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Review

Advances in Breeding, Bioprospecting, and In Vitro Culture of *Laelia* Orchid Species

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Abstract: Orchids (Orchidaceae) are plants that are highly appreciated by their beautiful flowers worldwide. Moreover, they represent a source of metabolites with applications in medicine and biotechnology. Within the Orchidaceae family, the *Laelia* genus is a group of orchid species from the Neotropics and is probably one of the most representative genera of America. *Laelia* orchids are cultivated by their splendid flowers and are widely used in orchid breeding. Here, we revise the use of the *Laelia* genus in orchid breeding and metabolite bioprospecting. We also analyze the use of plant tissue culture (PTC) as an alternative to conventional propagation and as a strategy for the recovery of those *Laelia* species threatened with extinction. We summarize and discuss the recent advances in the application of different PTC techniques for mass multiplication based on asymbiotic germination, organogenesis, protocorm-like bodies development, and somatic embryogenesis, and the advances of in vitro conservation by cryoconservation and the use of slow-growth promoting hormones. Finally, we suggest future directions and venues in research for *Laelia* species.

Keywords: orchids; *Laelia* species; mass propagation; in vitro conservation; bioprospection

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1. Introduction

Orchidaceae is the second largest family of flowering plants and is one of the biggest families in the Monocotyledoneae class. It includes 700–880 genera and more than 25,000 species [1–3]. Orchids are cosmopolitan plants but are distributed preferentially in tropical and subtropical forests. They are appreciated worldwide for their splendid flowers and are known for their medicinal, food, ritual, and ecological properties [1,3,4]. To size the economic value of orchids, from 1996 to 2015, the legal global trade was calculated at more than 1.1 billion of artificially propagated live plants [5]. Along with this formal world trade, orchids that are sold in local markets, usually smuggled, should also be considered. This demanding market for orchids, their accelerated loss due to habitat destruction, modification or fragmentation, and illegal extraction have become major threats for orchid species conservation [5,6]. In consequence, during 2018, at least 948 orchid species were found in The International Union for Conservation of Nature's Red List of Threatened Species, of which 56.5% were classified as threatened with extinction [7]. Under this scenario, governments, the scientific community, and society have been carrying out multiple efforts to implement field and laboratory strategies focused on conservation and propagation of orchids.

In this review, first we highlight the importance of Laelia genus as a genetic resource for orchid breeding and bioprospecting. Second, we summarize and discuss research data of plant tissue culture (PTC) applied to this small genus within the Orchidaceae family, which is highly valued in local markets for an ancestral ritual use and is one of the most appreciated in the horticultural industry. We provide an update on the advances in the diverse PTC techniques applied to the *Laelia* orchids for conservation and mass propagation. Finally, we highlight future directions, opportunities, and challenges of research for the *Laelia* species.

2. *Laelia* Genus as a Biocultural Resource and Source of Variability for Orchid Breeding and Metabolite Bioprospecting

Laelia spp. stands out due to the beauty, color, and size of its flowers, and they are probably the most representative orchids of America, especially of Mexico [8,9] (Figure 1). The *Laelia* genus was established by Johh Lindley in 1831 [10] using *Laelia grandiflora* as the species type (La Llave & Lex.), which is a synonym of *L. speciosa* (Kunth) Schltr. The current taxonomy for *Laelia* orchids is controversial and widely discussed among orchid taxonomists. Although some proposals using DNA sequences for updating the *Laelia* taxonomy have been carried out [11], the most accepted circumscription recognizes 25 species within this genus (Table 1), which have been grouped based on morphological characteristics and geographic distribution [12–15].

Laelia orchids have been highly valued since ancient times [16]. For example, in Mexico, *L. speciosa*, *L. anceps*, and *L. autumnalis* are highly valued for their beauty and are widely used in multiple religious ceremonies [8,17,18]. This ornamental value of the *Laelia* genus has also been long recognized by orchid breeders; this genus, together with *Sophrinitis* and *Brassovola*, is one of the three main genera used for genetic improvement programs [9]. With 200,000 different types, orchid hybrids represent a huge market value and take second place in the top ten ranking of orchid taxa commercially traded worldwide [5,9]. The most preferred orchid hybrids are those with attractive flowers regarding color, size, inflorescence shape, plant size, precociousness, and season-independent flowering [3,9,19–21]. *Laelia* spp. has been traditionally used in these breeding strategies to transmit mostly color traits. In Table 1, we describe the main flower characteristics (petal color and size, inflorescence size and fragrance) of *Laelia* spp. and which species have been used in intrageneric crossings. Species with large inflorescences and flowers with colors ranking from white to dark rose/lilac seem to be preferred by orchid breeders (Figure 1). The frequent use of *L. anceps* ssp. *anceps*, *L. rubescens*, *L. autumnalis*, and *L. speciosa* to generate primary T1 orchid hybrids is remarkable (Table 1). Other species such as *L. aurea* and *L. superbiens* have been less used but could be attractive to produce genetic variability due to flower color or inflorescence size (Table 1). *Laelia* spp. has also been used as parentals in breeding that involves more than two genera to produce intergeneric hybrids. The multiple intergeneric hybrids involving *Laelia* genus are listed in Table A1 (Appendix A). At least 14 distinct genera have been used in crossings with the *Laelia* genus to produce bigeneric hybrids that subsequently derive in hybrids involving more than four different genera (Table A1). Although most hybrids reported for the *Laelia* genus are artificial, hybrids also occur naturally, and three hybrids have been reported thus far: *Laelia* × *oaxacana*, *Laelia* × *tlaxiacoensis*, and *Laelia* × *meavei*. The first hybrid is reported as a natural cross between *L. halbingeriana* and *L. anceps*; the second from *L. albida* and *L. furfurea* as parents, and the last one is the offspring of *L. dawsonii* and *L. rubescens* [13–15]).

