and 'Lady'^[26–32].

Chinese researchers have also made strides in recent years in cultivating new anthurium varieties^[33–35]. Some of these varieties have received new variety rights and are commercially available, such as potted flower varieties 'Xiaojiao', 'Baixue Gongzhu', 'Fu Rui', 'Caixia', 'Xu Ri', 'Chao Tianjiao', 'Shuang Guan', 'Xia Yan', 'Zi Yun', 'Cai Xia', 'Rising Sun', 'Sunshine', 'Crystal Love', and 'Spring Dawn'.

Resources available for molecular breeding - transcriptomics and functional genes

Anthurium transcriptomics

Researchers have estimated the genome size of *A. andraeanum* to be 4.7 Gb using flow cell cytometry^[20]. Despite the absence of a published genome sequence for *A. andraeanum*, de novo transcriptome analysis has emerged as a crucial method for acquiring genetic insights^[36]. This approach proves particularly valuable in elucidating the genetic composition and regulatory mechanisms of anthurium species. Currently, many transcriptomes of anthurium have been reported (Table 1), predominantly focusing on pivotal signaling pathways and genes associated with traits such as spathe color, flower development, and stress resilience.

Comparative analyses of transcriptomes from different anthurium cultivars have been conducted to investigate the mechanisms governing anthocyanin biosynthesis. For instance, studies have compared transcriptomes of *A. andraeanum* 'Alabama', alongside its anthocyanin-deficient mutants to understand the regulation of anthocyanin biosynthesis^[37,38]. Similarly, researchers have explored the genetic basis of color variations among different-colored spathes of anthurium varieties^[43,44]. Analogous investigations have been conducted on leaf color. Transcriptome and small RNA sequencing of *A. andraeanum* 'Sonate' and its leaf color mutant revealed a range of differentially expressed genes (DEGs) and miRNAs^[42,46]. Moreover, a study related to the organ-specific transcriptome profiling of metabolic and pigment biosynthesis pathways in *Anthurium amnicola* Dressler, the progenitor species of anthurium, provided a comprehensive evaluation of the mechanisms involved in pigment synthesis in anthurium plants^[45].

By analyzing the transcriptomes, researchers gained insights into the signaling pathways and key genes associated with the cold stress resistance of anthurium. In *A. andraeanum* 'Alabama', researchers identified 4,363 DEGs under cold treatment and examined changes in metabolic pathways during prolonged stress treatment^[36]. Another study compared the transcriptomes of cold-tolerant cultivar *A. andraeanum* 'Elegant' and cold-susceptible cultivar *A. andraeanum* 'Menghuang', pinpointing 9,132 DEGs involved in cold response mechanisms enriched in pathways like plant hormone signaling, trehalose metabolism, and ribosomal proteins^[40]. Additionally, RNA-Seq analysis following the treatment

of anthurium seedlings with Putrescine (Put), a polyamine, identified 1,840 DEGs associated with defense, abscisic acid response, cold response, and oxidative stress response^[39].

The findings contribute to our understanding of these traits and provide valuable information for the development of breeding strategies aimed at cultivating anthurium varieties with improved characteristics.

Spathe color

The pigmentation of anthurium spathes primarily comprises anthocyanins, flavonoids, and chlorophyll^[47–49]. These pigments, present in varying types and proportions, determine the different color variations in anthurium spathes, ranging from red, pink, orange, coral, white, and green to obakes. Red, orange, pink, and coral spathes contain mainly cyanidin-3-rutinoside (red) and geranium-3-rutinoside (orange), with their ratios varying among different cultivars. White spathes lack anthocyanins but contain a substantial amount of flavone 6-C-glycoside derivatives. Green spathes predominantly feature chlorophyll. Notably, delphinidin (blue) has not been detected in *A. andraeanum*^[47–49].

The biosynthesis pathway responsible for anthocyanin production is well-established and conserved across plant species. In anthurium, key structural genes involved in anthocyanin synthesis have been identified, such as *AaCHS*, *AaDFR*, *AaF3H*, *AaANS*, *AaF3'H*, *Aa5*, *3GT*, *AaCHI*, and *AaC4H*^[50–55]. Transcription factors (TFs) play crucial roles in regulating spathe coloration by controlling the structural genes. Initially, the putative genetic factors M, O, and R have been identified as regulators of spathe color. The dominant *R* gene

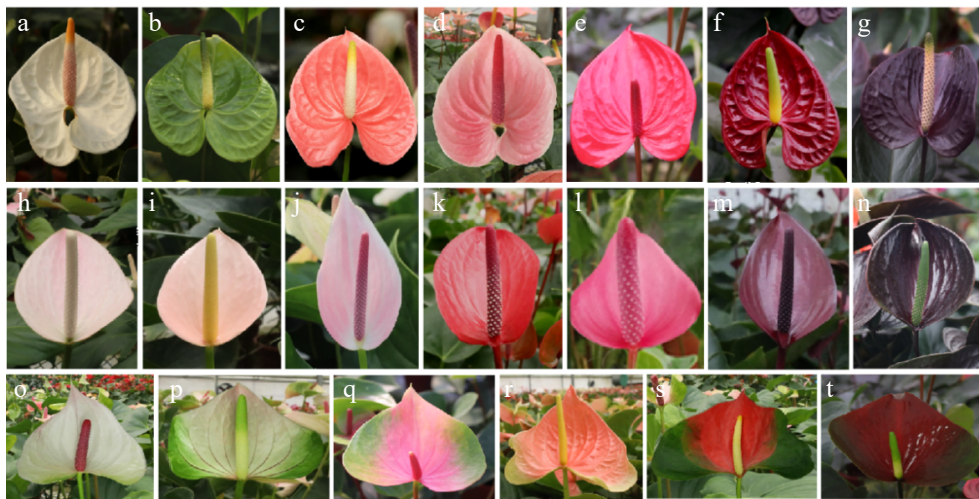


Fig. 3 Typical spathe colors and types in anthurium. (a)–(g) Display standard-shaped spathes in various colors. (h)–(n) Present tulip-shaped spathes in different colors. (o)–(t) Feature obake (bio-colored) spathes. The cultivar names corresponding to (a)–(t) can be found in [Supplementary Table S2](#).

