horticulturae

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Review

Advances in Orchid Biology: Biotechnological Achievements, Translational Success, and Commercial Outcomes

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Abstract: Orchids constitute the largest and most diverse group of flowering plants and are classified in the family Orchidaceae. Exhibiting significance as the most exotic and ubiquitous flowering plant, the cultivation of orchids on a commercial level is gaining momentum worldwide. In addition to its ornamental and aesthetic value, the orchid industry has successfully generated employment for people in developing countries. Recent advances in biotechnological interventions in orchids have substantially contributed to the development of exotic varieties with novel traits, not to forget the inputs of traditional plant breeding methods and tissue culture approaches. In addition, the scientific developments in orchid biology have remarkably bridged the knowledge gaps in areas of orchid classification, phytochemistry, and cultivation strategies. This has facilitated the commercialization of novel varieties, opening new avenues in the orchid industry, and their global marketing as cut flowers and artificially propagated plants. Orchids constitute the first floriculture crops that revolutionized the orchid industry; however, they also hold several challenges in the natural propagation and conservation of several species that are on the verge of extinction. International organizations like CITES have come forward to address challenges associated with illegal global trade and indiscriminate use of orchid varieties, aiming for conservation and legal commercial goals. This thematic review is one-of-a-kind in providing comprehensive insights into the emerging momentum of orchid biology and how its globalization projects to considerably impact the orchid industry in the coming times. However, it is imperative to understand the challenges in the cultivation and conservation of orchid varieties and ensure legislative guidelines both on domestic and global levels to ensure a multipronged approach to the conservation and commercialization of orchids.

Keywords: aesthetic value; biotechnological interventions; commercial trade; conservation; micropropagation; transgenic orchids

Citation: Tiwari, P.; Sharma, A.; Bose, S.K.; Park, K.-I. Advances in Orchid Biology: Biotechnological Achievements, Translational Success, and Commercial Outcomes. *Horticulturae* **2024**, *10*, 152. https://doi.org/10.3390/horticulturae10020152

Academic Editor: Anna Lenzi

Received: 31 December 2023
Revised: 30 January 2024
Accepted: 1 February 2024
Published: 6 February 2024

1. Orchid Biology: Recent Aspects and Emerging Perspectives

The emerging benefits and recognition of orchids for mankind have led to substantial research in the present decade. Considered one of the most fascinating and diversified plant families globally, Orchidaceae comprises more than 8000 genera and 35,000 natural and artificial hybrid species distributed globally [1,2]. Within the family Orchidaceae, 70% of species are epiphytic and constitute two-thirds of global epiphytes [3]. Of the remaining orchid species, 25% are terrestrial and 5% require support for growth [4]. With specialized structures and properties, orchids continue to fascinate researchers as they have since time immemorial. The peculiar features demonstrated by orchids comprise specialized pollination, thin non-endospermic seeds, diversified habitats, mycorrhizal-dependent germination, and adaptive mechanisms, among others [5].

Presently, advances in orchid biology and biotechnologies have substantially contributed to the development of new cultivars and hybrids with multiple ornamental values, contributing to the rapidly growing market and demand for exotic varieties. From 2007 to 2012, the cost of fresh orchid cuttings and buds traded was estimated to be 483 million US dollars [6]. According to statistics, orchids are imported and exported by many countries, amounting to 504 million US dollars in 2012 [6]. In addition, orchids are also harvested and traded for medicinal value and food components. On a commercial level, *Phalaenopsis* is the most important orchid genus, with a market share of 79% among all global orchids. The European market is defined as highly competitive, with multiple cultivation prospects and a commercial value of 182 million potted plants of more than EUR 620 million [7]. The success in the cultivation and marketing of *Phalaenopsis* has been achieved via micropropagation and breeding approaches in many countries, including the Netherlands, Taiwan, Thailand, etc. [8]. In addition, *Oncidium*, *Vanda*, *Dendrobium*, and *Cymbidium* are other popular orchid genera grown and marketed worldwide as cut flowers [8]. *Vanilla planifolia* (vanilla orchid) is an interesting orchid species that produces edible fruit and vanillin, a sought-after commodity across the globe.

The present era has witnessed unprecedented advancements in promoting orchid cultivation, attributed to the dynamic progress in biotechnological interventions. Figure 1 illustrates advanced biotechnologies in orchids facilitating multi-faceted trait improvement. Table 1 provides a comprehensive account of research studies on orchids for generating hybrids with high-value traits. Their multi-faceted importance in floriculture, the food sector, and medicine has substantially contributed to orchid commercialization, with a multi-million-dollar global market [5,6]. The growing demand for exotic varieties and the conservation of threatened species necessitates new scientific technologies such as novel flower varieties, biotic/abiotic stress tolerance, and efficient propagation [5,8]. New frontiers in plant science have focused on advanced studies in orchids including genetic manipulations, proteome studies, and functional genomics, among others [1,2,5] for desired outcomes. Moreover, high-throughput technologies have facilitated studies on orchid phytochemicals, achieved by high-performance liquid chromatography (HPLC), nuclear magnetic resonance (NMR), mass spectrometry (MS), and others. Recent advances in the development of HPLC-DAD and MS have facilitated the precise detection of bioactive components in biological samples and novel compounds with pharmacological attributes.

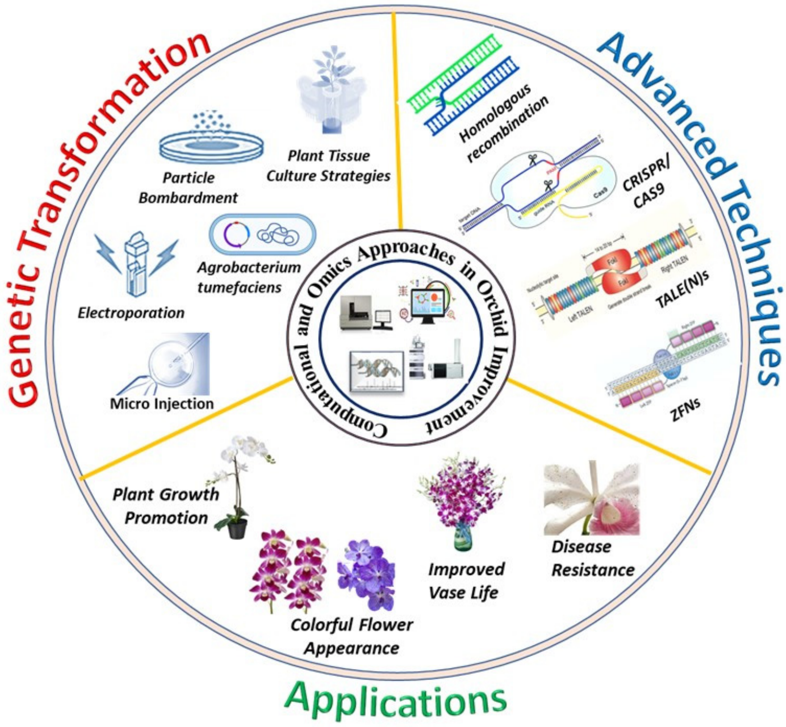

Figure 1. Advanced biotechnologies in orchids facilitating multi-faceted trait improvement.

Table 1. A comprehensive account of research studies on orchids for generating hybrids with high-value traits.

Orchid Genus	Biotechnological Interventions	Research Outcome	Reference
Oncidium sp.	*A. tumefaciens*-mediated transformation of OMADS1 gene RNAi-induced silencing of PSY gene Particle bombardment of construct pCB199 plasmid	Increased flowering and more flowers White flowers Disease resistance	[9] [10] [11]
Phalaenopsis sp.	RNAi-mediated silencing (virus-induced gene silencing) of the PeUFGT3 gene	Decreased anthocyanin and variation in flower color	[12]
Phalaenopsis amabilis *Coelogyne pandurata* Lindley	*A. tumefaciens*-mediated transformation of the orchid *A. tumefaciens*-mediated transformation of the KNAT1 gene	Transgenic orchids with the highest frequency of shooting Micropropagation of orchid species	[13] [14]
Cymbidium sinense	*A. tumefaciens*-mediated transformation of CsFT gene	Early flowering	[15]
Vanda sp.	Sonication-assisted *Agrobacterium*-mediated transformation (SAAT)	Enhanced disease resistance	[16]
Dendrobium Phalaenopsis	*Agrobacterium*-mediated transformation of gusA, nptII, hptII marker genes	Successful insertion of genes in transgenic orchid	[17]
Phalaenopsis sp.	*A. tumefaciens*-mediated transformation of eGFP (fluorescent) gene Particle bombardment of *EgTCTP* gene	Hygromycin resistance, early initiation of primordial shoots in the transformed PLBs	[18,19]
Cymbidium niveo-marginum	*A. tumefaciens*-mediated transformation of gfp, hptII, ORSV CP genes	Enhanced virus resistance	[20]
Phalaenopsis sp.	Genetic transformation of orchid with *Vitreoscilla* hemoglobin (vhb) gene via injection of DNA solution into immature capsules	Transgene with better metabolism and growth	[21]
Erycina pusilla	*A. tumefaciens*-mediated transformation of MSRB7 gene	Enhanced disease resistance	[22]
Dendrobium Sonia 'Earsakul'	RNAi-induced silencing of *DseDFR* and *DseCHS-B* genes	Anthocyanin accumulation was restricted in transgenic orchid	[23]
Cattleya sp.	*Agrobacterium*-mediated genetic transformation with an *Odontoglossum* ringspot virus replicase gene	Enhanced virus resistance	[24]
P. amabilis	Genetic transformation of lipid transfer protein-encoding gene	Improved adaptation to cold stress	[25]
Phalaenopsis aphrodite	*A. tumefaciens*-mediated transformation of Pha21 gene	Enhanced virus resistance	[26]
Phalaenopsis sp.	Genetic transformation of *Phalaenopsis* via pollen tube pathway	Transgenic orchid with improved traits	[27]
Dendrobium sp.	Electro-injection of foreign DNA into protocorms	Transgenic orchid with improved traits	[28]
Oncidium sp.	Genetic transformation of *pflp* gene	Resistance against *E. carotovora* pathogen	[29]