In addition to ornamental purposes, some *Laelia* species are used in traditional medicine, and recently, the metabolites responsible for biological activities are being identified. In Mexico, roots of *L. anceps* and *L. speciosa* roots are utilized for avoiding abortion and for hypertension treatment [35]. Bioassay-guided fractionations have led to the identification of 2,7-dihydroxy-3,4,9-trimethoxyphenantrene and gigantol in *L. anceps* and *L. speciosa* roots, respectively; both compounds have vasorelaxant effects [35,36]. Similar effects have been reported for methanol extracts of *L. autumnalis* [37]. Recently, seven compounds have

been isolated from leaves and pseudobulbs of *L. marginata*, including phenantrenoid 9,10-dihydro-4-methoxyphenanthren-2,7-diol, which showed antiproliferative activity in vitro, whereas the flavone rhamnazin has been proven effective against Zika virus [38].

Some orchids offer resin-like materials to pollinators, such as *Heterotaxis superflua*, an orchid from the Amazonian rainforest. This resin-like material is rich in mucilage, starch, and sugars and is collected by bees for nest construction [39]. In *Dendrobium* species, the chemical composition and genomics underlying biosynthesis of polysaccharide-rich mucilage with glue properties have been studied, and the biotechnological applications have been prospected [40,41]. In the *Laelia* genus, some species are also known as a source of adhesives. In Mexico, *L. speciosa* and *L. autumnalis* are traditionally used to obtain an adhesive-type substance by maceration of pseudobulbs, which is used as glue during manufacturing of musical instruments and feather mosaics [42,43]. Unfortunately, the chemical composition and properties of these compounds remain unknown thus far.

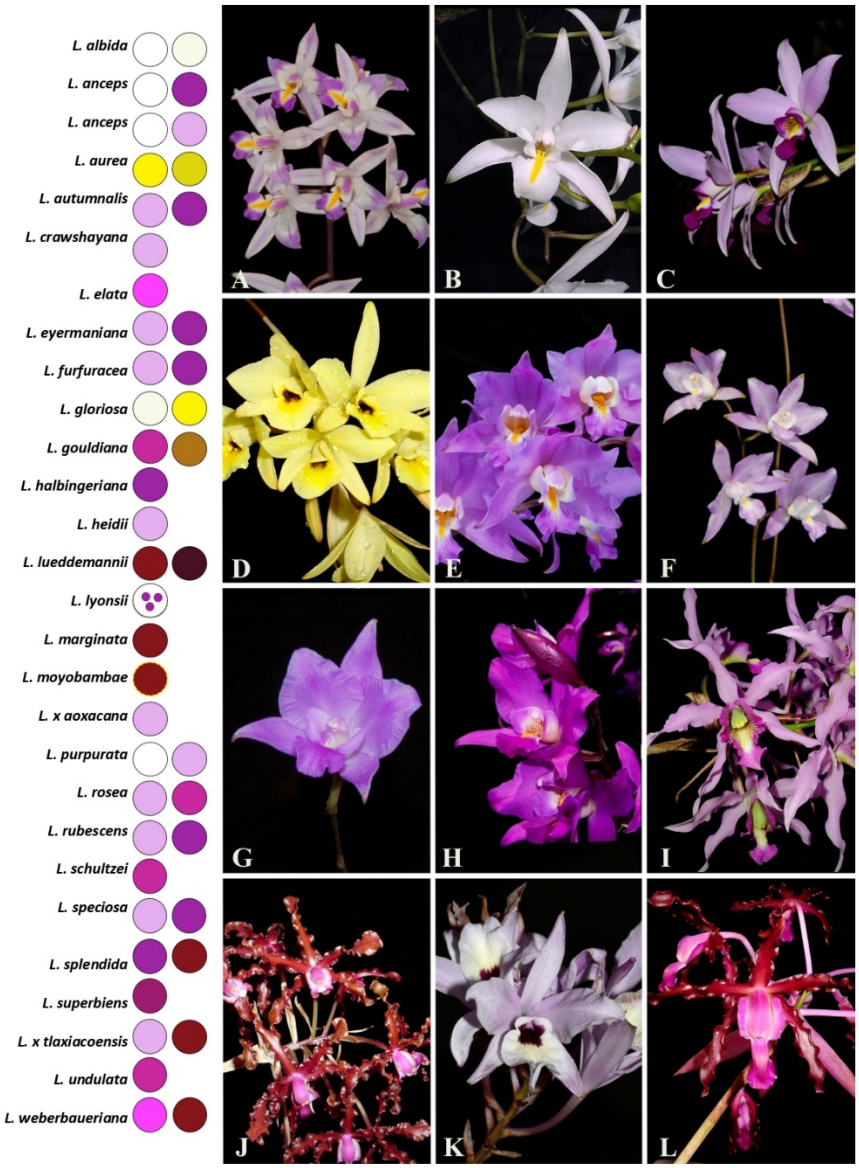

Figure 1. Flower diversity in *Laelia* genus. Left: schematization of the main colors in floral structures for the *Laelia* genus. Right: (**A**,**B**) *L. albida*, (**C**) *L. anceps*, (**D**) *L. aurea*, (**E**) *L. crawshayana*, (**F**) *L. eyermaniana*, (**G**) *L. furfuracea*, (**H**) *L. gouldiana*, (**I**) *L. halbingeriana*, (**J**) *L. lueddemannii*, (**K**) *L. rubescens*, (**L**) *L. splendida*. Photos credits: (**A**,**F**,**G**) Eduardo Pérez-García, (**B**,**D**,**E**,**H**–**J**,**L**) Germán Carnevali, (**C**,**K**) Jos Monzn.

Table 1. Species included in the *Laelia* genus: local names, inflorescence characteristics, and breeding use.