Table 1. List of the reported transcriptomes of anthurium.

Source	Tissue	Number of unigenes/ miRNAs	Mean length (bp)	Accession number (NCBI)	Ref.
'Alabama'/'Xueyu'	Spathe	111,674	987	SAMN08322140–SAMN08322145	[37]
'Alabama'/anthocyanin-loss mutant	Spathe	47,563	652	Not released	[38]
'Alabama'	Leaf	37,396	1,356	Not released	[39]
E (cold-tolerant)/MH (cold-sensitive)	Leaf	132,108	648	PR-JNA973051	[40]
'Alabama'	Callus	225,752	1,299	SRP152774	[41]
'Sonate'	Leaf	41,017	768	GBKP00000000	[42]
Eight anthurium cultivars	Spathe	62,013	200	SAMN34164547–SAMN34164553 SAMN35719425	[43]
'Sasha'/'Honduras'/'Rapido'	Spathe	151,652	91	Not released	[44]
'Alabama'	Stem, leaf	44,382	60	E-MTAB-1955	[36]
<i>A. amnicola</i>	Root, spathe, leaf, spadix	19,458	No data	SAMN03839010–SAMN03839021	[45]

is the putative regulator of *CHS*, *F3H*, and *ANS*, dominate *O* gene is the putative regulator of *DFR*, and *M* gene is the regulator of *F3'H*^[56]. Subsequently, both MYB and bHLH type TFs are proven to be involved in spathe color regulation. Researches indicate that AaMYBs, such as AaMYB1, 2, 4, 5, and 6, positively regulate anthocyanin biosynthesis by influencing the expression of anthocyanin synthesis genes^[56–60]. For instance, overexpression of *AaMYB6* in tobacco promotes the accumulation of anthocyanin pigments in filaments through activating the expression of *NtF3'H*, *NtDFR*, *NtANS*, and *NtUGT*, potentially interacting with AabHLH1^[56]. Conversely, AaMYB3 negatively regulates proanthocyanin accumulation in tobacco by downregulating the expression of *NtDFR* and *NtANS*, possibly through interaction with AabHLH1^[61]. Additionally, overexpression of *AabHLH1* in an *Arabidopsis tt8* mutant restores the proanthocyanin-deficient seed coat phenotype^[61]. Several genes related to chlorophyll synthesis in anthurium have also been reported. Li et al. suggested that reduced *AaMYB2* expression leads to white-colored spathes by increasing *AaLAR* and *AaANR* expression, while enhanced *AaMYB124* expression contributes to green spathes by upregulating *AaHemB* and *AaPor*^[43].

Furthermore, correlation analyses of miRNA and mRNA expression patterns have identified several miRNA-mRNA interaction pairs that potentially act as negative regulators in anthocyanin accumulation, including miR156b/miR529-SPL17, miR408-blue copper protein-like gene, miR858-MYB3-like, and miR164-NAC100 pairs^[62].

Fragrance

Research has shown that the fragrance in anthurium germplasm resources comes from species like *A. armeniense*, *A. fragrantissimum*, *A. lindenianum*, *A. ochranthum*, and *A. roseospadix*^[19]. The primary aroma substances in anthurium include oxygenated monoterpenes and monoterpene hydrocarbons such as α -pinene, β -pinene, limonene, and linalool^[19]. Studies on anthurium aroma are limited, focusing on the relationship between aroma compounds and genes involved in terpene metabolism pathways. Wei et al. investigated aroma components in *A. andraeanum* 'Alabama' and 'Mystry', and observed the higher expression levels of aroma synthesis genes in aromatic varieties 'Alabama' compared to the non-aromatic 'Mystery', including *AaDXS*, *AaDXR*, *AaMDS*, *AaHDS*, *AaTPS*, *AaDAHPS*, *AaADT2*, *AaPAL1*, and *AaPAL2*^[63]. Transcriptome sequencing has also been used to identify candidate genes associated with aroma compound synthesis. Xia utilized Illumina Hiseq 2005 technology to analyze the transcriptome of *A. andraeanum* 'Mystery' and 'Alabama' across various tissues, and identified several genes involved in terpene metabolism including *AaDXR*, *AaMCT*, *AaHDS*, *AaLIS*, *AaGPPS*, and *AaPAL*^[64]. It is worth noting that while certain genes related to floral fragrance synthesis have been cloned in specific varieties, such as *AaDXS* and *AaDXR*, the sequences of other genes are still based on transcriptome data.

Stress resistance

Both abiotic and biotic stresses negatively impact the growth and development of anthurium plants, sometimes leading to plant death. These stress conditions affect overall growth rates, yields, and increase cultivation costs.

Anthurium, being a tropical flower, is particularly sensitive to low temperatures. Researchers have extensively studied its cold resistance through exogenous treatments, transcriptome analysis, and gene function identification. For instance, exogenous putrescine (put) activated the arginine-polyamine pathway under chilling stress, enhancing arginine decarboxylase activity and gene expression, while inhibiting polyamine decomposition^[65]. Transcriptome analysis identified 39 cold-inducible transcription factors (TFs) in *A. andraeanum* 'Alabama', including members of the AP2/ERF,

NAC, MYB, and bZIP families^[36]. Proteins involved in protein synthesis, energy metabolism, and hormone signaling were found to play crucial roles in cold resistance, such as ribosomal proteins, HSPs, and HsfA^[40]. Some genes in anthurium have been proved to play roles in cold tolerance. For instance, heterologous overexpression of *AaAPRR2* in *Arabidopsis* were shown to increase photosynthetic pigment accumulation and enhance salt stress tolerance^[66]. Heterologous expression of *AabHLH35* were proven to improve cold and drought tolerance in *Arabidopsis*^[67]. A cold-induced factor, AnAPX, enhanced cold tolerance in tobacco against cell membrane damage. Furthermore, the heterologous overexpression of *Aa-miR158* in *Arabidopsis* enhanced cold stress tolerance by increasing antioxidant enzyme activity and elevating reactive oxygen species (ROS) levels^[68].

