




## Review

# Transcriptional Regulations and Hormonal Signaling during Somatic Embryogenesis in the Coconut Tree: An Insight

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**Abstract:** The coconut palm (*Cocos nucifera* L.) is a perennial, cross-pollinated, oil-bearing tropical forest tree. Recently, the demand for coconut goods has surged to 5 to 10 times its former value; however, coconut production is in jeopardy. Coconut senility is one of the most apparent factors that influence productivity. Adequate replanting is urgently required to maintain the growing demand for coconut products. However, coconut palm mass replanting might not be possible with traditional approaches. To overcome this snag, micropropagation via somatic embryogenesis (SE) has enormous potential for proficient clonal propagation in the coconut palm. During SE, the stimulation of cell proliferation, acquisition of embryogenic cell competence, and induction of somatic embryos undergo a series of developmental events. This phenomenon requires regulation in gene expression patterns and the activation of specific signaling pathways. This review summarizes gene regulatory mechanisms involved in the cell cycle, dedifferentiation, totipotency, embryo initiation, and meristem development during somatic embryo formation. Plant hormonal signal transduction is also highlighted during the formation of SE in coconut.

**Keywords:** *Cocos nucifera* L.; clonal propagation; gene regulation; micropropagation; replanting; senility



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## 1. Introduction

The coconut palm (*Cocos nucifera* L.), known as the “tree of life,” is considered one of the most important tropical forest tree species consumed by human beings, as it allows the elaboration of more than 100 products and by-products [1–3]. Coconut is the source of virgin oil, fresh kernel, coconut milk, husk, and shell charcoal [4,5]. Around 10 million smallholder farmers cultivate coconut palms worldwide on 12 million hectares of tropical and subtropical areas [6]. Recently, its importance has grown, commercially, fast for several high-value products, such as packed coconut water [7,8]. Primarily, coconut production is decreased by senility (aging) when the coconut palms reach 40–70 years of age [9]. Secondly, its production declines due to natural calamities (typhoons, tsunamis) and biotic factors like an attack of red palm weevil (*Rhynchophorus ferrugineus olivier*), lethal leaf yellowing (Bogia coconut syndrome), and cadang-cadang [10–13].

Moreover, most of the 12 million hectares dedicated to the coconut are senile [14]. The lack of quality plant material, nursery establishment, and seed distribution for replanting is a leading cause of low yield. On the other hand, the increase in market demand for coconut products has been noticed in recent years. Therefore, replanting with genetically improved coconut cultivars is urgently required to maintain supply to meet the growing demand for coconut products [15,16]. At a meeting of the International Coconut Genetic Resources Network (COGENT), it was decided to replant coconut palms on a large scale to fulfill the growing demands [17]. It is challenging to produce billions of coconut plants to meet

the rising demand for food. The use of the traditional propagation method results in an inadequate supply of planting material.

A single coconut palm could produce 50 to 80 fruits per year. Coconut propagation through seed is a slow method that takes decades (12–16 years). This limitation is especially evident for coconut; new plantings from seeds are genetically diverse, and their phenotypic variation within plantations hinders agronomic practices [18]. In this frame, promoting homogenous planting materials for the coconut industry through vegetative propagation would alleviate the problem. It is relatively easy to use the dwarf coconut genotype as a mother tree because the heterozygosity of tall varieties induces a high degree of heterozygosity in hybrid progenies [19–21]. Therefore, mass propagation as an outcome of *in vitro* regeneration through somatic embryogenesis (SE) is a better choice to satisfy the rising demand [22–24].

SE is a method of asexual reproduction widely used for large-scale clonal propagation in various tree species (coconut, oil palm, date palm) with long reproductive cycles from one single explant [25–28]. Micropropagation by SE enables the generation of multiple genetically identical embryos while eliminating the need to wait for the next reproductive season. A broad range of explants is utilized to initiate SE [29–31], such as immature leaves, roots, shoot apical meristems, zygotic embryos, inflorescences, plumules, and unfertilized ovaries [32,33]. Although SE in coconut is an applicable and promising tissue culture technique, there is still a bottleneck due to the recalcitrant nature of coconut tissues. The efficiency of the number of explants developing embryogenic callus and the frequency of somatic embryos created per embryogenic callus remains poor. These constraints result in more embryogenic callus production and toil to gain greater yields [34]. In the SE process, cell-to-plantlet formation is followed by various factors, such as medium composition, explant type, plant growth regulators (PGRs), heterogenous response, and acclimatization procedure [35,36]. In the last two decades, significant efforts have been made to develop and optimize propagation methods of coconut plantlets through SE [37]. Researchers are using *in vitro* techniques to understand how somatic cells can grow into new and independent clonal organisms [25,38].