Species/Local Names	Inflorescence Characteristics	Breeding Use	References
L. albida Bateman ex Lindl. "Huichila", "Lirio de San Francisco" (Lily of San Francisco), "Monjitas" (Little nuns), "Tzicxóchitl", "Flor de tatanachtle".	10–90 cm long, with flowers (21–30 × 10–20 mm) with petals and sepals white or cream and lip-pale to dark-rose colored. With sweet strong honey fragrance.	>15 F1 hybrids reported.	[8,22]
L. anceps sp. *anceps* "Calaverita" (Little skull), "Lirio de todos los Santos" (Lily of All the Saints".	25–75 cm long, with big and showy flowers (73–120 × 55–80 mm) that ranges in color from completely white to dark rose-purple. Sweet and weak fragrance.	>150 F1 hybrids reported.	[8,23]
L. anceps ssp. *dawsonii* J. Anderson "Huichila".	40–70 cm long, with big and showy flowers (73–130 × 55–90 mm), than vary in color from white to pale pink, with thin or heavily marked purple lines the lip throat. Weak, sweet and floral fragrance.	Not reported.	[8,24]
L. aurea A.V.Navarro The golden Laelia.	10–40 cm long, with showy flowers (70–110 × 70–130 mm) with sulfur-yellow to golden-yellow sepals and petals. Weak fragrance, similar to roses.	1 intrageneric hybrid with *L. speciosa*.	[8,25]
L. autumnalis (Lex.) Lindl. "Flor de las ánimas" (Flower of all souls), "Flor de todos santos" (Flower of All the Saints), "Flor de encino" (Oak flower), "Flor de la calavera" (Flower of the skull), "Lirio de San Francisco" (Lily of San Francisco).	40–100 cm long, with big and showy flowers (38–67 × 14–27 mm), with sepals and sepals rosy-purple or lilac color. Weak to strong fragrance.	>26 F1 hybrids.	[8,26]
L. crawshayana Rchb.f. "Lirio" (Lily)	10–70 cm long, with big, showy and rosy flowers (38–53 × 20–28 mm). Pleasant fragrance.	Not reported.	[8]
L. elata (Schltr.) J.M.H.Shaw Not known.	55 cm long, with big, showy and pink flowers.	Not reported.	[27]
L. eyermaniana Rchb.f. "Kiki", "Flor de peña" (Flower of the cliff), "Flor" or Lirio de San Miguel" (Flower or Lily of San Miguel), Eyerman's *Laelia*.	20–100 cm long, with big and showy, flowers (30–48 × 16–27 mm), with rosy or lilac color petals and sepals. Floral and intense fragrance.	Not reported.	[8]
L. furfuracea Lindl. "Lirio de San Francisco" (Lily of San Francisco), "Monja" (nun), "Gihtsl".	15–28 cm long, with big, showy, rosy or rosy-lilac flowers (37–48 × 20–35 mm). Harsh fragrance, similar to ordinary soap.	3 hybrids.	[8]
L. gloriosa (Rchb.f.) L.O.Williams The glorious Schomburgkia	120 cm long, with big and showy flowers, with colors that varies from pale cream to bright yellow.	Not reported.	[28]

Table 1. *Cont.*

Species/Local Names	Inflorescence Characteristics	Breeding Use	References
L. gouldiana Rchb.f. "Santorum", "Flor de Muerto" (Flower of the dead), "Monjitas" (Little nuns).	40–75 cm long, with big, showy flowers (46–54 × 26–30 mm) with sepals and petals with fiery purple or dark magenta color. Intense floral-aromatic fragrance.	13 F1 hybrids.	[8]
L. halbingeriana Salazar & Soto Arenas Not known.	48–70 cm long, with big, showy, and lilac flowers (60–80 × 11–15 mm) with reticulate magenta veining.	Not reported.	[29]
L. heidii (Carnevali) Van den Berg & M.W.Chase Not known.	Flowers (50 mm long) with pink floral bracts.	Not reported.	[27]
L. lueddemannii (Prill.) L.O.Williams. Not known.	45–100 cm long, flowers (26–39 × 5–7.8 mm) with brown to chocolate-colored petals and sepals, with purple lip. With fragrance.	Not reported.	[27]
L. lyonsii (Lindl.) L.O.Williams Not known.	1.5 m long, flowers (30–50 long), with purple-spotted white petals.	Not reported.	[30]
L. marginata (Lindl.) L.O.Williams Not known.	60–110 cm long, flowers with sepals and petals chestnut brown	Not reported.	[30]
L. moyobambae (Schltr.) C.Schweinf. Moyobamba Schomburgkia	More than 30 cm long, with flowers (15 × 9 mm), petals with lip rose-colored, and sepals brown with yellow margins.	Not reported.	[30]
Laelia × *oaxacana* Salazar & R.Jiménez Not known.	80–135 cm long, with flowers with rosy-lilac sepals and petals.	Not reported.	[13]
L. purpurata Lindl. & Paxton Purple-stained *Laelia*	30–37.5 cm long, showy flowers with variable color depending on horticultural forms: sepals, petals and lip ranking from white to pink color. With anise fragrance.	Not reported.	[31]
L. rosea (Linden ex. Lindl.) C.Schweinf The rosy *Schomburgkia*	60 cm long, with rosy-pink flowers (4–5.1 × 14 mm).	Not reported	[27]
L. rubescens Lindl. "Flor de Jesús" (Flower of Jesus), "Huichila rosada", "Flor de la Concepción" (Flower of the Conception).	15–75 cm long, flowers (26–44 × 9–7 mm) with white, slightly rosy or rosy lilac coloration. Weak and floral fragrance.	>50 F1 artificial hybrids and 2 natural hybrids.	[8,32]
L. schultzei (Schltr.) J.M.H.Shaw Schultze's Schomburgkia	60–100 mm long, flowers with pink floral bracts.	Not reported.	[27]
L. speciosa (Kunth) Schltr "Flor de Mayo" (May's flower), "Estrella de Belén", "Flor de Todos los Santos" (Flower of All the Saints).	15–25 cm long, with 1–2 large and showy flowers (60–90 × 25–50 mm) with a pale to dark pink-lilac to purplish coloration. Weak fragrance that resembles that of violets.	19 artificial hybrids.	[8]