Table 1. *Cont.*

Orchid Genus	Biotechnological Interventions	Research Outcome	Reference
Dendrobium sp.	Genetic transformation of Firefly Luciferase gene	Transgenic orchid glows in the dark	[30]
Dendrobium sp.	Sense and anti-sense constructs used for genetic transformation	Enhanced vase life of transgenic orchid	[30]
Phalaenopsis sp.	Genetic transformation of ß-1,3-endoglucanase gene	Transgenic orchid is resistant to fungus	[31]
Calanthe sp.	Seed imbibition; electroporation of GUS, NPT II gene	Transgenic orchid with improved traits	[32]

However, overexploitation and the complex life cycles of orchids account for key challenges: unsustainable/illegal collection, climatic fluctuations, and threatened habitats. According to IUCN Global Red List statistics for 948 orchid species, 56.5% were classified as threatened in 2017 (The International Union for Conservation of Nature, 2017). Furthermore, attributing to their complicated lifestyles, orchids present a major challenge for restoration/conservation and highlight an immediate requirement for integrated conservation measures on broader levels (Table 1).

In the Cypripedioideae (the slipper orchids) subfamily, 90% of species were reported threatened due to over-harvesting and a decline in habitats by the Global Red List [33]. Vogt-Schilb et al. [34] studied orchid species and distribution on Mediterranean islands and reported a turnover in the composition of the species due to alterations in land usage and variation in species distribution due to changes in worldwide levels [35]. The unsustainable harvesting of orchid species represents a crucial factor. The indiscriminate use and collection of notable orchid genera, namely *Renanthera*, *Paphiopedilum*, *Cattleya*, and *Phragmipedium*, have resulted in their classification as being severely threatened. To curb the rising illegal trade of commercial varieties, more than 70% of orchid species were categorized in the appendices of the Convention on International Trade in Endangered Species (CITES) [36], a fruitful global initiative toward restoration. However, considering that many other orchid species are smuggled/traded across international borders for food, medicines, and horticulture, attempts are being made to understand/estimate the unauthorized export of orchids (under CITES) [37,38]. The steps toward orchid conservation and the development of new varieties should address the conservation of habitats, proper monitoring, and the implementation of guidelines for protection, and ensure legal marketing/global trade of multi-attribute varieties. The thematic review discusses the growing significance of orchids on a global platform with an emphasis on orchid biotechnologies to develop exotic varieties via conventional and modern strategies. In addition, the contributions of international and domestic organizations in monitoring illegal orchid trade and ensuring guidelines for conservation are extensively discussed. The preservation of orchid biodiversity via scientific approaches, contributions of computational resources in orchid biology, guidelines for marketing/trade at the domestic/global levels, and translational success stories define the underlying themes of the article.

2. Research Methodology: Literature Retrieval, Compilation, and Analysis

The conceptualization, implementation, and review writing spanned a time frame of 3–4 months. For the comprehensive study, an exhaustive literature survey and analysis were performed. Several literature databases, including PubMed (https://pubmed.ncbi.nlm.nih.gov (accessed on 28 January 2024) and Google Scholar (https://scholar.google.com (accessed on 28 January 2024), were used to retrieve research and review papers discussing various aspects of basic orchid biology and emerging biotechnologies for orchid cultivation, conservation, and genetic engineering studies. Efforts were also made to understand and discuss the impact of globalization and legislative guidelines at global/domestic levels for curbing illegal orchid trade and ensuring a legal framework for orchid cultivation and trade.

3. Conventional Versus Modern Approaches for Orchid Cultivation and Conservation

Orchid cultivation is gaining momentum attributed to the development of new orchid varieties with unique features of colors and appearance. To bridge this demand and supply gap, both traditional and molecular breeding approaches are employed with consistent efforts. The traditional breeding approaches of orchids, although time-consuming, have remained the mainstream approach for orchid breeding until now. The traditional breeding of orchid varieties includes their propagation through seeds, division of large clumps, offshoots or keikis, cutting, and air layering [39,40]. However, the increased demands of unique traits like flower/foliage color, morphology, and enhanced shelf life cannot be attained by traditional cultivation approaches including crossbreeding-mediated hybridization and mutation [1]. In recent years, these limitations have been actively addressed with the help of modern breeding approaches via transgenic molecular breeding approaches.

3.1. Classical Breeding Strategies

3.1.1. Crossbreeding

Orchid genera *Phalaenopsis* and *Oncidium* are widely grown orchids for commercial production. Orchids are both self-pollinated and cross-pollinated species. However, the self-pollinating species sometimes produce a smaller number of seeds than cross-pollinated flowers [1,41]. Crossbreeding or hybridization using both natural and artificial approaches splendidly integrates the excellent traits of two parents in their hybrid offspring. One of the oldest natural orchid hybrids, *Phalaenopsis intermedia,* which is a result of a cross between *P. aphrodite* and *P. rosea,* was described in 1853. Meanwhile, the first commercial artificial hybrid orchid *Calanthe dominyi* was developed as a cross between *C. masuca* and *C. furcate* [42,43]. The production of these commercial natural and hybrid orchids was achieved using crossbreeding approaches. However, several factors including hybrid combination fertility, targeted traits quality assessment, and superior hybrid offspring selection play an important role and must be considered [44]. The generation F_1 derived from the cross between parents with targeted contrasting traits usually has large phenotypic differences from their parents. For example, the F_1 generation derived from the parent having a large flower and short flowering time compared to the parent having a small flower and long flowering time, viz. *Ionmesa* Popcorn 'Haruri', produces flowers with distinct notable differences from its parents. However, hybrids sometimes bear problems associated with germination; for example, the occurrence of intraspecific < intrageneric < intergeneric degree of genetic relationship in hybrid *Cymbidium* seeds results in difficult seed germination and culturing [45]. Similar problems associated with the hybridization process, parent incompatibility, and post-fertilization embryo abortion failing the distinct hybridization have been reported [46]. Commercial orchid cultivation suffers from several associated breeding barriers such as the large and complex polyploid genome, slow growth, and long life cycle; consequently, it takes a long period to generate new cultivars using cultivation through the traditional breeding system. The low transformation efficiency makes the development of new varieties with desired traits a challenging task [47,48]. For example, the high commercial value orchid *Phalaenopsis* takes more than 2 years to switch from the vegetative to the reproductive phase [49]. Therefore, the applicability of these conditions remains to be studied in major commercial orchid species. Seed germination is one of the key aspects of the traditional breeding system, as it is directly associated with the efficient success of crossbreeding; therefore, in-depth studies are required for a deeper understanding of the seed germination mechanisms and plant developmental characteristics of an effective breeding system. Hence, a suitable cultivation approach is required for hybrid seeds developed from crossbreeding and stable growth of the hybrid population.

3.1.2. Selection Breeding

Selection breeding differentiates from crossbreeding where hybrid selection is based on natural variations in traits [50]. Selection breeding specifically concerns three important genetic parameters: genetic correlations between traits, trait heritability, and interactions between genotypes and the environment [1]. Like classical orchid breeding strategies of crossbreeding and selection breeding, biotechnological interventions have resulted in the origin of mutational breeding and molecular marker-assisted breeding approaches for orchids.