Anthurium plants are susceptible to various bacterial and fungal diseases during cultivation, including bacterial blight, bacterial wilt, rhizoctonia root rot, phytophthora, and black nose disease^[69]. Among these, bacterial blight, primarily caused by *Xanthomonas axonopodis* pv. *dieffenbachiae* (*Xad*), is the most severe bacterial disease affecting anthurium and was first reported in Brazil in 1960^[70]. In the disease-resistant *A. andraeanum* 'Acropolis', transcriptome sequencing was used to investigate the signaling pathways involved in disease resistance and the roles of hormone signaling pathways in enhancing disease resistance. Furthermore, ten WKRY genes potentially associated with *Xad* resistance were identified^[71]. To enhance the resistance of the susceptible *A. andraeanum* 'Tian Tang Fen' to *Xad*, the cephalosporin-based cutting peptide *Shiva-1* was introduced into 'Tian Tang Fen'. The obtained transgenic plants exhibited improved resistance to bacterial leaf blight^[72]. These findings highlight the potential for genetic modification and targeted interventions to enhance stress resistance in anthurium plants, offering a promising approach to mitigate the impact of adverse stresses in cultivation.

Approaches applicable to anthurium breeding

Anthurium is a widely cultivated ornamental plant of significant commercial value, with its market competitiveness sustained through the development of new cultivars exhibiting enhanced traits, including improved spathes (shape, color, and size), leaves (shape, color, and size), plant stature, fragrance, stress tolerance, and prolonged flowering duration. Currently, hybrid breeding remains the dominant method in the cultivation of new varieties of *Anthurium andraeanum*, with approximately 90% of mainstream varieties on the market being the result of hybridization.

Crossing breeding

Anthurium is a cross-pollinated plant with hermaphroditic and protogynous characteristics during floral development^[13]. Due to its highly heterozygous genetic background, significant segregation occurs in the F1 generation, providing numerous opportunities for selection. Based on these characteristics, various potted and cut flower series have been developed through crossbreeding, featuring differences in spathe size (4–6 cm, 7–11 cm, 11–13 cm, 13–15 cm, 15–17 cm, 17–19 cm), spathe color (black, brown, green, orange, pink, purple, red, white, yellow), spathe shape (cupped, heart-shaped, mini, obake, standard), plant height (7–24 cm), and low-temperature tolerance (average, below average, excellent, good), among others. The commercialized anthurium varieties undergo a lot of steps, including target identification, parent selection, hybridization, F1 generation evaluation, tissue culture asexual reproduction, field evaluation, final selection, registration, and release. This process typically takes eight to 10 years. Some varieties are the result of multiple crosses or backcrosses, which can

take up to 15 years to achieve, like *A. 'White Lady'*, which is achieved through multiple interspecies hybridization [*A. andraeanum* '*Uniwai*' × *A. lindenianum*) × *A. amnicola*] × (*A. andraeanum* × *A. antioquiense*)^[35,73].

Hybrid breeding methods include intraspecific, interspecific, and intergeneric hybridization. Most commercial varieties are produced through intraspecific crosses, such as '*Xiao Jiao*', '*Xia Yan*', and '*Cherry Red*', have gained market prominence due to the stability and efficiency of intraspecific hybridization (Table 2). Interspecific hybridization also plays a crucial role in cultivating new anthurium varieties. For example, Sheffer & Kamemoto used 57 anthurium species as materials for distant hybridization and formulated 1,529 combinations, ultimately obtaining 344 distant hybrids with a success rate of 22.5%^[35,74]. Many anthurium cultivars are original from two or more native species, such as '*Pink Champion*', '*White Lady*', '*Centennial*', and '*New Era*', are the result of interspecific hybridization, highlighting its importance in expanding *Anthurium* diversity^[75] (Table 3). While intergeneric hybridization has been explored, it often results in problems like infertility and abnormal growth, limiting its widespread application. However, some success has been achieved through techniques like embryo rescue technology, which has facilitated the creation of hybrids between different genera^[76].

The reproduction of newly acquired germplasm mainly relies on asexual reproduction, which preserves the desirable traits of the germplasm, ensuring its continuity and further utilization.

Molecular marker assisted breeding

Molecular markers play a key role in *A. Anthurium* breeding, particularly in areas such as assisting with the selection of target traits, evaluating germplasm resources, and determining parental relationships. Effective molecular markers have been reported in flower color and fragrance breeding for the early screening of these traits in hybrid progeny. For example, Jiang constructed 10 flower color pools using 60 *A. Anthurium* resources and identified six molecular markers linked to flower color. Zhu used markers SSR10 and SSR126 for marker-assisted selection of red spathe in 96 progeny from the cross of *A. 'Mystral'* × *A. 'Alabama'*, achieving accuracy rates of 75.9% and 71.9%, respectively^[82]. Zhu also identified the fragrance-associated marker SSR27 and applied it to hybrid progeny populations from two different crosses, with accuracy rates of 87% and 69%, respectively^[82].