Table 1. *Cont.*

Species/Local Names	Inflorescence Characteristics	Breeding Use	References
L. splendida (Schltr.) L.O.Williams The splendid Schomburgkia.	55 cm long, flowers (100 mm long) with violet and dark copper-colored floral bracts.	Not reported.	[33]
L. superbiens Lindl. The gorgeous Schomburgkia.	75–120 cm long, with big and showy flowers (60–102 × 9–16 mm), with variation in color but mostly with dark color (tepals rose-lilac, with purple violet lines in sepals). Weak, soap-like fragrance.	8 artificial hybrids.	[8]
Laelia × *tlaxiacoensis* Solano & Cruz-García Not known.	33–57.5 cm long, with rose-lilac or magenta flowers.	Not reported.	[14]
L. undulata (Lindl.) L.O.Williams The undulate *Schomburgkia*.	60–180 cm long, with showy flowers with pinky floral bracts. With fragrance.	Not reported.	[33]
L. weberbaueriana (Kraenzl.) C.Schweinf Weberbauer's *Schomburgkia*.	80 cm long, with flowers with brown-pink floral bracts.	Not reported.	[34]

F1, first filial (F) generation.

3. In Vitro Culture of *Laelia* Species

PTC, defined as the aseptic culture of cells, organs, and their components under controlled in vitro conditions [44], is a biotechnological tool that has been successfully applied to recovery, conservation and clonal propagation of orchids [45–48]. Since the development of a method for asymbiotic germination by Lewis Knudson in 1921 [49], PTC has become highly diversified in orchid species. In the following sections, we describe advances reported in PTC applied to *Laelia* spp. (Figure 2; Table 2), from asymbiotic germination to somatic embryogenesis (SE), all aimed toward in vitro conservation and mass multiplication.

3.1. Asymbiotic Seed Germination

In orchids, thin and non-endospermic seeds limit sexual reproduction [63,64]. In nature, it is calculated that out of one million seeds, only 10 to 15 germinate, and a maximum of two seedlings turn into adult plants [65]. Asymbiotic germination under in vitro culture conditions has been used for eight *Laelia* species thus far, showing this to be an effective alternative to increased germination and survival rates while maintaining genetic diversity. Furthermore, asymbiotic germination is a powerful technique for establishing aseptic cultures for other in vitro downstream purposes [18,48,66,67].

In Table 2, we summarize the conditions for asymbiotic germination for *Laelia* species reported thus far. Two crucial factors for in vitro germination, capsule age and culture media composition, identified in all the protocols analyzed, are discussed as follows. Since almost all orchid species have dehiscent dry capsules [68], choosing capsules with closed valves that ensure no contamination but with already viable seeds is a challenge. Conversely, the chemical composition of culture media may determine if these viable seeds can germinate or not. To assess timing of collecting *Laelia* capsules, the most common strategy is testing capsules collected at different weeks after pollination (WAP) since capsule maturity positively controls seed viability, as reported recently [59]. For *L. albida*, *L. anceps* ssp. *dawsonii*, *L. marginata*, *L. purpurata*, and *L. rubescens*, the highest germination rates have been found in seeds from full-ripe capsules [22,53,57,59,69] or from close to this stage, namely 9 to 12 WAP. For *L. speciosa*, contrasting data have been reported. For example, Lavrentyeva and Ivannikov [50] found better results using seeds from immature fruits, while Ávila-Díaz et al. [60] indicated that higher rates of germination were found in seeds from older capsules (9 WAP). These last authors also indicated that germination can be promoted in immature seeds if basal media are supplemented with 6-benzylaminopurine (BAP) at 2.2 µM and darkness, but the development of protocorms was not observed [60].

Knudson C (KC) medium [70] and Murashige and Skoog (MS) medium [71] have been the most frequent basal media tested for asymbiotic germination of *Laelia* species (Table 2). KC medium has been evaluated for *L. albida*, *L. anceps*, and *L. purpurata* [22,50,57], while MS medium has been found adequate for *L. autumnalis*, *L. marginata*, *L. rubescens*, and *L. tenebrosa* [18,58,62,69]. These two media, KC and MS, have different nitrogen (N) contents; in KC medium, N is found at 16.04 mM, whereas in MS medium, N is found at 60.01 mM [72]. High N concentrations have an inhibitory effect on asymbiotic germination, but its magnitude seems to be species-dependent [72–74]. For example, KC inhibits seed germination completely in *L. rubescens* [59] but yields germination rates ranging from 70% to 90% in *L. albida* [22]. In basal media with low N concentration or used at diluted concentrations, e.g., Phytamax or 1/2 MS, peptone is usually added as an extra N or amino acid source [72,74–76]. Peptone addition has been assayed in *L. anceps* and *L. rubescens*, yielding high germination rates [50,59]. In other *Laelia* species such as *L. albida* and *L. purpurata*, organic N has been supplemented using potato starch [22] or ripe banana pulp [57], respectively.

Table 2. Overview of different PTC techniques applied to *Laelia* species.