3.1.3. Mutation Breeding

The mutational breeding approach utilizes physical and chemical mutagens to improve individual traits and will shorten the breeding cycle in orchids. Mutational breeding has produced several orchids with improved traits, viz. aroma, higher medicinal content, enhanced shelf life, and stress resistance [43]. Polyploidization using colchicine and other mutagen treatments is one of the key approaches used for mutation in orchids such as *Cymbidium*, *Dendrobium*, *Oncidium*, and *Phalaenopsis* [51–56]. The higher levels of genomic heterozygosity can allow the enhanced mutation rate in a short time duration; however, the random and unpredictable nature of mutagenesis can take place throughout the genome which can lead to other physio-morphological problems in orchid mutants. Therefore, a lot of studies are still required to understand the basis of mutation breeding in orchids for the identification of suitable genotypes, explants, mutagen types, and their optimized dose concentration to produce mutant orchids with desired traits.

3.1.4. Molecular Marker-Assisted Breeding (MMAB)

The molecular marker-assisted breeding approach utilizes the accuracy of molecular biology tools and techniques for fast, accurate, and environmental-influence-free orchid breeding and natural and artificial hybrid selection [57]. The MMAB uses the most prevalent, versatile, and high-potential markers such as restriction fragment length polymerase (RFLP), amplified fragment length polymerase (AFLP), insertional simple sequence repeats (ISSR), and single nucleotide polymorphism (SNP) markers [1]. Most of these markers are widely used in modern orchid breeding and have achieved good results. Li et al. [58] developed a set of wide-range genic SSR markers in *Cymbidium ensifolium* to evaluate the genetic relationship and trait mapping in the orchid population. These SSR markers facilitate the identification of genetic relationships and have been successively used for the identification of root growth mechanisms and secondary metabolites-related gene identification, along with flower shape and color-related genes in *Phalaenopsis* [59,60]. Similarly, SNP markers were also utilized to construct integrated genetic maps of the *Dendrobium* genome along with the identification of several important QTL sites [61]. Although MMAB has played an important role as a modern orchid breeding approach, it mainly targets phylogenetics for determining genetic relationships between orchid species. Therefore, co-integrated approaches of traditional, and modern orchid breeding strategies and biotechnologies are required for improved orchid breeding.

3.2. In Vitro Orchid Propagation in Plant Tissue Culture

In vitro micropropagation provides a convenient and feasible approach for orchids, especially for orchid seeds that are difficult to germinate and grow in a natural environment [40]. Also, it provides a platform for biotechnologies for orchid improvements and genetic engineering. In vitro micropropagation represents a promising tool for the conservation of several threatened and endangered orchids and has been successfully applied in several species such as *Paphiopedilum armeniacum*, *Bulbophyllum nipondhii*, *Paphiopedilum insigne*, and *Anoectochilus elatus* [62–65].

In the last decades, plant tissue cultures have been instrumental in the rapid propagation and ex situ conservation of orchids, using different methods and explants including flower stalks, shoot tip nodes, stem bids, root tips, and rhizome segments [66]. The composition of culture media plays a major role in in vitro seed germination and micropropagation using different explants [67,68]. For example, Murashige and Skoog (MS) medium enhances germination in the orchid *Geodorum densiflorum*, whereas Knudson C medium [69] is more suitable for *Paphiopedilum* seeds compared to other orchid-specific culture media [70]. It was also observed that a low concentration of mineral salts in MS medium (viz. ½ MS or ¼ MS) promotes seed germination in some terrestrial orchids [71,72]. The constituents of culture media, especially plant growth regulators, auxins, and cytokinins, have a significant impact on the growth, germination, and development of orchid seeds and explants in vitro [73,74]. Along with the plant growth promoters, the addition of organic nutrient sources like coconut water and potato extract in culture media was also found to promote orchid in vitro seed germination [63,75].

The different orchid species show great variations in physiological and morphological features, requiring different conditions for growth in plant tissue culture. Different species respond differently to growth factors (depending on the genotype), and some are recalcitrant in in vitro conditions [76]. In terrestrial orchids, such as *Paphiopedilum* and *Cypripedium*, meristem explant survival and PLB induction are difficult. In addition, a method developed for a particular species may not work for another species. Therefore, for targeted genetic transformation, a plant regeneration protocol must be developed for a particular plant genotype [76], and the identification of variations in genotype must occur before plant transformation is necessary. The subsequent discovery of asymbiotic seed germination (for in vitro plant propagation) has been widely employed to develop orchid plants in vitro and direct somatic embryogenesis [77], totipotent callus induction, shoot-bud formation from different explants, PLB formation from cell suspension culture, and others, which have immensely contributed to the micropropagation and creation of transgenic hybrids [5].

3.3. Cryopreservation Techniques

Low temperature and dry storage-based preservation are key approaches to orchid germplasm conservation [78,79]. However, this low temperature and dry storage-based method is successful for 1 to 6 months of germplasm preservation but fails to provide high viability of germplasm under preservation for longer durations [80,81]. Cryopreservation is the best germplasm preservation approach as all the metabolic and physiological processes cease at the temperature -196 °C [82]. The pretreatment of orchid seeds and pollens germplasm through vitrification, desiccation, and encapsulation–dehydration methods of removing the cell water content before cryopreserving in liquid nitrogen are employed [83,84].

3.3.1. Vitrification

Sakai [85] introduced the technique of vitrification typically used for the longer preservation of immature and mature orchid seeds with higher than average water content. The vitrification method uses a high osmolarity vitrification solution containing glycerol, dimethyl sulfoxide, and ethyl glycol as cryoprotectants. The seeds for preservation are kept in this high osmolarity vitrification solution that reduces the intracellular water content of seeds and vitrified by penetration of these cryoprotectants through osmoregulation, thus reducing the freezing temperature and preventing cells from ice nucleation injuries [84,86]. Vitrification has helped in the conservation through cryopreservation of immature and high-water-content seeds of several orchid genera, viz. *Bletilla*, *Cymbidium*, *Dendrobium*, *Encyclia*, *Phaius*, and *Vanda* [82].

3.3.2. Desiccation

Desiccation-based cryopreservation is found to be more suitable for mature orchid seeds. The process of desiccation includes the slow drying of seeds under a controlled desiccation rate under constant relative humidity or drying with silica gel or with $CaCl_2.6H_2O$ salt solution to reduce the water content of the seeds before preserving them in liquid nitrogen [82]. Several orchids, viz. *Bletilla formosana*, *Caladenia flava*, *Dactylorhiza fuchsii*, *Diuris fragrantissima*, *Eulophia gonychlia*, *Gymnadenia conopsea*, *Orchis coriophora*, *Paphiopedilum rothschildianum*, *Pterostylis sanguinea*, *Thelymitra macrophylla*, and *Dendrobium candidum*, were successively cryopreserved using the desiccation technique [82,87].

3.3.3. Encapsulation–Dehydration

Encapsulation–dehydration, a technique developed for artificial seed production, is the third method for cryopreservation [88]. The encapsulation–dehydration approach uses the in vitro cultured orchid plant tissues, seeds, and embryos, partially desiccated with silica beads or airflow of the laminar bench to reduce the cellular water content. These partially dried tissues are trapped and encapsulated in sodium alginate beads before keeping them in liquid nitrogen for cryopreservation [87]. The encapsulation–dehydration techniques are generally applied to a few orchids, viz. *Cyrtopodium hatschbachii* and *Oncidium bifolium* [89,90].

3.4. Genetic Engineering and Generation of Hybrids with 'High-Value' Traits

Genetic engineering in orchids confers 'high-value' traits to the hybrids with desired characteristics and has been attempted in the genera viz. *Phalaenopsis, Cattleya, Cymbidium, Dendrobium, Oncidium, Paphiopedilum,* and *Vanda*, with documented translational success. PLBs derived from shoot tip cultures are used as target material for transformation in *Phalaenopsis* sp., while protocorm has also been frequently used [91]. A relatively large number of transgenic plants can be generated by protocorm transformation due to the presence of thousands of seeds in one fruit of *Phalaenopsis* sp. However, to achieve a successful outcome, it is indispensable to improve the transformation efficiency for efficient orchid breeding. Furthermore, the genetic engineering procedures in orchids are applied through either particle bombardment or *Agrobacterium*-mediated transformation to achieve the delivery of the desired gene. The initial genetic transformation studies were limited to the biolistic-mediated transformation [92,93]. The very first successful *Agrobacterium*-mediated genetic transformation was achieved in the orchid genera *Phalaenopsis* expressing the GUS gene construct [94]. The *Agrobacterium*-mediated genetic transformation was found to be more efficient than the biolistic-mediated genetic transformation in terms of incorporation of low copy number genes at transcriptionally active chromosomal regions [95].