Molecular markers are increasingly used to assess the genetic diversity of *Anthurium* germplasm and to explore genetic relationships and variations among different varieties or wild species. This aids in identifying valuable gene resources and provides insights for selecting optimal hybrid parents. Bliss & Suzuki^[20] attempted to

Table 2. Information of some reported intraspecific hybrids of *A. andraeanum*.

Species/cultivars	Parent materials	Origin	Ref.
'Bai xue Gongzhu'	'Pink Champion' × 'Colorado'	Guangzhou Flower Research Center, China	MARA
'Zhao Xia'	'Toscane' × 'Colorado'	Guangzhou Flower Research Center, China	MARA
'Xu Ri'	'Pink Champion' × 'Fiesta'	Guangzhou Flower Research Center, China	MARA
'Xiao Jiao'	'Texana' × 'Sierra'	Guangzhou Flower Research Center, China	[77]
'Shuang Guan'	'Pink champion' × 'Orange champion'	Guangzhou Flower Research Center, China	[78]
'Xia Yan'	'Arizona' × 'Dakota'	Chinese Academy of Tropical Agricultural Sciences, China	[79]
'Victory Flag'	'Tropical' × 'Choco'	Chinese Academy of Tropical Agricultural Sciences, China	[80]
'Ming nong Yue hua'	'Sempre' × 'Big Beauty'	Sanming Academy of Agricultural Sciences, China	[75]
'Royal champion' ^a	'Dakota' × 'Sierra'	the Netherlands	MARA
'Cherry Red' ^a	'Red hot' × 'Kozohara'	Hawaii, USA	MARA
'Kapoho Welo'	'Acropolis' × 'Tropic Fire'	Hawaii, USA	[81]
'Red hot'	'Southern Blush' × 'Lady Jane'	Hawaii, USA	[27]
'Tropic', 'Sunrise'	'Anuenue' × 'Soga Orange' 'Obake'	Hawaii, USA	[23]
'Apapane'	UH931 × 'Tropic Fire'	Hawaii, USA	[23]
'I'iwi'	UH931 × 'Tropic Fire'	Hawaii, USA	[23]
'Lē'ahi'	UH931 × 'Blushing Bride'	Hawaii, USA	[23]

^a Indicates that the information about this variety comes from The International Gardening Association. MARA: The Science and Technology Development Center of the Ministry of Agriculture and Rural Affairs of the People's Republic of China (www.nybjkfzxx.cn/p_pzbh/sub_gg.aspx?n=21).

Table 3. Information of reported interspecific hybrids of *A. andraeanum*.

<i>A. Andraeanum</i> cultivars	Parent materials	Origin	Ref.
'Southern Blush'	<i>A. andraeanum</i> × <i>A. amnicola</i> × <i>A. andraeanum</i> 'Lady Jane'	Hawaii	[24–26]
'Hokuloa'	<i>A. antioquiense</i> × <i>A. andraeanum</i> 'Tatsuta'	Hawaii	[23]
'Manoa mist'	<i>A. antioquiense</i> × <i>A. andraeanum</i> 'Marian Seefurth'	Hawaii	[23]
'Sundial'	(<i>A. amnicola</i> × <i>A. andraeanum</i>) × ((<i>A. antioquiense</i> × (<i>A. antioquiense</i> × <i>A. andraeanum</i>)) × <i>A. andraeanum</i> 'Lady Jane')	Hawaii	[23]
'Pink Champagne'	<i>A. andraeanum</i> 'Anuenue' × <i>A. amnicola</i>	the Netherlands	[23]
'New Era'	A494 × <i>A. andraeanum</i> × <i>A. antioquiense</i> × pink UH507	Hawaii	[23]
'Blushing Bride'	(<i>A. andraeanum</i> (pink) × <i>A. antioquiense</i>) × <i>A. andraeanum</i>	Hawaii	[23]
'Maggie Inouye'	((<i>Uniwai</i> × <i>A. kamemotoanum</i>) × <i>A. formosum</i>) × <i>A. amnicola</i>	Hawaii	[23]
'Princess Aiko'	<i>A. antioquiense</i> × <i>A. Andraeanum</i> 'Tatsuta'	Hawaii	[23]
'Electron'	Unnamed seedling × seedling 94-4:(7-2:(3-1:(<i>A. amnicola</i> × <i>A. andraeanum</i>) × 4-1:(<i>A. antioquiense</i> × 1-1:(<i>A. antioquiense</i> × <i>A. andraeanum</i>)))) × <i>A. andraeanum</i> 'Lady Jane')	Hawaii	[23]
'Mini Gem'	'ARCS' × <i>A. amnicola</i>	Hawaii,	[23]
'Kalapana'	'Diamond Jubilee' × 'Paradise Pink'	Hawaii,	[23]
'White Lady'	((('Uniwai' × <i>A. lindenianum</i>) × <i>A. amnicola</i>) × (<i>A. andraeanum</i> × <i>A. antioquiense</i>))	Hawaii,	[23]
'Hilo Moon'	'Tropic Mist' × (<i>A. antioquiense</i> × 'Marian Seefurth')	Hawaii	[23]
'Waimea'	'Paradise Pink' × (<i>A. antioquiense</i> × 'Marian Seefurth')	Hawaii	[23]

distinguish various anthurium varieties using genome size as a differentiator. The findings suggested that genome sizes could reflect the species contributing to the pedigree of the cultivars but were inadequate for distinguishing genetic relationships between varieties^[20].