Species/Source of Explant	Medium Composition	Incubation Conditions	Key Results	References
Asymbiotic germination				
L. albida Mature seeds.	KC medium + potato starch (20 g·L^{-1}).	24 ± 2 °C, photoperiod 16 h light/8 h dark, and 35 µmol m^2 s^{-1} for radiation.	70–90% germination.	[22]
L. anceps Immature seeds.	KC medium + peptone (2 mg·L^{-1}), potassium hummate (50 mg·L^{-1}), and activated charcoal (1 mg·L^{-1}).	25–26 °C, photoperiod 16 h light/8 h dark, and relative moisture of air 70%.	ND.	[50]
L. anceps ND.	MS medium.	ND.	ND.	[51]
L. anceps ND.	0.5X MS medium.	25 ± 2 °C and 50 µmol m^{-2} s^{-1} for radiation.	ND.	[52]
L. anceps ssp. *dawsonii* Mature seeds.	MS, KC media + NAA, BAP, and IAA 2 mg·L^{-1} of each.	Photoperiod 16 h light/8 h dark and 22 µmol m^2 s^{-1} for radiation.	100% germination.	[53]
L. anceps ssp. *dawsonii* Mature seeds.	MS medium.	25 °C, photoperiod 16 h light/8 h dark.	95% germination.	[54]
L. autumnalis ND.	MS medium.	Photoperiod 16 h light/8 h dark and 45 µm m^{-2} s^{-1} for radiation.	ND.	[18]
L. autumnalis ND.	MS medium.	24 ± 1 °C, photoperiod 16 h light/8 h dark, and 40 µmol m^{-2} s^{-1} for radiation.	ND.	[55]
L. eyermaniana Mature seeds.	0.5X MS medium.	25 ± 1 °C, photoperiod 16 h light/8 h dark 25, and 46 µmol m^{-2} s^{-1} for radiation.	ND.	[56]
L. purpurata ND.	KC medium + banana pulp (90 g·L^{-1}).	ND.	ND.	[57]
L. rubescens Mature seeds.	MS medium.	25 °C, photoperiod 16 h light/8 h dark.	62.5% germination.	[58]
L. rubescens Immature seeds.	KC medium + peptone (2 mg·L^{-1}), potassium hummate (50 mg·L^{-1}), and activated charcoal (1 g·L^{-1}).	25–26 °C, photoperiod 16 h light/8 h dark.	ND.	[50]
L. rubescens Immature and mature seeds.	MS, 0.5X MS, KC, VW media, Phytamax.	25–26 °C, photoperiod 16 h light/8 h dark, and 40 µmol m^{-2} s^{-1} for radiation.	88% germination.	[59]

Table 2. *Cont.*

Species/Source of Explant	Medium Composition	Incubation Conditions	Key Results	References
L. speciosa Mature seeds.	MS medium.	Photoperiod 16 h light/8 h dark and 130 µmol m^{-2} s^{-1} for radiation.	60% germination.	[60]
L. speciosa Mature seeds.	MS medium.	Photoperiod 16 h light/8 h dark and 130 µmol m^{-2} s^{-1} for radiation.	ND.	[17]
L. speciosa Immature seeds.	MS, 0.5X MS media.	24 ± 2 °C, photoperiod 16 h light/8 h dark, and 43 µmol m^{-2} s^{-1} for radiation.	100% germination.	[61]
L. tenebrosa ND.	MS medium.	ND.		[62]
Callus formation				
L. anceps ssp. *dawsonii* Seeds.	MS medium + NAA, BAP, and IAA 2 mg·L^{-1} of each.	Photoperiod 16 h light/8 h dark and 33.78 µmol m^{-2} s^{-1} for radiation.	Embryogenic friable callus.	[53]
L. speciosa Leaf segments obtained from in vitro plants.	MS medium + BAP (2.5 mg·L^{-1})	25 ± 1 °C, photoperiod 16 h light/8 h dark, and 36 µmol m^{-2} s^{-1} for radiation.	High-quality callus with a light green appearance.	[17]
PLBs proliferation				
L. anceps Seeds.	KC medium + of peptone (2 mg·L^{-1}), potassium hummate (50 mg·L^{-1}), and activated charcoal (1 mg·L^{-1}).	25–26 °C, photoperiod 16 h light/8 h dark, and relative moisture of air 70%.	Protocorm formation at bases of leaf primordiums and bud squamules.	[50]
L. anceps Protocorms.	MS medium + BAP (3 mg·L^{-1}).	25 ± 2 °C, photoperiod 16 h light/8 h dark, and 50 µmol m^{-2} s^{-1} for radiation.	Formation of 50.6 PLBs by explant.	[51]
L. rubescens Seeds.	KC medium + peptone (2 mg·L^{-1}), potassium hummate (50 mg·L^{-1}), and activated charcoal (1 mg·L^{-1}).	25–26 °C, photoperiod 16 h light/8 h dark, and relative moisture of air 70%.	Protocorm formation at bases of leaf primordiums and bud squamules.	[50]
L. speciosa **Leaves**	MS medium + 2.5 mg·L^{-1} NAA and 1 mg·L^{-1} BAP.	Photoperiod 16 h light/8 h dark and 36 µmol m^{-2} s^{-1} for radiation.	Development of seedlings was successfully obtained in MS supplemented with 0.5 mg·L^{-1} of NAA and 0.1 mg·L^{-1} of gibberellic acid.	[17]

Table 2. *Cont.*

Species/Source of Explant	Medium Composition	Incubation Conditions	Key Results	References
Somatic embryogenesis				
L. anceps ssp. dawsonii Seeds.	MS medium + NAA, BAP, KIN, and IAA 2 mg·L^{-1} of each.	Photoperiod 16 h light/8 h dark and 20.2 µmol m^{-2} s^{-1} for radiation.	High number of somatic embryos after 3 subcultures (45 day of each).	[53]
L. anceps ssp. *dawsonii* Seeds.	MS medium + NAA, BAP, and IAA 2 mg·L^{-1} of each.	Photoperiod 16 h light/8 h dark and 33.8 µmol m^{-2} s^{-1} for radiation.	High multiplication rate of somatic embryos after 8 weeks of subculturing.	[23]

PLBs, protocorm-like bodies; KC, Knudson; MS, Murashige and Skoog; NAA, napthaleneacetic acid; BAP, 6-benzylaminopurine; IAA, indole-3-acetic acid; KIN, kinetin; ND, not determined.

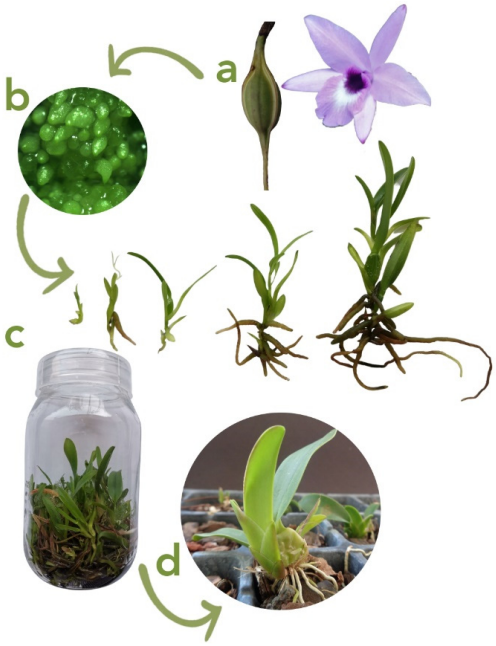

Figure 2. Overview of asymbiotic germination and in vitro growth of seedlings of *Laelia rubescens*. (**a**) Flower and ripe capsule. Capsules can be collected 10–12 weeks after pollination, providing seeds with high viability. (**b**,**c**) Early phases during asymbiotic germination and in vitro seedling development. Peptone as a nitrogen source is suggested for asymbiotic germination and seedling development. (**d**) Acclimatization of seedlings. Pictures not to scale.