The last decade has documented genetically engineered orchids through *Agrobacterium*-mediated genetic transformation systems in *Phalaenopsis, Dendrobium, Cymbidium, Oncidium,* and *Vanda* [18,96–99]. The genetic engineering approaches in orchids are not only restricted to the overexpression of heterologous genes for the desired traits but also gene silencing to knock out genes in *Dendrobium* 'Sonia' and *Oncidium* hybrids [100]. Now, with the availability of the complete genomes of *Dendrobium officinale* and *P. equestris*, the genetic engineering approaches facilitate CRISPR/Cas9-mediated genome editing in different orchid species [101]. Liu et al. [100] delivered a phytoene synthase-RNAi construct into PLBs of *Oncidium* hybrid. The downregulation of PSY and geranyl synthase genes was observed in the transgenic orchid, and endogenous levels of abscisic acid and gibberellic acid were decreased in dwarf plants [100]. In another study, *Agrobacterium*-mediated insertion of KNAT1 (a key gene for bud apical meristem differentiation) and AtRKD4 (a key gene for embryonic differentiation) into the orchid genome induced organogenesis and bud development, thereby improving the yield of native and transgenic orchids.

4. Biotechnological Interventions in Orchids: Existing and Upcoming Trends

Biotechnological approaches play a key role in the development of ornamentals with improved floral and 'high-value' attributes and are often employed to alter flower color, fragrance, appearance, disease resistance, and shelf life, among others [79,102].

4.1. Promoting Growth Vigor and Flowering

Desired traits can be selected in orchids with the help of genetic engineering along with controlling the flowering time, fragrance, flower color, and vase life [103]. Table 2 discusses flowering mechanisms in diverse orchids as exemplified by key representative genes and their multiple functions. Figure 2 illustrates the biological roles of MADS-box genes in controlling flowering in the *Arabidopsis* and Orchid plants.

Table 2. Flowering mechanisms in diverse orchids as exemplified by key representative genes and their multiple functions.

Orchid Genus	Gene Name(s)	Functional Role(s)	Reference
Dendrobium	DOH1: HOMEOBOX1	Floral transition and flower development	[104]
Dendrobium	DOSOC1	Promotes early flowering	[105]
Dendrobium	DnVRN1	Floral induction	[106]
Dendrobium	DnAGL19	Flowering regulation	[107]
Dendrobium	DOFT	Inflorescence and flower development	[108]
Dendrobium	DOAP1	Formation of floral meristems	[109]
Dendrobium	DOFTIP1	Promotes flowering	[108]
Doritaenopsis	DhEFL4	Requirement for photoperiod perception and circadian function	[110]
Oncidium	*OMADS1*	Induced precocious flowering	[111]
Oncidium	OnTFL1	Encoding floral activator	[112]
Phalaenopsis	PeMADS6	Flower longevity and ovary development	[113]
Phalaenopsis	PhalCOL	Early flowering phenotype	[54]
Phalaenopsis nation	PeSEP	Floral organ determination	[114]
Phalaenopsis	PaFT1	Precocious flowering	[115]
Phalaenopsis	PhapLFY	Flower initiation	[116]
Phalaenopsis 'Formosa rose'	*ORAP11* and *ORAP13*	Both genes are highly expressed during the early stages of floral buds and vegetative organs	[117]
P. aphrodite	*PaAP1-1* and *PaAP1-2*	*PaAP1-1* is expressed in the inner whorls of the pollinia and pedicel and *PaAP1-2* is expressed in the pedicel only	[118]
Cymbidium ensifolium	CeMADS	Reproductive organ development such as stamen and carpel development and function in the meristem	[119]

The very first genetic engineering attempts in *Oncidium* and *Odontoglossum* orchids were carried out to enhance growth and vase life through the mutant ethylene receptor gene [120]. *Oncidium* and *Odontoglossum* are commercially less viable orchids than *Phalaenopsis* due to their reduced vase life. Raffeiner et al. [120] engineered an ethylene receptor mutant gene *etr1-1* from *Arabidopsis* under the control of a flower-specific promoter to reduce the sensitivity of transgenic orchids toward the exogenous ethylene, thus providing a prolonged vase life. In similar attempts, a virus-induced gene silencing approach was applied in *P. equestris* by suppressing the *P. equestris* UDP glucose–flavonoid 3-O-glucosyltransferase (PeUFT3), which significantly faded the flower color by decreasing the anthocyanin content and altered the flower pigmentation due to reduced anthocyanin biosynthesis [121]. Similarly, genetic engineering in orchids was successfully used to generate the adaptive response against cold stress in *P. amabilis* by introducing the cold-inducible lipid transfer protein (LTP) gene from rice. To alter growth and morphology, genes like the class 1 Knox DOH1 gene and *Dendrobium* Sonia cytokinin oxidase DSCKX1 gene were introduced and overexpressed in *Dendrobium* under in vitro conditions, leading to abnormal multiple shoot developments and reduced cytokinin content [122–124]. These plants demonstrated slow shoot growth with an improved rooting system. These studies proved the utility of the DSCKX1 gene as a growth rate-manipulating gene in the development of orchids.

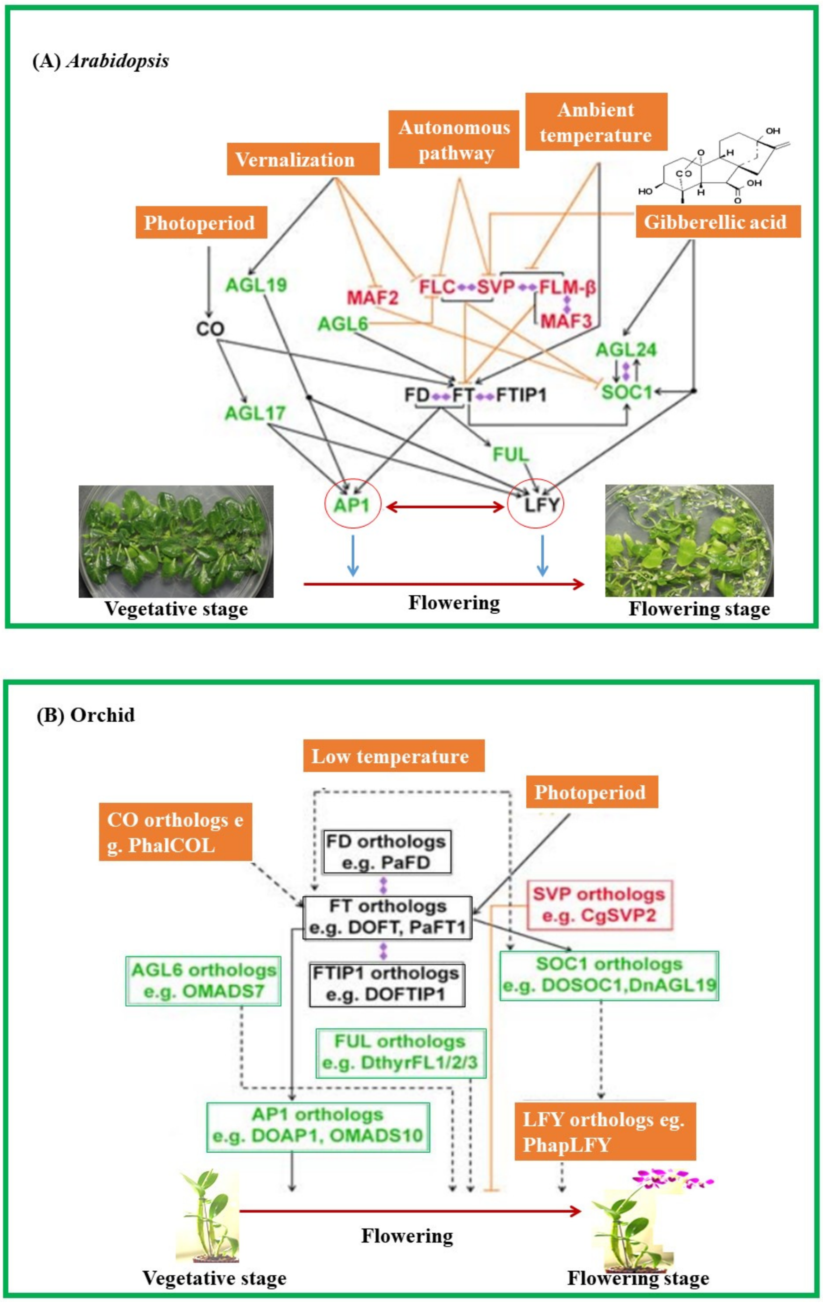

Figure 2. Biological roles of MADS-box genes in controlling flowering in the *Arabidopsis* and Orchid plants. (**A**) In *Arabidopsis*, the MADS-box genes including SOC1, FLC, SVP, and AGL24 integrate signals for flowering from environmental and endogenous cues. (**B**) In orchids, orthologous genes of SOC1, AGL6, SVP, and AP1 have been isolated and functionally characterized either in heterologous systems (e.g., *Arabidopsis*) or orchids and shown to be involved in promoting flowering. MADS-box transcription factors that function as flowering activators and suppressors are shown in green and red, respectively, whereas the remaining flowering regulators are shown in black boxes. Promoting and repressive flowering is indicated by black arrows and orange T bars, respectively. The dashed lines with arrows indicate possible positive regulation based on the studies using a heterologous system. Double-ended diamond arrows indicate protein–protein interactions. AGL6; AGL17; AGL19; AGL24; AP1; CO; FLC; FLM; FT; FTIP1; FUL; LFY, MAF2; SOC1; SVP. Abbreviations: AGL—AGAMOUS-LIKE; AP—APETALA; CO—CONSTANS; FLC—FLOWERING LOCUS; FLM—FLOWERING LOCUS; FTIP—FT-INTERACTING PROTEIN; FUL—FRUITFULL; LFY—LEAFY; MAF—MADS AFFECTING FLOWERING; SOC—SUPPRESSOR OF OVEREXPRESSION OF CONSTANS; SVP— SHORT VEGETATIVE PHASE.