Molecular markers offer a more effective means of investigating genetic relationships. Isoenzymes, the earliest protein markers used in anthurium genotyping, exhibited limited variability and low polymorphism^[83]. DNA markers such as microsatellites or simple sequence repeats (SSR) and inter-simple sequence repeats (ISSR) have proven more effective. Wang & Chuang^[84] used four SSR loci to classify 27 diverse genotypes into three main clusters. Srisamoot & Padsri^[85] used 10 ISSR markers to assess genetic diversity among 26 cultivars, identifying significant genetic variation and high diversity. Their analysis, which revealed 122 bands with 113 polymorphic ones, resulted in an average polymorphism percentage of 91.64%, and clustered the cultivars into two main groups with a Cophenetic Correlation Coefficient (CCC) of 0.92^[85]. Khan & Pankajaksan^[86] used RAPD markers to analyze the genetic similarity among 12 cultivars, finding that intra-clustering within the two major clusters reflected their genetic backgrounds. Wang et al.^[87] utilized SRAP markers to analyze the genetic relationship among 33 cultivars and identified a considerable genetic diversity. The clustering patterns were closely linked to the color and morphology of the spathe. In contrast, other studies have reported inconsistencies between molecular markers and genetic diversity. For example, Souza Neto et al.^[88] used seven RAPD and 17 ISSR markers to evaluate the genetic diversity of 20 anthurium cultivars revealing wide genetic divergence, but genotype clustering did not match the morphological data. Nowbuth et al.^[7] evaluated the genetic variation among 24 cut-flower anthurium cultivars using RAPD markers and found low genetic variation, with clustering analysis showing no correlation with morphological traits.

Additionally, molecular markers help identify the genetic relationships between parent plants, preventing issues like progeny decline caused by inbreeding. By analyzing genetic distance and gene complementarity between parents, molecular markers can also be used to predict heterosis. Molecular markers have been developed as a DNA fingerprinting technique (DFP) to confirm the phylogenetic relationships among morphologically similar potted cultivars. Ranamukhaarachchi et al.^[18] used RAPD as a DFP tool to determine the phylogenetic relationships among nine morphologically similar anthurium potted cultivars. They successfully identified close genetic correlations and shared specific DNA bands between these varieties and three potential parent species. However, the DFP tool is primarily useful for confirming relationships among known cultivars and their potential parent species.

Furthermore, researchers have constructed a genetic linkage map for *Anthurium* using molecular markers, facilitating more effective marker-assisted selection (MAS) and improving the process of hybrid parent selection. Venkat et al.^[89] used a double-pseudo test cross-mapping strategy with RAPD, ISSR, and SRAP markers to create genetic linkage maps for two species, *A. ornatum*, and *A. andreanum*. The map for *A. ornatum* consisted of 10 linkage groups and a doublet spanning 1,233.5 cm length, incorporating a total of 85 markers. The map for *A. andreanum* consisted of 12 linkage groups covering 1,023.5 cm length with 78 markers. Another map for *A. andraeanum* based on SRAP markers and 94 F1 individuals from a 'Pink Champion' × 'Dakota' cross, consisted of 19 linkage groups covering 1,689.5 cm length with 254 markers^[90].

Currently, the limited genome information and insufficient research on genetic maps for crucial traits in anthurium hinder the rapid progress of the anthurium breeding industry. Hybrid breeding is still the primary method used, but integrating molecular

marker-assisted selection could enable more efficient and accurate screening of target traits, thereby shortening the breeding period. Therefore, developing effective molecular markers and constructing detailed genetic maps offer significant potential to advance anthurium breeding.

Prospective and promising approaches in anthurium breeding

In recent years, significant advancements have been made in biotechnology and related fields, leading to important progress in mutation breeding, ploidy breeding, and molecular breeding. Although these breeding methods are still in the research phase, each offers unique advantages and holds great potential. In the future, they are expected to play a pivotal role in the development of new varieties of *A. andraeanum*, warranting considerable attention and anticipation. Mutation breeding leverages physical, chemical, and other factors to induce heritable variations in *A. andraeanum*, creating opportunities to develop new varieties with distinct traits. Ploidy breeding, which alters the ploidy level of the plant's chromosomes, aims to produce varieties with superior growth characteristics and enhanced ornamental value. Meanwhile, molecular breeding employs advanced transgenic technologies to selectively improve specific traits of *A. andraeanum*.

Mutation breeding

Mutation breeding is a technique that induces genetic variation in plants by applying physical or chemical factors. This process typically involves selecting individuals with desirable traits from the mutated population to cultivate new varieties. In the case of anthurium, gamma ray radiation is commonly used as a physical mutagenesis method to generate new germplasm exhibiting novel traits such as dwarfism, distinctive spotted leaves, or enhanced stress resistance. Studies have indicated that different tissues of anthurium exhibit varying sensitivities to irradiation, with higher irradiation doses leading to more significant inhibition of the experimental material. Liang et al.^[91] reported that the half-lethal dose of radiation for adventitious buds of anthurium ranged from 30 to 40 Gy, while for callus tissue, it was between 10 and 20 Gy. Similarly, Peng et al.^[92] observed that the half-lethal dose of radiation for callus tissue was approximately 20–30 Gy, whereas for tissue culture seedlings, it ranged from 30–40 Gy. Researchers also noted that the regenerated plants following radiation exhibited stunted growth and slower development, with the degree of growth inhibition increasing with the radiation dose. Other radiation treatments have also been applied in anthurium mutation breeding. A¹³⁷Cs (Caesium) source was utilized to apply γ radiation to different tissues of *A. andreanum* 'Nitta', including seeds, callus, and leaf explants^[93]. Morphological changes were observed in the materials treated with ¹³⁷Cs at a dose of 5 Gy, while 15 Gy was found to be lethal. Subsequently, comprehensive researches were conducted building upon the acquisition of mutants through mutagenesis. *A. andreanum* 'Angel' plants exposed to 10 Gy gamma radiation displayed the highest percentage of mosaic leaves when^[94]. Furthermore, an effective amplified fragment length polymorphism (AFLP) marker was then developed for differentiating irradiated clones in *A. andreanum* 'Angel'^[94]. Additionally, mutants were successfully generated from petiole callus tissue of *A. andreanum* 'Sweet Heart' using a 1.5 Gy dose of ⁶⁰Co treatment^[82]. Cytological analysis of these mutants revealed various chromosomal variations, including bridges, micronuclei, fragments, and chromosomal hysteresis. Exposure of *A. andreanum* 'Alabama' callus to 30 Gy of ⁶⁰Co radiation resulted in mutants with stable inheritance and notable changes in leaf color, leaf shape, and spathe color^[95]. Researchers also

developed random amplified polymorphic DNA (RAPD) molecular markers to effectively distinguish between the mutants and their parent plants.