3.2. Callus Culture

The callus, defined as a mass of proliferating and pluripotent cells [77], has been used for plant regeneration and clonal propagation, but if kept undifferentiated, it also represents an easy and scalable way to produce secondary metabolites for pharmaceutical purposes [17,78]. Callus formation involves cellular undifferentiation and a high cell division rate, which depend on explant type, genotype, culture medium composition, hormone type, and concentration [79,80]. Although callus culture is a commonly used PTC technique in high market-valued genera such as *Phalaenopsis*, *Dendrobium*, *Vanda*, and *Oncidium* [46,81,82], in *Laelia* orchids, it has only been tested in *L. anceps* ssp. *dawsonii* and *L. speciosa*, using seeds or leaf-like initial explants, respectively [17,53]. For *L. anceps*, friable calli were obtained from seeds germinated in MS medium supplemented with 2 mg·L^{-1} of 1-napthaleneacetic acid (NAA), BAP, and indole-3-acetic acid (IAA), 45 days after sowing [53]. In *L. speciosa*, callus induction was only observed when 6-month-old leaf segments of in vitro plantlets were used as initial explants. After 60 days of culture, light-green colored calli were obtained using 2.5 mg·L^{-1} BAP as the best treatment [17]. In both *Laelia* species, callus culture was used as tool for mass propagation via subsequent SE (*L. anceps*) or protocorm-like bodies (PLBs) regeneration and development (*L. speciosa*) [17,53].

3.3. In Vitro Conservation

Besides plant propagation and genetic improvement, in vitro PTC has been used as a tool for short-, medium-, and long-term storage of elite or critically endangered germplasm, by using technologies that imply encapsulation/cryoconservation or slow-growth conservation of several propagules, namely seeds, embryos, apical and axillary buds, microshoots, nodal segments, microplantlets, calli, and PLBs [83–86]. During cryoconservation, plant material is stored in liquid nitrogen (LN) (−196 °C) or in the vapor phase (from −150 to −196 °C) [87]. By using seeds or pollen, significant advances have been reported in cryoconservation for the genera *Dendrobium*, *Phalaenopsis*, *Cymbidium,* and *Cattleya* [87,88]. In the case of orchid seeds used for ultra-low freezing purposes, desiccation and use of plant vitrification solutions (PVS) as cryoprotectans are key pre-treatments for keeping via-

bility [87,89]. In *Laelias*, seed cryoconservation has only been assayed in *L. autumnalis* and *L. speciosa* thus far [55,90]. For these species, the best treatments for seed desiccation implicate air-drying and silica gel (sodium silicate). In *L. speciosa* seeds, the use of PVS2 (glycerol 30% + ethylene glycol 15% + dimethylsulfoxide + 0.4 M sucrose) or PVS3 (glycerol 50% + sucrose 50% at 0.4 M) negatively affects seed viability and asymbiotic germination [90], contrary to reports for PLBs in other orchid species [91–93]. Recently, PVS2 was used successfully in *Encyclia cordigera*, keeping seed viability at 93.79% after LN exposure [94]. Assays with PSV2 and PVS3 in *Laelia* species are preliminary, and therefore, evaluation of different exposure times to these solutions and the use of other cryoprotectant agents commonly used in vitro cryoconservation, namely dimethylsulfoxide, ethylene glycol, glycerol, and sucrose [95], have to be tested. These results will be key factors during the development of vitrification-based cryopreservation protocols for *Laelia* orchids.

Another strategy for in vitro conservation during short to medium-long periods (few months to 2–3 years) is slow growth without subculturing [96]. A combination of 7.4 µM BAP and 5.3 µM NAA has been suggested as adequate for conservation of PLBs of *L. albida* [22], but a detailed protocol is still needed. In contrast, a full protocol using asymbiotic germination-derived plantlets that allows in vitro conservation and regeneration was reported for *L. anceps* recently. Paclobutrazol at 2 $mg \cdot L^{-1}$ is an effective treatment for producing reduced growth of shoots and roots with a 90% survival rate [52].

3.4. PLBs Proliferation

In the PTC of orchids, one of the most interesting processes observed under specific conditions is the formation, proliferation, and regeneration of PLBs. These explants are excellent for mass multiplication of orchids in semisolid media and bioreactor systems. Currently, PLBs are used as models to dissect genetic circuits involved in regeneration and metabolite production in orchids under in vitro conditions [46,97–99]. Although PLB formation has been observed in many *Laelia* species, especially in those germinated asymbiotically [17,59], few protocols for enhancing their in vitro proliferation have been reported thus far. In *L. speciosa*, PLB proliferation was obtained after 60 days of subculture of leaf-derived calli in a MS medium supplemented with 2.5 $mg \cdot L^{-1}$ NAA and 1 $mg \cdot L^{-1}$ BAP [17]. Lavrentyeva and Ivannikov [50] reported a single medium for PLB proliferation for *L. anceps*, *L. lobata*, *L. lundii*, *L. mantiqueirae*, *L. purpurata*, *L. rubescens*, and *L. sincorana*: basal buds of shoots in a MS medium supplemented with 5 $mg \cdot L^{-1}$ BAP, 2 $mg \cdot L^{-1}$ NAA, 100 $mL \cdot L^{-1}$ peptone, 15% coconut milk, and 1.5 $g \cdot L^{-1}$ activated charcoal. This protocol should be revised and optimized for members of the *Laelia* genus, as it is long known that a morphogenic response to in vitro culture is a species-dependent process. In *L. superbiens*, PLB formation has been observed in shoots after 30 days of incubation with thidiazuron and meta-topolin, both at 0.44 µM; however, this effect has not been quantified [100].