4.2. Diagnosis of Pathogens

Most orchid species are faced with challenges of extinction due to global environmental changes and overexploitation; however, microbial pathogens equally threaten orchid cultivation. The most common pathogen–fungal species are namely leaf spots from *Nigrospora oryzae*, leaf spots from *Cladosporium cladosporioides*, wilt from *Fusarium oxysporum*, blight with root rot from *Phytophthora capsica*, anthracnose from *Colletotrichum gloeosporioides*, the black spot from *Alternaria alternata*, leaf spots from *Phyllosticta capitalensis*, and leaf spots from *Phoma multirostrata*. Also, sometimes, endophytes can work as conditional pathogens for orchids [79,125,126]. Biotechnological advancements have provided the solution through modern disease diagnosis techniques, allowing detection within the laboratory and in the field.

Droplet polymerase chain reaction (dPCR) is an innovative PCR-based disease diagnosis technique that utilizes the Taq DNA polymerase to unwind targeted DNA sequences from a complex test through a pre-validated primer/probe test [127]. Along with the PCR-based nucleic acid amplification detection technique, an advanced spectroscopy method is also applied for disease diagnosis in orchids. Surface-Enhance Raman Spectroscopy (SERS) is a Raman scrambling-based non-destructive and developing laser-based spectroscopy method that utilizes resistance tests and atomic tests for pathogen detection in plants [128]. DNA hybridization and colorimetric biosensor-based approaches are being extensively researched to establish a rapid, real-time disease diagnosis tool [129]. Similarly, an advanced chip-based integrated microfluidic system has been developed for automated rapid virus detection, through nucleic acid amplification. This approach was utilized to identify the most prevalent orchid virus, *Cymbidium mosaic virus* (CMV), with the purification of pathogen-specific RNA from the diseased sample. The isolated RNA is amplified to cDNA, and its optical detection is achieved using reverse transcription loop-mediated isothermal amplification (RT-LAMP) for the detection of the pathogen in the sample [130].

4.3. CRISPR/Cas and Advanced Genome Editing in Orchids

Recent advances in the development of genetic manipulation techniques have completely revolutionized orchid biotechnologies and opened new avenues in 'hybrid' generation with desired characteristics. Gene editing has been performed in ornamental genera, *Dendrobium* and *Phalaenopsis,* with low efficiency; however, CRISPR/Cas9 genome editing research in orchids aims to facilitate the development of key orchid phenotypes. Tong and coworkers [131] attempted a high-efficiency CRISPR/Cas-based editing of *Phalaenopsis*, wherein two CRISPR/Cas methods were employed to introduce three MAD sites (MADS44, MADS36, and MADS8) together in pYLMADS8_36_44 [132] and vector and single in separate vectors (P1300_MADS8, P1300_MADS36, and P1300_MADS44 [133] for the production of multiple mutants in *P. equestris* MADS-box genes [131]. The genetic manipulation of orchids has witnessed some success with the establishment of genetic transformation systems and the creation of transgenic mutants with the desired traits; however, the poor transformation efficiency of orchids defines a major challenge, and limited knowledge about the gene function and breeding further adds to the limitations. Further insights and research on achieving better transformation efficiency are needed for the success of transgenic technologies in orchids. Semiarti and coworkers [134] developed a CRISPR/Cas9 KO system for molecular breeding in *P. amabilis*. The Phytoene desaturase 3 (PDS3) gene was successfully integrated into the transformants and showed pale leaf color, and the study showed prospects for functional gene editing in orchids. As a step further, Xia et al. [135] successfully developed a multiplex genome editing system in *Phalaenopsis* orchids and protoplast-based screening, highlighting advanced precision breeding in orchids. The CRISPR/Cas9 tool was employed for editing endogenous genes in the *D. officinale* genome [136]. The study showed efficient genome editing in *D. officinale* paving the way to create novel varieties.

5. Ethnomedicinal and Edible Importance of Orchids

Represented as the diversified plants among the angiosperms, orchids are cultivated for their attractive flowers and exotic varieties. Initially cultivated as ornamentals for their multi-colored and attractive flowers, the medicinal applications of orchids are gaining momentum in the present time. Studies have reported the initial cultivation of orchids by the Chinese and documented orchids for their medicinal properties and use [137]. Researchers have traced orchid history and their medicinal uses to 120 million years ago, probably cultivated for their health-promoting effects [66]. Early documented evidence was found in the literature of Japan and China, approximately 3000 to 4000 years ago; they are regarded as pioneers in describing the medicinal attributes of different orchid species [138,139]. Shennung, a Chinese legend, described *Dendrobium* and *Bletilla striata* species in the book *Materia Medica* in the 28 century BC [138]. The Indian traditional system also reported the pharmacological uses of orchid species, namely *Dendrobium macraei*, *Orchis latifolia*, and *Eulophia campestris*, among others, in Ayurveda [140]. The key genera of medicinal orchids are as follows: *Ephemerantha*, *Eria, Galeola*, *Cymbidium*, *Cypipedium*, *Nevilia*, *Thunia*, *Bletilla*, and *Anoctochilus*, with new orchid varieties being discovered [102,141,142].

The medicinal properties of orchids are gaining popularity and different species are increasingly employed for medicinal attributes, attributed to the presence of diverse phytochemicals present in different species. Alkaloids have been reported in several medicinal orchids and demonstrate antimicrobial functions. Multiple studies in recent times have focused on the isolation of phytochemicals with medicinal attributes from different species and comprise Cypripedin, Orchinol, Nidemin, Hircinol, Loroglossin, and Jibantine. A comprehensive overview of key orchid species, plant parts, phytochemicals, and their ethnobotanical significance has been discussed. Table 3 provides key examples of orchids with medicinal properties and their multi-faceted ethnobotanical attributes.

Table 3. Key examples of orchids with medicinal properties and their multi-faceted ethnobotanical attributes.

Scientific Name	Found in	Habitat	Plant Part	Medicinal Attributes	Reference
Aerides multiflora Roxb.	India	Epiphytic	Roots, Leaves	Wound and cuts, Antibacterial	[143]
Calanthe triplicata	India	Terrestrial	Flowers, roots	Anti-inflammatory, Diarrhea, Gastric disorders	[144]
Brachycortis obcordata (Lindl.) *Summerh.*	----	Terrestrial	Roots	Dysentery	[66]
Dendrobium chrysanthum	China	Epiphytic	Leaves	Skin diseases, Anti-pyretic, Immunoregulatory	[145]
Bulbophyllum umbellatum Lindl.	Asia	Epiphytic	All plant parts	Increase congeniality	[66]
Orchis latifolia L.	India Iran Afghanistan	Terrestrial	Roots	Diabetes, Dysentry, Malnutrition, Diarrhea	[146]
Maxillaria densa	Mexico	Epiphytic	All plant parts	Analgesic, Relaxant	[147]
Cymbidium aloifolium (L.) Sw.	Asia	Epiphytic	Bulbs, Rhizomes	Dislocated bones and fracture	[148]
Acampe papillosa	India	Epiphytic	Roots	Rheumatism, Syphilis Neuralgia	[149]
Arundina graminifolia (D. Don) *Hochr.*	Nepal Thailand China Japan	Terrestrial	Roots	Bodyache	[150]
Anoectochilus formosanus Hayata	Taiwan	Terrestrial	Tubers	Abdominal pain, Nephritis, Hypertension, Anti-inflammatory	[151]