During SE, cells regenerate as a whole plant via comprehensive reprogramming. This reprogramming requires regulation in gene expression patterns and the initiation of specific signaling pathways. As the initial step in coconut SE, competent cells of cultured explants respond to inductive signals (PGRs or stress) and induce dedifferentiation. The endogenous level of PGRs increased during the initial stages of SE. The combined action of genes and undifferentiated cells led to embryogenic development [39]. The cellular changes induced by inductive signals are crucial to initiate the process. However, several studies highlight the complexity of developmental stages and identify critical components involved during SE. The general notion applies to many species [38], but understanding the molecular mechanism during SE and its regulation is critical in coconut.

## 2. Somatic Embryogenesis System in Coconut

Under *in vitro* conditions, somatic cells developed a structure similar to the zygotic embryo without the fusion of gametes [22]. The first study of coconut SE was performed in the 1980s using immature leaves, zygotic embryos, and inflorescences as an explant [40,41]. Chan [42] published an effective SE protocol based on plumule explants from coconut. Some studies have reported a reproducible regeneration method for plumule explants based on the multiplication of embryogenic callus and SE (Table 1) [33,43]. Numerous factors can induce SE, and most are associated with stress, including nutrient starvation, wounding, cold, heat, osmotic shock, water deficit, heavy metals, medium culture dehydration, ultraviolet radiation, and pH [39,43–50].

In coconut palm, SE involves three main stages; the induction of embryogenic callus (cell cycle, dedifferentiation, and totipotency), somatic embryo development (meristem maintenance), and plantlet maturation [51]. The stimulation of cell proliferation, acquisition of embryogenic cell competence, and induction of somatic embryos undergo a series of

development events [25]. PGRs are incredibly involved in the whole process of SE, such as initiation and meristem maintenance. Particularly, 2,4-dichlorophenoxyacetic acid (2,4-D), which controls and balances endogenous indole-3-acetic acid levels, and cytokinin (CK) are crucial to most species experiencing SE (Table 1) [52–55].

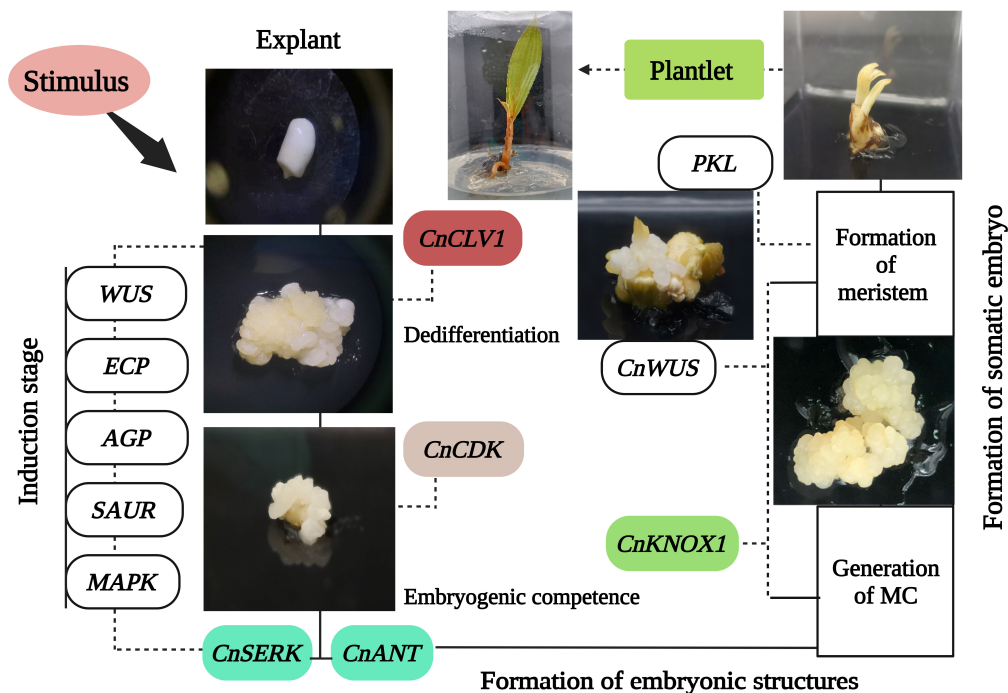
**Table 1.** Coconut explant type, medium composition, and plant growth regulators.