These findings indicate that a preliminary physical mutation breeding technology system for anthurium has been established, with radiation proving effective in increasing the frequency of genetic variation compared to natural conditions. However, there have been no reports of anthurium varieties selected through this method being successfully integrated into commercial production.

Ploidy breeding

Polyploid breeding involves using artificial or natural mutations to double the chromosome number in cells, aiming to create superior varieties with desired traits. In nature, *Anthurium andraeanum* and related species are typically diploid ($2n = 30$). Cultivating polyploid anthuriums can enhance their ornamental value and environmental resistance. Current methods for inducing polyploidy in anthuriums include chemical induction and sexual hybridization, primarily aimed at developing new germplasm with extended flowering periods, larger flowers, and improved stress resistance.

Colchicine is commonly used in chemical methods, targeting young explants, callus tissues, protocorms, clustered buds, and somatic embryo cells. In the 1950s and 1960s, Hawaiian researchers pioneered ploidy breeding for anthuriums, successfully using colchicine to double chromosomes^[96]. Zhang et al. achieved up to a 45.5% tetraploid induction rate in leaf-induced callus tissue with 0.2 g·L⁻¹ colchicine for 14 d^[33]. Similarly, Tian et al. achieved the highest tetraploid induction rate of 17.5% by treating *A. andraeanum* 'Alabama' leaf callus tissue with 0.2 g·L⁻¹ colchicine for 15 d^[97]. Aerial root regeneration clumps also exhibited the capability to produce polyploid plants, with a 63.3% induction rate achieved by subjecting them to 0.3% colchicine treatment for 7 h^[98]. Additionally, other chemical inducers are also showed effective in inducing anthurium polyploidy. Chu et al. found that sulfamethoxazole, fluralin, and colchicine can induce polyploidy in tissue-cultured *A. andraeanum* 'Dakota' seedlings. They achieved induction rates of 48.72% with 15 mg·L⁻¹ sulfamethoxazole for 7 d, 71.79% with 100 mg·L⁻¹ fluralin for 5 d, and 62.96% with 0.5% colchicine for 5 d^[99].

Sexual hybridization, which crosses different species or chromosomal groups, also produces polyploid offspring with desirable traits. Triploid varieties such as potted anthurium varieties 'Guifei' and 'Feizixiao', developed from tetraploid *A. andraeanum* 'Pink Champion' and diploid 'Tropical', exhibit enhanced stress resistance and superior characteristics compared to their parent varieties.

Haploid breeding is also an important technique in ploidy breeding, allowing for the production of homozygous plants with specific desired traits. This process involves several steps: haploid induction, chromosome doubling, and the selection of superior homozygous plants. In the case of *A. andraeanum*, a specialized technical system utilizing plant tissue culture has been developed to induce haploid plants from anthers^[100]. Winarto & Teixeira da Silva^[101] developed an efficient anther or half-anther culture system for *A. andraeanum* 'Tropical', by optimizing various steps such as anther separation timing, sterilization methods, and callus induction. They also studied the ploidy levels of the anther cultures and explored the relationship between haploid production and genotype^[101–116]. Their study revealed morphological and cytological variations in *in vitro* plantlets and acclimatized *ex-vitro* plants from anthurium half-anther culture^[102,103]. These variations included differences in plant size, peduncle length, spathe position, bud type and number, spathe and spadix color, and spadix length. Cytological variations showed different ploidy levels: 23%–29% haploids, 5%–10% aneuploids, 56%–69% diploids, and 3%–4% triploids^[103].

The obtained haploid plants were then treated with colchicine to develop doubled haploid (DH) plants, with a 65% success rate using 0.05% colchicine for 10 d, and an 80% success rate using 0.25% colchicine for 7 d^[106]. The successful establishment of haploid cultures from *A. andraeanum* 'Tropical' enabled the development of similar techniques for other cultivars, such as 'Carnaval', 'Casino', 'Laguna', and 'Safari'^[101,104–107].

Despite these advancements, the random nature of haploid breeding still presents challenges in targeted trait improvement and no new *A. andraeanum* varieties have been reported through haploid breeding so far.

Transgenic breeding

Transgenic breeding involves introducing exogenous genes or modifying the expression of endogenous genes to achieve specific traits, offering advantages over traditional breeding methods by enabling rapid, stable, and targeted development of new varieties or species. However, in *A. anthurium*, genetic modification is still in the stage of system establishment and optimization. As early as 1991, Kuehne et al. began exploring Agrobacterium-mediated transformation systems for anthurium using various explants, including internodes, leaves, petioles, and roots^[117,118]. Their efforts led to the successful introduction of *neo* and *att* genes into *A. andraeanum* 'Anuenue' using internodes and roots^[119,120]. Subsequently, other reporter and functional genes were transferred into different anthurium cultivars such as 'Arizona', 'Pink Champion', 'Marian Seefurth', and others (Table 4). To date, there have been more than 20 reports on the genetic transformation and transgenic breeding of anthurium, attempting to improve traits like color, flowering period, abiotic resistance, and biotic resistance^[121,122] (Table 4). The explants used included etiolated internodes, leaves, petiole, roots, etiolated shoots, callus, and somatic embryos. The key transformation techniques included Agrobacterium-mediated transformation, pollen tube pathway, and gene guns.