Table 3. *Cont.*

Scientific Name	Found in	Habitat	Plant Part	Medicinal Attributes	Reference
Epidendrum mosenii	Korea China	Mostly epiphytes, some terrestrial	Stem	Antinociceptive	[152]
Gastrodia elata	Asia	Heterotrophic	All plant parts	Epilepsy, Tetanus, Neuroprotective	[153]
Habenaria pectinata D. Don	India	Terrestrial	Tubers	Snake-bite treatment, Arthritis	[154]
Cypripedium elegan Reichenb .f. Nep	Asia America	Terrestrial	Roots	Epilepsy, Spasms, Rheumatism	[66]
Dendrobium densiflorum Lindl.	India	Epiphytic	Pseudobulbs	Skin diseases	[155]
Eulophia nuda Landl.	India	Terrestrial	Tubers	Bronchitis, Tumors	[156]
Malaxis acuminta D. Don	India	Terrestrial	Pseudobulbs	Antioxidant, Anti-aging	[157]
Vanda roxburghii	India	Epiphytic	Leaves	Anti-pyretic, Sciatica, Bronchitis	[158]
Vanilla planifolia	Mexico	Epiphytic	Sheath	Rheumatism, Hysteria, High-fever	[159]
Satyrium nepalense	India Nepal	Terrestrial	Tubers	Malaria, Dysentry	[160]
Bletilla striata	Taiwan Nepal China	Terrestrial	Tubers	Cancer, blood disorders, Tuberculosis	[161]
Cymbidium goeringii	Asia Australia	Epiphytic	Whole plant	Diuretic	[162]
Coeloglossum viride	England	Terrestrial	Rhizome	Neuroprotective	[163]
Goodyera discolor	Asia	Terrestrial	Whole plant	Antihepatotoxic	[149]
Gymnadenia conopsea	Europe Asia	Terrestrial	Tubers	Anti-allergic, Aphrodisiac	[164]
Pholidota yunnanensis	China	Epiphytic	---	Antioxidant	[165]
Orchis laxiflora Lam.	Europe, Africa, Asia	Heterotrophic	Bulbs	Bronchitis, Diarrhea	[166]
Luisia zeylanica Lindl.	India, Sri lanka Thailand	Epiphytic	Leaves	Wound healing, Treating burns	[145]
Pholidota pallida Lindl.	India	Epiphytic	Roots Pseudobulbs	Analgesic	[167]
Thunia alba (Lindl.) Rchb. F	India Myanmar Thailand	Epiphytic	All plant	Treatment of dislocated bones	[66]
Zeuxine strateumatica (L.) *Schltr.*	China Japan India	Terrestrial	Tubers Roots	Tonic	[168]
Trudelia cristata (Lindl.) *Senghas*	India Bangladesh Bhutan	Epiphytic	Leaves Roots	Wound healing, Treatment of dislocated bones	[66]
Vanda tessellata (Roxb.) *Rchb. f.*	India Sri lanka Burma	Epiphytic	Leaves Roots	Rheumatism, Anti-pyretic	[169]
Platanthera sikkimensis (Hook. f.) *Kraenzlin.*	India	Terrestrial	Pseudobulbs Bulbs	Analgesic	[66]
Pleione humilis (Sm.) D. Don	India	Epiphytic	Pseudobulbs	Wound healing, Tonic	[170]

The beneficial effects of phytochemicals from orchids on human health have been well known since ancient times and include anti-inflammatory, neuroprotective, antimicrobial, anticancer, hypoglycemic, anti-rheumatic, and wound-healing properties among other significant effects [141]. Traditional Chinese medicine suggested the routine use of *B. striata*, *D. nobile*, and *G. elata* for medication, with different *Dendrobium* species widely used in China to cure various diseases [171]. Moreover, the tubers of *B. striata* were widely used in traditional systems for the treatment of pneumono-phthisis and pneumonorrhagia, in addition to treating gastritis and duodenal ulcers, bleeding, hemoptysis, and tuberculosis. In addition, Ayurvedic literature reported the active use of orchids in herbal formulations, viz. *Habenaria intermedia*, *Malaxis muscifrea*, *Habenaria edgeworthi*, and *Malaxis acuminata*, which were active ingredients in Chavyanprasa [169]. Similarly, pseudobulbs and tubers of key species, namely *Zeuxine strateumatica*, *Habenaria*, *Orchis mascula*, *Eulophia*, *Orchis latifolia*, and *Cymbidium aloifolium*, were used as restorative therapy in several diseases, with a discussion of key orchid species found in Table 3. Studies have reported the isolation of more than 100 bioactive alkaloids from orchids [141,166,172] and the pharmaceutical constituents comprise Dendrocandin-A, Dendrocandin B, Phenanthrenes, Bulbophythrins A, Bulbophythrins B, Nobilin-E, Nobilin-D, Rotundatin, Ochracinone, Ochracinanthrone, Ochrolic acid, Ochrolone, and many more that have recently been discovered [173–179].

The flavonol and flavonoid components (of medicinal significance) isolated from orchid species include Apigenin 7-O-glucoside, 8-C-p-hydroxybenzylquercetin, Scutellarein 6-methyl ether, Apigenin-6-O-β-d-glucopyranosil-3-O-α-l-rhamnopyranoside, Quercetin, Chrysin, Homo-isoflavone, etc. [180,181]. The emerging medicinal importance of orchids has necessitated the need for clinical validations [181,182]. A clinical trial by Khouri et al. [183] suggested the efficacy of plant extract (*Orchis anatolica*) in improving fertility in male mice. In another study, constituents from the orchid *Scaphyglottis livida* were evaluated as relaxants of heart contractions in mice. The study further showed that stilbenoids limited aortic contractions and led to vasodilation and relaxation and are supposed to have major potential in cardiac treatment [184]. A terrestrial orchid, *Eulophia epidendraea*, is traditionally used for wound healing, tumors, and antidiarrhoeal activity, attributed to the presence of terpenoids, saponins, alkaloids, etc. [185,186]. *Dendrobium* and its bioactive constituents display effective hepatoprotective and immunomodulatory functions [187]. *Gastrodia elata* and its active ingredients have been widely used to treat rheumatism, brain disorders, inflammatory diseases, and headaches, due to the presence of Gastrodin, Gastrodioside, Vanillin, β-sitosterol, Vanillyl alcohol, and ρ-hydroxybenzyl alcohol [188,189].

In China and other Asian countries, multiple orchids have been employed to develop functional food products since 1990. The bioactive constituents and micronutrients present in orchid tubers make them a nutritional supplement in Cameroon and African countries [190]. Fonmboh and coworkers [191] provided literature insights into the medicinal and edible properties of wild root tuber orchids in Cameroon. While the medicinal properties of multiple orchid species are well known, the use of orchids as food constituents and flavoring agents makes them a key economic resource in food industries. In recent times, studies exploring the orchid flora in South Africa have investigated the edible properties and constituents facilitating the orchid trade. Orchid tubers are used as a food source and harvested from the wild species. The tubers are processed as a sausage and locally named chikande and chinaka, relished by the local Mawai population [192]. In addition, tubers are added as ingredients in soups and included in dishes in international hotels [193]. In Cameroon, orchids are mainly epiphytic, and the edible orchids belong to the genera *Disa*, *Satyrium*, and *Habenaria*. Moreover, new food products have been developed from *Dendrobium* and *Gastrodia* spp. Food items and healthy drinks as functional food have been processed from the flower and stem of *D. officinale* and another *Dendrobium* sp. [194]. A key example is the use of *G. elata* tubers in soup and *Cymbidium* flowers in healthy drinks and herbal tea [195,196]. In east and central Africa, tubers of the terrestrial orchids are used to prepare 'Chikanda', a traditional cake recipe. 'Salep' is another food ingredient in ice cream and drinks, mainly consumed in Turkey and adjoining countries [37]. While edible orchids represent an alternative food source in countries in the Global South, Zambian, Tanzanian, and Malawi people consume orchid tubers for food and trade [197]. In a key study, the nutritional content of wild orchid species from Tanzania was studied and included fiber (2.7%), protein (5.36 g), minerals ash (2.2%), and fat (1.57%), among others, highlighting the use of edible orchids as a functional food. Additionally, the concerns about malnutrition in children/infants can be treated by products developed from orchids [37]. The powdered form of tubers of *Orchis mascula* is used as a food component in 'Salep' beverage or the Turkish food 'Dondurma'. In Turkey, ice creams from orchid constituents, known as 'Dondurma', are relished by the locals. Other popular food items prepared from different edible orchids comprise flavor rum from the dried leaves of *Jumellea fragrans* in Reunion Island, underground tubers of *Gastrodia sesamoides* as food in Australia, and Chikanda from *Satyrium cursoni* [40]. *V. planifolia* is found in tropical lowlands and inhabits Central America, Brazil, and Mexico [198]. Regarded as endangered by IUCN [199], the plant is the main source of vanilla, a food flavoring agent. While vanillin comprises 80% of total bioactive metabolites in the pods of *V. planifolia*, vanillic acids such as 4-hydroxybenzoic acid and vanillic alcohols such as Guaiacol, 4-hydroxybenzaldehyde, etc. are the other metabolites [200]. A chromosome-scale *V. planifolia* genome was reported by Hasing and coworkers [201] that revealed gene variants that affect the pathway of vanillin biosynthesis and bean quality and facilitate orchid breeding for improved traits.