Coconut Variety	Explant Type	Medium Composition	Plant Growth Regulators	Reference
Malayan Red Dwarf × Tagnanan	Rachilla	Y3 medium, gelrite (3 g/L), AC (2.5 g/L)	2,4-D, BAP (0.3 mM) and GA <sub>3</sub> (0.0046 mM)	[37]
Jamaican Malayan Dwarf	Rachilla and stem	3 basal medium and sucrose (6.8%), agar (0.39%)	2,4-D (0.1 µM), BAP (5 µM), and GA <sub>3</sub> (10 µM)	[56]
West Coast Tall	Rachilla, stem, and foliage	Y3, AC (0.25%), sucrose (5%), agar (0.6%)	2,4-D (452 µM), NAA (2.69 µM), BAP (8.88 µM), kinetin (4.65 µM)	[57]
Green Malayan Dwarf	Plumule	Y3, gelrite (3 g/L), AC (2.5 g/L), sucrose (50 g/L)	2,4-D (6 µM) and (300 µM BAP)	[58]
MYD, Makapuno, XXD and PB121	Plumule	Y3, agar (2.5 g/L), vitamins	2,4-D and BAP	[59]
Green Malayan Dwarf	Plumule	Y3, gelrite (3 g/L), AC (2.5 g/L)	2,4-D and BAP	[43,60]
Sri Lanka Tall	Plumule	BM72, sucrose (4% w/v), agar (0.8%)	2,4-D	[61]
Malayan Dwarf	Plumule	Y3, gelrite (3 g/L), AC (2.5 g/L)	2,4-D (1 µM) and BAP (50 µM)	[42]
Sri Lanka Tall	Immature embryo	BM72, AC (0.25%), sucrose (40 g/L), agar (0.8%)	2,4-D (24 µM), ABA (2.5–7.5 µM), and cytokinin (2–10 µM)	[62]
Batu Layar Tall	Mature embryo slice	M2, AC (2.5 g/L), sucrose (0–100 g/L), agar (7.5 g/L)	2,4-D and ABA	[47]
Typica	Embryo	AC (0.25%), sucrose (30 g/L), agar (0.8%)	2,4-D (8 µM and 2 µM), BAP (10 µM) and kinetin (10 µM)	[63]
West Coast Tall	Young embryo	Gamborg's B5 medium, agar (0.7%)	IAA, NAA, 2,4-D, BAP or kinetin (0.5 mg/L to 5 mg/L)	[64]
Malayan Yellow Dwarf (MYD) × West African Tall	Young foliage tissue	Sucrose (30 g/L), agar (0.8%), vitamins	2,4-D, TCPP, and BAP	[41]
MYD × WAT, WAT × MYD and MYD	Immature inflorescence	Y3, AC (2 g/L), sucrose (116.8 mM), vitamins	2,4-D and BAP (10 <sup>−5</sup> M)	[45]
PB 121 (MYD × WAT)	Immature inflorescence	Modified MS macronutrients, AC (3 g/L), agar (7.5 g/L) Nitsch micronutrients, vitamins, EDTA (26 mg), iron (24.9 mg), ascorbic acid (100 mg/L), malic acid (100 mg/L), adenine sulfate (30 mg/L)	2,4-D and BAP	[44]
Malayan Yellow Dwarf	Immature inflorescence	Y3, AC (2.5 g/L), sucrose (30 g/L)	2,4-D, spermine (0.01 µM), auxin (500 µM), and water (10%)	[65]
Sri Lanka Tall	Inflorescence	CRI 72AC (0.1%), sucrose (40 g/L)		[66]
Sri Lanka Tall	Unfertilized ovary	CRI 72, agar (2%)	2,4-D and ABA (5 µM)	[67]
Dwarf Green	Leaf and inflorescence	Euwens medium, sucrose (60 g/L), TDZ (1.0 mg/L), 2-ip (1.0 mg/L)	2,4-D (60 mg/L) and BAP (2 mg/L)	[36]

## 2.1. Gene Regulatory Mechanism during the Development of SE

Somatic embryogenesis includes the action of a complex signaling network and the reprogramming of gene regulation in a precise way (Table 2) [68]. Gene identification and regulation analysis help us to uncover the SE process in coconut. During SE, epigenetic modifications also play a significant role in cell fate transition and the transmission of genetic information through cell division (Figure 1). Transcriptome analysis was performed on *C. nucifera* (west coast tall cultivar) embryogenic calli obtained from plumular explants [69]. After transcriptome analysis, fourteen SE-related genes have been identified

in *C. nucifera*; mitogen-activated protein kinase (MAPK); embryogenic cell protein (ECP), AP2/ERF-domain-containing transcription factor, WRKY transcription factor, *Aintegumenta* (ANT), *somatic embryogenesis receptor-like kinase* (RLK) SERK, *PICKLE* (PKL), *CLAVATA1* (CLV), glutathione s-transferase (GST), late-embryogenesis-abundant protein (LEC), *WUSCHEL* (WUS), and germin-like protein (GLP). Six developmental stages were selected to analyze these gene expression patterns (PKL, WRKY, SERK, GST, CLV, WUS, GLP) via quantitative real-time PCR (qRT-PCR) (Table 2).