3.5. Organogenesis-Mediated Regeneration

Organogenesis has been assayed in three *Laelia* species: *L. anceps*, *L. gouldiana*, and *L. superbiens*. In all of them, the most responsive initial explants were those obtained from plantlets previously germinated in vitro but not those collected from ex vitro mature plants [54,100,101]. In *L. anceps*, leaves collected from in vitro plantlets were used as initial explants, and after 90 days, a MS medium complemented with 10 $mg \cdot L^{-1}$ BAP and 5 $mg \cdot L^{-1}$ KNO_3 yielded the highest rate of PLB formation [54]. Similarly, leaf segments of *L. gouldiana* have been used to regenerate shoots; in this case, the medium consisted of MS salts and 0.1 $mg \cdot L^{-1}$ NAA and 45–75 days of induction [101]. Temporary immersion bioreactors have also been used to establish organogenesis in *Laelia* species. The RITA® system was tested in *L. superbiens* to obtain shoots directly from plantlets without an intermediate callus phase or PLBs [96]. In this case, although the combination RITA® bioreactor + half strength MS enriched with 100 $mL \cdot L^{-1}$ coconut water was more efficient for enhancing shoot biomass than other assayed treatments, a higher number of shoots were quantified in semisolid media + full strength MS containing 100 $mL \cdot L^{-1}$ coconut

water. In both treatments, these effects were positively affected by using 0.44 µM BAP and 1 mg·L^{-1} chitosan [100].

3.6. Somatic Embryogenesis

Having considered the forefront of PTC because of its capacity to provide a large number of plants in a shorter time than organogenic approaches [102], SE is one of the most important techniques for mass propagation of orchids [103]. Paradoxically, in the *Laelia* genus, SE has been little explored, and only *L. anceps* ssp. *dawsonii* has been tested for SE response. In this species, indirect SE has been obtained from callus derived from asymbiotically germinated seeds. Optimum induction conditions for embryogenic calli consisted of MS supplemented with NAA, BAP, kinetin and IAA (2 mg·L^{-1} each) [23,53]. The reports indicate that kinetin may be excluded, and the induction medium still works efficiently [104]. Growth of germinated somatic embryos was promoted by using a Vacint and Went (VW) medium, containing 2 mg·L^{-1} BAP, 1 mg·L^{-1} IAA and 0.2% activated charcoal [104].

4. Summary and Perspectives

Contrary to what was thought considering the ornamental value of *Laelia* spp., PTC has been applied to less than a half of all the species described in the genus. PTC is not only focused on those species with the most showy and colorful flowers, namely *L. anceps*, *L. speciosa*, *L. eyermaniaca*, and *L. gouldiana*, but also on endangered or extinction threatened species such as *L. rubescens*. The progress in PTC techniques developed for *L. anceps* ssp. *dawsonii* is noteworthy, including in vitro conservation [52], asymbiotic germination [50,53], micropropagation [54], PLBs proliferation [50,51], indirect ES [23,53,104], and even synseeds [104]. This increasing interest of PTC on *L. anceps*, which is not reflected for any other species of orchids, is explained by its wide use as a cut flower, its intense use in orchid breeding, and for being a highly vulnerable orchid due to an accelerated loss of its habitat.

By analyzing the PTC literature reported thus far, it seems that PTC has been used for conservation using mostly asymbiotic germination, and to a lesser extent, by cryoconservation. Other technologies such as synseeds have been little developed for *Laelia* spp., although protocols are well established for PLB production or SE for some species, e.g., *L. anceps*, which may provide excellent propagules. Regarding mass propagation using PTC techniques, there is much work to be performed in the *Laelia* genus. Only three species, *L. anceps*, *L. speciosa*, and *L. rubescens*, have protocols reported for PLB multiplication, and only one species, *L. anceps*, has been assayed for SE. Neither temporary immersion systems for micropropagation have been evaluated in any *Laelia* species. A published thesis is available online for *L. superbiens* propagation using RITA® [100]; however, a peer-reviewed protocol has not been reported thus far.

Bioprospecting approaches on the *Laelia* genus for metabolite discovery with biomedical purposes have set out the necessity of developing other PTC techniques such as cell suspensions. For example, it may be interesting to assess the potential of producing secondary metabolites with vasorelaxant effects in cell suspension cultures (CSC) of *L. anceps* or *L. speciosa* roots. Although CSC as a platform to produce high-value metabolites on a large scale still has some limitations [105], the successful establishment of precursor-enriched CSC from *Dendrobium fimbriatum* to induce accumulation of secondary metabolites [106] shows a promising future for other orchid-derived CSCs.

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Appendix A

Table A1. Simple and multiple *Laelia* hybrids generated by artificial crossing. This information in this table is provided by [21,105].