6. Computational and Omics Approaches in Orchid Biology

The discovery of new orchid species and their emerging prospects has necessitated the need to address the knowledge gaps and improve the understanding of key areas in orchid biology. The last few decades have witnessed substantial contributions of computational and omics approaches in providing comprehensive insights into orchid genomes and the molecular and physiological mechanisms, respectively.

Omics refers to a group of disciplines in the areas of genomics, transcriptomics, proteomics, and metabolomics, among others, which contribute to a better understanding of the roles and pathways of different molecules in living organisms [202]. Genomics provides an overview of the complete set of genetic instructions provided by DNA. Orchid genomes are typically larger than those of most model plants and there is remarkable variability in genome size across the family, with the amount of nuclear DNA varying by up to 168-fold [203]. It is difficult to analyze *Phalaenopsis* orchid via genomics due to its large genome and long life cycle. Lin et al. [204] employed the flow cytometry method for the estimation of DNA content in *Doritis pulcherrima* Lindl. and *Phalaenopsis* 'Blume' species. The results showed variation in genome size within 18 *Phalaenopsis* species. Further, new commercial hybrids were produced via chromosome doubling [21] and can be used for the comparative assessment of DNA content, providing insights into the evolution of *Phalaenopsis* orchids and assisting the orchid breeders in the selection of parent varieties for the hybridization process. Further, to understand the relationship and molecular characterization of different species, sequence-based microsatellite markers were used [205]. Ko and coworkers [206] employed polymorphic microsatellite markers for delimiting species within the *Phalaenopsis* genus.

Transcriptome studies were performed in *C. ensifolium* pooled flower buds and mature flowers [207]. The *Cymbidium sinense* mature plant transcriptome was studied for the identification of genes associated with floral development [208]. MicroRNAs (miRNAs) are short RNA molecules that regulate gene expression in eukaryotes, and they influence physiological mechanisms such as development, cell proliferation, cell death, and differentiation [209,210]. The different techniques used for the study of the entire "miRNome" allow for exploring these novel mechanisms of gene expression regulation [210]. In *Orchis italica* inflorescence, miRNome revealed the presence of conserved and novel miRNAs. The *insilico* search for the possible miRNA targets showed a conserved miRNA cleavage site within the four OitaDEF-like transcripts, which experimentally validated for OitaDEF2 [209]. This result reveals that miRNAs play an important role in the diversification of the organs of the perianth in orchids through the inhibitory regulation of the clade-2 DEF-like gene. Different mechanisms might act to regulate the expression level of the other DEF-like genes, suggesting the existence of lineage-specific regulatory mechanisms contributing to the functional specialization of the DEF-like clades in orchids. Advances in next-generation sequencing (NGS) technologies and new algorithms have improved the computational analysis of genome-scale RNA-seq transcriptomes [211–213]. The characterization of the plant transcriptome provides useful information into genomic features and functions, including protein-coding/noncoding gene transcripts and alternative splicing for species that lack reference genomes [214,215]. In recent years, genomic and transcriptomics studies have been performed for orchids, namely *Dendrobium* ssp., *Erycina pusilla*, *Phalaenopsis* ssp., and *Orchis italica*, among others, that provided key insights into the functional role of genes in polyploidy, MADS-box genes diversification, flower development, etc., enriching our knowledge [7].

To accommodate the increasing amount of orchid transcriptome data and house more comprehensive information, the Orchidstra 2.0 database was created with a new database system to store the annotations of 510,947 protein-coding genes and 161,826 noncoding transcripts, including 18 orchid species belonging to 12 genera in 5 subfamilies of Orchidaceae. The Orchidstra 2.0 database showed that RNA-seq-based gene expression data showed that the KNOX genes were highly expressed in the developing flower stalks at its early stage and in germinating seeds in *P. phrodite* and mesocarp tissues of the developing vanilla six- and eight-week-old pods in *V. planifolia* [213].

The fungal association affects both the symbiotic and asymbiotic germination of orchids. Liu and coworkers [216] studied the large-scale transcriptome dataset of *Anoectochilus roxburghii* (Wall.) Lindl. seeds for both symbiotic and asymbiotic germinated seeds. The study identified forty-nine genes involved in regulation, of which six genes were differentially expressed in symbiotic germination vs. asymbiotic germination, suggesting the induction or suppression of these six genes by fungi. Valadares et al. [217] characterized 88 proteins related to energy metabolism, cell rescue and defense, molecular signaling, and secondary metabolism in *Oncidium sphacelatum* Lindl. at different trophic stages of symbiotic germination. In addition, the proteomic analysis showed the upregulation of proteins that are involved in purine recycling, ribosome biogenesis, energy metabolism, and secretion in *O. sphacelatum*.

The proteomic studies on orchids focused on flower development and tissue culture studies for mass production. By elucidating developmental processes in orchids, omics approaches can assist with breeding, genetic improvement, conservation, and commercial production in orchids. Comparative proteomics analyses of pollination response in the endangered orchid species *Dendrobium chrysanthum* were carried out [218]. For a better understanding of the mechanism of pollination in *D. chrysanthum*, the differentially expressed proteins (DEP) between the self-pollination and cross-pollination pistil of *D. chrysanthum* were investigated via two-dimensional electrophoresis (2-DE) coupled with tandem mass spectrometry [218]. A total of 54 DEP spots were identified in the two-dimensional electrophoresis (2-DE) maps between the self-pollination and cross-pollination. Gene ontology analysis revealed an array of proteins belonging to the functional categories: metabolic process (8.94%), response to stimulus (5.69%), biosynthetic process (4.07%), protein folding (3.25%), and transport (3.25%). The identification of these DEPs at the early response stage of pollination provides new insights into the mechanism of pollination response and assists in the conservation of the orchid species [218]. By proteomics techniques (LC–MS/MS, LTQ (HPLC)), flower labellum tissues sampled from *Ophrys exaltata subsp. Archipelagi*, *O. garganica*, and *O. sphegodes* were used for the identification of candidate genes for pollinator attraction and reproductive isolation (e.g., genes for hydrocarbon and anthocyanin biosynthesis and regulation and the development of floral morphology) [219]. Proteomic studies (employing 2 DE MALDI ToF/ToF) were performed in the *C. ensifolium* flower (structures including labellum and inner lateral petals proteins) [220]. In another study, the DNA-binding properties and protein–protein interactions of the floral homeotic MADS-box protein complexes in *P. equestris* were analyzed by a Yeast two-hybrid system [221].

Reports on the molecular mechanisms of mycorrhizal association and seed germination in orchids are limited. So, the question will be, is there any difference in seed development and germination between orchids and other flowering plants at the molecular level or not?

Chen et al. [222] reported that some genes such as PaMADS39 and PaMADS51 belong to the Ma-subclass of type I MADS-box genes and are detected at the cellularization stage of developing endosperm during seed development. These genes are closely related to *Arabidopsis* (AGL23 and AGL62.1) and they have similar expression patterns in reproductive tissues when fertilization occurs and embryo development initiates. MIKC-type genes were identified from streptophyte lineages, revealing new insights into their evolution and development relationships. The study reported that MIKC-type genes might play a role in seed germination in *D. officinale*. Some MIKC genes from *D. officinale* showed different expression during seed germination, including SVP and SQUA subfamily genes, as well as the MIKC gene, and these genes have the same role in other flowering plants [223]. So, it was concluded that the expression pattern in seed germination of orchids was like other plants, like *Arabidopsis*.

7. Strategies/Guidelines for Orchid Conservation and Utilization

The commercialization of orchid species has witnessed a tremendous upsurge in recent times. The classification of the orchid trade has been performed accordingly: specialist growers-driven market—people who have a collection of orchid species and purchase diverse hybrids and species; and the mass-market trade—comprising casual buyers of potted varieties and easily cultivated varieties. The demand for rare orchid varieties in the floriculture market has partially led to the illegal trade. However, casual buyers sometimes purchase unknowingly with prices like plants that are artificially propagated [224]. Initially, the orchid varieties were sold and purchased in the local markets, but with the advent of e-commerce platforms, the orchid species availability has increased to both online and offline sellers in the networks.

International/National Guidelines for the Preservation of Orchid Biodiversity

On a global level, the trade of all orchid species is monitored by CITES, and legal marketing (to a considerable level) particularly for artificially propagated plants occurs according to the established guidelines. However, the rising incidences of illegal trade have severely hampered the orchid industry. Southeast Asia, an orchid-rich habitat, contributes to a significant share of wild species collection, [225] and countries in Southeast Asia as well as the United States, Europe, and Japan are the emerging specialist markets. However, in the present time, there has been a tremendous upsurge in the illegal trade of commercial orchid varieties; for example, *Paphiopedilum* spp. highlights the risk of extinction and are categorized as "critically endangered" by CITES owing to extensive reports of over-collection. CITES has three distinct Appendices for different species. Appendix I contains species threatened with extinction conditions, whose international trade is possible only under exceptional conditions. Presently, Appendix I lists two genera of orchids, *Paphiopedilum* and *Phragmipedium,* representing 240 species, more than 180 varieties, and 30 natural hybrids, along with *Aerangis ellipsis*, *Dendrobium cruentum*, *Laelia jongheana*, *Laelia lobata*, *Peristeria elata*, and *Renanthera imschootiana*. The rest of the orchids are listed in Appendix II, which includes the species not necessarily threatened with extinction conditions, and Appendix III, which contains species that are protected in one country at least. This extensive protection of orchids makes them the largest plant family protected under CITES [226]. Along with the conservation and protection under CITES, there are several orchid societies around the globe aiding cultivation and conservation efforts under the two major approaches, i.e., in situ conservation and ex situ conservation.