However, research on transgenic anthurium has primarily resulted in plants capable of detecting exogenously inserted genes through molecular biology methods, with no significant observable phenotypic changes reported so far. This lack of phenotypic change may be due to the minor effects of individual genes or unforeseen issues arising from the long growth cycles of the plants.

Conclusions and prospects

A. andraeanum is a tropical ornamental plant of great economic importance. This article provides a review of the research progress on the origin, germplasm resources, genetic resources, and breeding methods of anthurium. Currently, there is limited research on anthurium, revealing many areas that require further exploration.

Germplasm innovation

Currently, cross-breeding is the primary method for developing commercial *A. andraeanum* varieties. However, commercial breeding efforts are often driven by consumer preferences and commercial interests, leading to overly concentrated breeding objectives and a narrow range of parental selection. As a result, many new varieties exhibit homogeneity, particularly in traits such as flower color (especially red), petal structure, and flower size. This focus on a few desired characteristics has led to a lack of diversity in recently launched varieties. Moreover, breeding institutions often keep their parent selection and breeding technologies confidential, hindering rapid advancements in new variety development.

The *Anthurium* genus, with over 1,000 species across 18 sections, offers a rich gene pool for breeding. Species of *A. andraeanum* from different regions have developed unique genetic resources, such as

Table 4. Transgenic research on anthurium.

Species/cultivars	Explants	Transformation methods	Transgene	Promoter	Transformation results	Ref.
<i>A. andraeanum</i>	Etiolated internodes, leaf, petiole	Agrobacterium	No data	No data	Tumors formed on etiolated internodes (32%), green leaves (2%), petiole explants (3%)	[17]
<i>A. andraeanum</i> , <i>A. lindenianum</i> , <i>A. karniotoanum</i>	Roots	Agrobacterium	<i>nptII</i> , <i>att</i> , <i>uidA</i>	CaMV35S; NOS	No data	[118]
<i>A. andraeanum</i> , 'Rudolph', 'UH1060'	Etiolated internodes	Agrobacterium	<i>nptII</i> , <i>att</i> , <i>uidA</i>	CaMV35S; NOS	Western analysis confirmed the expression of atacin protein in callus induced from laminae of regenerated kanamycin resistant 'Rudolph' plantlets	[119]
<i>A. andraeanum</i> 'Anueue'	Roots	Agrobacterium	<i>att</i> , <i>neo</i>	CaMV35S; NOS	1.3%	[120]
<i>A. andraeanum</i> , <i>A. lindenianum</i> , <i>A. karniotoanum</i>	Etiolated internodes	Agrobacterium	<i>nptII</i> , <i>uidA</i>	CaMV35S; NO	No data	[123]
<i>A. andraeanum</i> 'Paradise Pink', Hybrid 'Tropic Flame'	Etiolated internodes	Agrobacterium	<i>Shiva-1</i> (with PR1 secretion signal)	Double CaMV35S	Stable (several-year-long) insertion and expression of <i>Shiva-1</i> gene in the transgenic lines by PCR, RT-PCR and ELISA	[124]
<i>A. andraeanum</i> 'Marian Seefurth', <i>A. andraeanum</i> 'Paradise Pink'	Etiolated shoots or leaf	Agrobacterium	Gene of Modified rice cysteine protease (D86)	No data	No data	[125]
<i>A. andraeanum</i> 'Arizona'	Leaf	Agrobacterium	<i>PhCHS</i>	CaMV35S; NOS	No data	[126]
<i>A. andraeanum</i> 'Arizona'; <i>A. andraeanum</i> 'Atlantic'	Petiole, etiolated internodes	Agrobacterium Gene gun	<i>LycB</i>	CaMV35S; NOS	No data	[127]
<i>A. andraeanum</i> 'T × P'; <i>A. andraeanum</i> 'Arizona'	Callus	Agrobacterium	<i>LycB</i>	CaMV35S; NOS	3.4%	[128]
<i>A. andraeanum</i> 'Arizona'	Petiole	Agrobacterium	<i>AtFT</i> , <i>PttFT1</i>	Double CaMV35S	Eight cell lines of AtFT transformed plants and one cell line of <i>PttFT1</i> transformed plants in the transgenic lines by PCR and GFP	[129]
<i>A. andraeanum</i> Red varieties	Leaf, callus	Agrobacterium	<i>AdAMP</i>	CaMV35S; NOS	Insertion by PCR, PCR sequencing.	[130]
<i>A. andraeanum</i>	Callus	Agrobacterium	<i>CBF1</i>	CaMV35S; NOS	No data (resistant healing tissues showed the highest survival and differentiation rates of 48.65% and 11.46%)	[131]
<i>A. andraeanum</i> 'Pink Champion'; <i>A. andraeanum</i> 'Robino Champion'	Leaf	Agrobacterium	<i>AtCBF3</i> ; <i>PaFT</i>	CaMV35S; NOS	<i>AtCBF3</i> : one transgenic plants were obtained; <i>PaFT</i> : 1 transgenic plants were obtained	[132]
<i>A. andraeanum</i> 'Pink Champion'	Leaf, root, callus	Agrobacterium	<i>CBF3</i>	CaMV35S; NOS	No data	[133]
<i>A. andraeanum</i> 'Sonate'	Leaf, callus	Agrobacterium	<i>DREB</i>	No data	11 transgenic plants were obtained	[134]
<i>A. andraeanum</i> 'Pink Champagne'	Leaf	Agrobacterium	<i>gfp</i> , <i>nptII</i>	CaMV35S; NOS	Seven transgenic plants were obtained	[135]
<i>A. andraeanum</i> 'Arizona'	Callus	Agrobacterium	<i>API-A</i> , <i>API-B</i> , <i>gfp</i> , <i>nptII</i>	CaMV35S; NO	1.71%	[136]
<i>A. andraeanum</i> 'Marian Seefurth', <i>A. andraeanum</i> 'Midori'	Embryogenic callus	Agrobacterium	<i>NPR1</i> , <i>nptII</i> , <i>NPRI</i> , <i>att</i> , T4 lysozyme, <i>Cowpea rypsin</i> inhibitor genes	CaMV35S; NOS	Up to nine selected lines/100 mg fresh weight of callus (for T4 lysozyme)	[137]
<i>A. andraeanum</i> 'Local Pink', <i>A. andraeanum</i> 'Pierrot', <i>A. andraeanum</i> 'Lydia', Sonata', <i>A. andraeanum</i> 'KAIRI2010', <i>A. andraeanum</i> 'Honduras', <i>A. andraeanum</i> 'Mirjam', <i>A. andraeanum</i> 'Tropical'	Leaf discs to test; cultivar effects; leaf, spathe and spadix to test explant and developmental stage effects	Agrobacterium	Gus plus with rice glycine-Rich protein signal peptide sequence	No data	Transient transformation Efficiency varied with anthurium cultivars from 0% ('Tropical') up to 83 ± optimization. After optimization, it reached 100% both in 'Local Pink' and 'KAIRI2010' (before optimization it was below 5%)	[138]
<i>A. andraeanum</i> 'Marian Seefurth'	Lamina somatic embryos and roots	Bombardment	<i>uidA</i>	Ubiquitin 2, Actin 1, Cytochrome C1 from rice Ubiquitin 1 from maize; CaMV35S	No data	[139]