Bigeneric Hybrids	Trigeneric Hybrids	Tetrageneric Hybrids	Pentageneric Hybrids	Hexageneric Hybrids
x Barkeria = Laeliokeria	x Barkeria x Cattleya = Laeliocattkeria	x Brassavola x Broughtonia x Cattleya = Otaara	x Brassavola x Broughtonia x Cattleya x Epidendrum = Hattoriara	x Brassavola x Cattleya x Caularthron x Guarianthe x Rhyncholaelia = Andersonara
x Brassavola = Brassolaelia	x Barkeria x Caularthron = Caulaeliokeria	x Brassavola x Cattleya x Encyclia = Bergmanara	x Brassavola x Broughtonia x Cattleya x Myrmecophila = Siebertara	x Brassavola x Cattleya x Encyclia x Guarianthe x Ryncholaelia = Maumeneara
x Broughtonia = Laelonia	x Brassavola x Cattleya = Brassolaeliocattleya	x Brassavola x Cattleya x Guarianthe = Garlippara	x Brassavola x Broughtonia x Cattleya x Prosthechea = Keishunara	x Brassavola x Cattleya x Myrmecophila x Pseudolaelia x Rhycholaelia = Paulandmarystormara
x Cattleya = Laeliocattleya	x Brassalova x Caularthron = Marvingerberara	x Brassavola x Cattleya x Myrmecophila = Jellesmaara	x Brassavola x Cattleya x Caularthron x Guarianthe = Ghillanyara	x Broughtonia x Cattleya x Caularthron x Encyclia x Psychilis x Rhyncholaelia = Warasara
x Caularthron = Caudalaelia	x Brassalova x Guarianthe = Guarilaelivola	x Brassavola x Cattleya x Rhyncholaelia = Keyesara	x Brassavola x Cattleya x Caularthron x Guarianthe = Ghillanyara	x Broughtonia x Cattleya x Caularthron x Guarianthe x Rhyncholaelia = Dodara
x Domingoa = Laegoa	x Brassvola x Rhyncholaelia = Rhynchovolaelia	x Brassalova x Caularthron x Guarianthe = Millerara	x Brassavola x Cattleya x Caularthron x Mrmecophila = Rolfwihelmara	x Cattleya x Caularthron x Epidendrum x Guarianhe x Rhyncholaelia = Dormanara
x Encyclia = Encylaelia	x Broughtonia x Cattleya = Laeliocatonia	x Broughtonia x Cattleya x Caularthron = Williamcookara	x Brassavola x Cattleya x Domingoa x Epidendrum = Kawamotoara	x Cattleya x Caularthron x Guarianthe x Myrmecophila x Rhyncholaelia = Kautskyara
x Epidendrum = Epilaelia	x Broughtonia x Guarianthe = Brolaelianthe	x Broughtonia x Cattleya x Encyclia = Sevillaara	x Brassavola x Cattleya x Encyclia x Guarianthe = Pynaertara	x Cattleya x Caularthron x Guarianthe x Psychilis x Ryncholaelia = Marycrawleystormara
x Euchile = Euchilaelia	x Cattleya x Caularthron = Laeliocatarthron	x Broughtonia x Cattleya x Epidendrum = Jewellara	x Brassavola x Cattleya x Encyclia x Prosthechea = Orpetara	
x Guarianthe = Laelianthe	x Cattleya x Encyclia = Catcylaelia	x Broughtonia x Cattleya x Guarianthe = Janssensara	x Brassavola x Cattleya x Myrmecophila x Prosthechea = Roezlara	
x Leptotes = Leptolaelia	x Cattleya x Epidendrum = Epilaeliacattleya	x Broughtonia x Cattleya x Rhyncholaelia = Viesara	x Brassavola x Cattleya x Myrmecophila x Pseudolaelia = Hayataara	
x Myrmecophila = Myrmecolaelia	x Cattleya x Euchile = Eucatlaelia	x Broughtonia x Caularthron x Guarianthe = Aberconwayara	x Broughtonia x Cattleya x Caularthron x Guarianthe = Denisara	
x Oerstedella = Oerstelaelia	x Cattleya x Guarianthe = Laeliocatanthe	x Cattleya x Caularthron x Encyclia = Lebaudyara	x Broughtonia x Cattleya x Encyclia x Rhyncholaelia = Bettsara	
x Prosthechea = Proslia	x Cattleya x Myrmecophila = Myrmecatlaelia	x Cattleya x Caularthron x Epidendrum = Pendletonara	x Broughtonia x Cattleya x Guarianthe x Rhyncholaelia = Dunstervilleara	

Table A1. *Cont.*

Bigeneric Hybrids	Trigeneric Hybrids	Tetrageneric Hybrids	Pentageneric Hybrids	Hexageneric Hybrids
x Psychilis = Laechilis	x Cattleya x Psychilis = Psylaeliacattleya	x Cattleya x Caularthron x Guarianthe = Ledienara	x Cattleya x Caularthron x Guarianthe x Rhyncholaelia = Jackfowlieara	
x Rhyncholaelia = Laelirhynchos	x Cattleya x Rhyncholaelia = Rhyncatlaelia	x Cattleya x Caularthron x Myrmecophila = Hasskarlara	x Cattleya x Encyclia x Guarianthe x Rhyncholaelia = Devriessara	
	x Caularthron x Encyclia = Encyarthrolia	x Cattleya x Caularthron x Rhyncholaelia = Meloara		
	x Caularthron x Epidendrum = Epicaulaelia	x Cattleya x Caularthron x Schomburgkia = Georgefara		
	x Caularthron x Guarianthe = Guarilaeliarthron	x Cattleya x Encyclia x Epidendrum = Bernardara		
	x Caularthron x Schomburgia = Schomcaulaelia	x Cattleya x Encyclia x Guarianthe = Stricklandara		
	x Epidendrum x Guarianthe = Laeliadendranthe	x Cattleya x Encyclia x Prosthechea = Mylamara		
	x Epidendrum x Rhyncholaelia = Rhyndenlia	x Cattleya x Encyclia x Rhyncholaelia = Appletonara		
	x Euchile x Guarianthe = Eulaelianthe	x Cattleya x Epidendrum x Guarianthe = Pabstara		
	x Guarianthe x Prosthechea = Laerianchea	x Cattleya x Epidendrum x Oerstedella = Rafinesqueara		
	x Guarianthe x Rhyncholaelia = Rhynchoguarlia	x Cattleya x Guarianthe x Prosthechea = Obrienara		
	x Guarianthe x Schomburgia = Guarlaeburkgia	x Cattleya x Guarianthe x Rhyncholaelia = Rechingerara		
	x Myrmecophila x Rhyncholaelia = Rhycopelia	x Cattleya x Guarianthe x Schomburgkia = Ottoara		
	x Prosthechea x Rhyncholaelia = Rhynchothechlia	x Cattleya x Myrmecophila x Rhyncholaelia = Claudiasauledaara		

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