On a worldwide level, several orchid species with ornamental attributes are traded in the legal trade of reasonable potted plants for non-specialist buyers, usually *Dendrobium* and *Phalaenopsis* genera, with the key exported countries being the Netherlands, Taiwan, and Thailand. Among the most popular products, cut flowers and orchid plants comprise the maximum share of the global platform, with less expertise and expenses involved in maintenance. The specialized trade includes specialists, and the consumers include specialists' growers with expertise in orchid cultivation who have a broad collection of exotic germplasms. According to statistics by CITES on legal orchid trade, orchid plants witnessed a large global export between 1996 and 2015 [225]. Considering no in-depth studies exist on the global levels of illegal orchid trade, only commercial harvesting of wild varieties from approximately 10 countries has been documented [225]. In Europe, the legal international market is declining, owing to the increasing costs of propagated orchid species and restrictions by CITES. Given the conservation and protection of several orchid varieties, guidelines have been issued on national/international levels for the preservation of orchid biodiversity. While individual countries have defined parameters and legislation for the cultivation, conservation, and marketing of wild orchids, the legal guidelines are more precise and defined at global levels. Some orchid species may be illegal for local/global trade in a few countries, while in others these may be allowed. On the global platform, 70% of the orchid species are classified in CITES, and a few species, namely *Peristeria elata*, *Dendrobium cruentum*, *Renanthera imschootiana*, *Laelia jongheana*, and *Paphiopedilum* sp. are classified in Appendix I, which identifies their trading as prohibited (CITES, Appendices I, II and III. https://cites.org/eng/app/E-Apr27.pdf accessed on 20 October 2023). In an international move, the decision was made to list orchids at the family level, considering the identification of 300–500 new orchid species annually [227]. With guidelines and initiatives being made at domestic and international levels for orchid conservation, the legal framework is still defined by complexity, as it is difficult to clearly define the legal or illegal nature of trade and therefore difficult to implement proper guidelines. In addition, the emergence of e-commerce platforms for online trading has further contributed to the rise in the unauthorized trading of orchids, with access to people across the globe and no clearly defined parameters for orchid trade. In a specific instance on a social media platform (2014), the trading of 46% of species for 150 orchid groups was performed in five languages [228]. In this direction, IUCN Species Survival Commission Orchid Specialist Group's Global Trade Programme has made efforts to streamline online orchid trading and report these incidents to concerned committees (Orchid Specialist Group Global Trade program, https://globalorchidtrade.wixsite.com/home/about-us (accessed on 28 January 2024)). Floraguard is an established project (established in 2017), aimed at implementing better policies to monitor the online trading of all plant species, including orchids (Floraguard, http://floraguard.org (accessed on 28 January 2024)). According to Article 038 of the Convention on Biological Diversity (1994), the rights of natural resources are under the jurisdiction of respective countries, allowing the maximum utilization of traditional knowledge and resources. Among others, the Nagoya Protocol (2010) includes international consent to deriving shared benefits from the utilization of genetic resources in a transparent manner, while the Cartagena Protocol (2003) on an international platform ensures the safe use and transport of living modified organisms (LMOs).

8. Translational Success, Restoration Initiatives, and Future Research

Research advances in the cultivation and commercialization of orchids have witnessed unprecedented success, witnessing an expanding global market. The *Phalaenopsis* orchid is cultivated and marketed worldwide, accounting for 500 million USD in the United States, Japan, and the Netherlands, among other countries. The statistics suggest that *Phalaenopsis* was the most exported orchid in 2018 (76.4%), followed by *Oncidium* (6.9%) and *Cymbidium* (3.2%) [8]. From the perspective of the Indian sub-continent, it has about 1350 species classified in 186 genera and represents approximately 5.98% of the orchid flora existing across the world. CITES (administered by the United Nations Environment Programme, located in Geneva, Switzerland) plays a pivotal role in the conservation measures for plant species, including orchids. Moreover, three approaches are primarily adopted for the conservation of genetic resources (in orchids) and are defined as follows: in situ conservation in sanctuaries, legislative guidelines, and ex situ conservation in botanical gardens. In addition to the above conservation measures, there are international laws and guidelines to preserve biodiversity and stop the bio-piracy of natural resources.

While significant success has been achieved on different levels from basic biology studies on orchids to implementing biotechnologies for sustainable living, the future directions in orchid research aim to address the knowledge gaps and bottlenecks in cultivation studies. The advent of genetic engineering and high-throughput sequencing defines a big boost in orchid research, enabling solutions to intriguing puzzles in orchid biology. While to date, 16 orchid genomes have been elucidated, a lot remains to be uncovered. Orchid genome sequencing has opened new avenues in multi-omics-guided studies for gene expression, mapping, and comparative genomics. The progress achieved in distinct areas has enabled information on the origin and diversification of orchids and the molecular mechanisms in growth stages, reproduction, and complex life cycles.

9. Concluding Remarks

In the present decade, the orchid industry has flourished with leaps and bounds on domestic and international platforms. The aesthetic and ornamental attributes of novel orchid species have gained the attention of plant biologists as well as agriculturists. To date, orchids have been cultivated for their cut flowers and artificially propagated varieties, with the multi-faceted applications of orchids in the food sector and medicine gaining global recognition in recent times. Plant tissue culture, breeding approaches, and biotechnologies have made substantial contributions in introducing and improving the plant traits of novel attributes and remarkably improved commercialization on a global platform.

Advances in whole genome sequencing have facilitated the understanding of orchid genomes, providing key insights into the cultivation of new orchid cultivars for commercialization. Furthermore, tools in genomics and proteomics employed for orchid genome assembly provided valuable insights about orchid genomes. The genomic insights showed gene function in heterozygosity, MADS-box gene diversification, and CAM photosynthesis evolution concerning physiological responses, flower development, and the effect of climatic fluctuations on the productivity of orchids [7]. Studies on the function and composition of SSRs and microRNAs in orchids' growth and development facilitate studies in functional genomics. Recent innovations in biotechnologies have opened new avenues in the development of ornamental plants with desired multi-faceted and novel attributes. Biotechnological interventions such as genetic engineering and in vitro tissue culture along with classical breeding approaches have been regularly employed to alter flower color, fragrance, appearance, disease resistance, and shelf life, as discussed with key examples. The progress in the development of scientific techniques such as HPLC-DAD and MS has facilitated the precise detection of bioactive components from multiple orchids and their emerging prospects in drug discovery and research. Omics biology-guided elucidation of important traits linked to gene families and their regulatory components has key potential to revolutionize orchid improvement. While advances in plant genome editing have enabled precise gene modifications and genome engineering, next-generation tools like the CRISPR-Cas9 system define the key potential for 'gene stacking', where multiple gene modification steps can be attempted in a single procedure [229]. Although limited genetic manipulation studies are attempted in orchids, these advanced tools offer great opportunities to design orchids with 'high-value' traits in the near future.

The cultivation and export of new orchid varieties are gaining momentum, with an expanding global market generating significant economic returns. However, with the unprecedented rise in exports and global orchid trade, rare and exotic varieties are over-harvested and illegally traded by suppliers across the boundaries. Restoration measures have been undertaken to safeguard the interests of people and orchid specialists through guidelines to monitor and prevent the indiscriminate use and trading of orchid species. The guidelines by CITES and the Convention on Biological Diversity and Wildlife Protection Act 1972, by the Government of India, have been successful in reducing bio-piracy and conservation of natural resources to a greater extent, introducing legislative measures and guidelines for monitoring the conservation and trade of wild orchid species. For the orchid industry to flourish, it is imperative to explore orchid biology and biotechnologies and to ensure legal international trade by implementing guidelines towards a multipronged approach for the conservation and commercialization of orchids.

Author Contributions: P.T. and K.-I.P. conceptualized the theme of the manuscript. P.T., A.S. and S.K.B. collected the data and wrote the manuscript. P.T. and K.-I.P. revised and improved the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Institutional Review Board Statement: This article does not contain any studies with human participants or animals performed by any of the authors.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: The authors extend their gratitude to their organizations for constant encouragement and support.

Conflicts of Interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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