stress-resistance genes and ornamental traits, through long-term adaptation to their environments. Integrating these genes into cultivated varieties could yield new characteristics and help prevent further homogenization.

Marker-assisted breeding can play a crucial role in improving genetic diversity. By analyzing genetic markers, breeders can select parents with distinct genetic profiles, thereby increasing genetic variation in offspring and reducing homogeneity. To address this, breeding efforts should focus on broadening parental selection, expanding breeding populations, and introducing new traits through distant hybridization. The use of effective marker-assisted selection can help shorten the breeding cycle and support the development of *A. andraeanum* varieties with greater diversity and new application values.

Breeding methods

In the field of *A. andraeanum* breeding, various techniques have been explored, but methods such as mutation and ploidy breeding show limited efficiency and high randomness in producing ideal varieties. In mutation breeding, when targeting specific traits (e.g., flower color) using similar mutagenic conditions (e.g., fixed doses of chemical mutagens), the resulting mutants often exhibit similar changes. To broaden the variation spectrum and uncover more valuable traits, new mutagenesis techniques, such as space mutagenesis and ion beam implantation, should be further explored. Combining these methods with modern biotechnologies like genome-wide selection can enable early and efficient screening of mutagenized populations, accelerating the development of superior varieties.

Transgenic breeding holds great potential to advance *A. andraeanum* breeding. However, most current transgenic experiments have not led to significant phenotypic changes, highlighting the importance of selecting appropriate target genes. Genome sequencing and QTL analysis will enhance the efficiency of identifying suitable genes for transgenic breeding. Additionally, challenges such as complex genetic backgrounds, long transformation cycles, and low transformation efficiencies remain. The choice of suitable receptor materials is crucial and requires further exploration. A promising solution to these challenges is the efficient somatic embryogenesis liquid culture system recently developed by Wang et al.^[140], which addresses issues of slow proliferation and low transformation rates. When combined with CRISPR gene editing, this system offers the potential for precise gene modification, leading to the creation of novel germplasms and even new varieties.

Genetic research

The lack of comprehensive genomic information has hindered the analysis of breeding and trait regulation mechanisms in *A. andraeanum*. Although the predicted genome size is 4.7 Gb, its complex genetic background presents significant challenges. To address this, sequencing local species and re-sequencing cultivated varieties will be more effective. Detailed genomic information is crucial for gene mapping, developing molecular markers, and understanding the genetic basis of key traits, which will aid in breeding new varieties.

Additionally, genomic data from other species in the Araceae family, such as *Zantedeschia elliottiana*^[141], *Amorphophallus konjac*^[142], *Colocasia esculenta*^[143], and *Pinellia ternata*^[144], can provide valuable insights for solving biological problems in anthurium.

The integration of multi-omics technologies, including transcriptomics, proteomics, and metabolomics, can offer a more comprehensive analysis of genetic information. This combined approach can systematically uncover the molecular regulatory networks behind key biological processes like growth, flower color formation,

and stress resistance. With this vast molecular data, breeders can identify key genes and regulatory elements linked to target traits, enabling efficient molecular breeding.

A. andraeanum exhibits unique traits such as its colorful and varied spathes, inflorescence colors, reproductive isolation, prolonged juvenile period, and extended ornamental period. Studying the mechanisms behind these features using interdisciplinary methods from horticulture, biology, genetics, and molecular biology can provide valuable insights for enhancing these traits.

International cooperation

Strengthening international cooperation and exchanges in anthurium breeding, facilitating the exchange of resources, technologies, and expertise, and improving the international variety registration and protection system are crucial for advancing the development of anthurium breeding.

Author contributions

The authors confirm contribution to the paper as follows: conception and supervision: Wei Q, Zhou X; data collection: Liu Y, Cai T, Guo H; image collection and processing: Xia Q, Yuan Y, Xie L; manuscript suggestions: Yi M, Su Q, Zhang Z, Zeng R; draft manuscript preparation: Liu Y, Wei Q, Cai T; manuscript reviewing and editing: Wei Q, Zhou X. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All data generated or analyzed during this study are available from the corresponding author on reasonable request.

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Conflict of interest

The authors declare that they have no conflict of interest.

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