**Figure 1.** Predicted molecular pathway of coconut somatic embryogenesis. *WUS*, *WUSCHEL*-related homeobox transcription factor; *MAPK*, mitogen-activated protein kinase; *ECP*, embryogenic cell protein; *ANT*, *Aintegumenta*; *SERK*, *PICKLE*; *CLV*, *CLAVATA1*; *LEC*, late embryogenesis abundant protein; *Arabinogalactan Protein* (*AGP*); *SAUR*, *Saur Family Protein*; *KNOX1*, *Class I Knotted-Like Homeobox*.

**Table 2.** Highly expressed genes during somatic embryogenesis in coconut.

Expression Pattern	Gene	Abbreviation	Reference
SE developmental stage	<i>WUSCHEL</i>	<i>CnWUS</i>	[69]
Callus tissues at the initiation stage of SE	<i>SOMATIC EMBRYOGENESIS RECEPTOR-like KINASE</i>	<i>CnSERK</i>	[70]
Early stages of callus formation	<i>CLAVATA</i>	<i>CLV</i>	[69]
Embryogenic calli	<i>AINTEGUMENTA-like</i>	<i>ANT</i>	[69]
Globular and coleoptilar SE growth	<i>KNOTTED-like homeobox</i>	<i>CnKNOX</i>	[71]
SE developmental stage	<i>GLUTATHIONE STRANSFERASE</i>	<i>GST</i>	[69]
Embryogenic callus and germinated embryogenic calli	<i>Cyclin-Dependent Kinases</i>	<i>CnCDK</i>	[72]
	<i>MITOGEN-ACTIVATED PROTEIN KINASE</i>	<i>MAPK</i>	[69]
	<i>APETALA2/ETHYLENE RESPONSIVE FACTOR</i>	<i>AP2/ERF</i>	[69]
	<i>SAUR Family Protein</i>	<i>SAUR</i>	[69]



Table 2. Cont.

Expression Pattern	Gene	Abbreviation	Reference
	EMBRYOGENIC CELL PROTEIN	ECP	[69]
	LATE EMBRYOGENESIS ABUNDANT PROTEIN	LEA	[69]
	ARABINO GALACTAN PROTEIN	AGP	[69]
SE developmental stage	WRKY transcription factor	WRKY	[69]
	GERMIN-LIKE PROTEIN	GLP	[69]
Embryogenic and non-embryogenic calli	MicroRNAs	miRNAs	[73]
SE developmental stage	PICKLE	PKL	[69]

The GLP, GST, PKL, WUS, and WRKY genes show high expression during the somatic embryo stage, whereas the CLV gene shows high expression during the initial phase of callogenesis. The *CnSERK* gene has significantly more expression in embryogenic callus formation than in SE. Some other reported genes, such as *Class I Knotted-Like Homeobox (KNOX1)*, *Cyclin-Dependent Kinases (CDK)*, *Saur Family Protein (SAUR)*, and *Arabinogalactan Protein (AGP)*, are essential for SE and were comprehensively analyzed via a traditional gene by gene approach [74]. Moreover, several *miRNAs (microRNAs)* and their targets were identified in embryogenic and non-embryogenic calli derived from plumular explants. This information details the gene regulatory mechanism involved in SE [75,76].

#### 2.1.1. Cell Cycle

Different developmental pathways are involved in cell division during cell cultures, such as unorganized callus and somatic embryo formation (Table 3). Coconut in vitro regeneration and cell cycling have been reported using different tissues [77]. The *CDK* genes are widely involved in cell division maintenance, cell proliferation, and the cell cycle in differentiated and developmental tissues [78–80]. Even though not all known kinases affect cell cycle progression, the first reported *CDK–cyclin* partners play a significant role in G1/S and G2/M checkpoints [81].

Table 3. Genes functional characterization in different developmental stages.

SE Development Stage	Gene	Coconut Dwarf Accession	Gene Accession	Molecular and Biological Function
Cell cycle	CDK	AZ04G0076960 AZ13G0236040	AT1G15570 AT1G18040 AT1G20930 AT1G76540	G2/M transition of the mitotic cell cycle, protein binding, regulation of cell cycle, regulation of G2/M transition of the mitotic cell cycle
Dedifferentiation	WUS	AZ11G0210850	AT2G17950	Stem cell population maintenance, DNA-binding transcription factor activity, protein binding
	CLV3		AT2G27250	Cell differentiation, cell–cell signaling involved in cell fate commitment, protein binding
	WOX5	AZ03G0055410	AT4G32980 AT3G11260	Positive regulation of stem cell population maintenance, response to auxin, DNA-binding transcription factor activity
	AIL	AZ01G0008180	AT1G72570 AT3G20840	DNA binding, regulation of transcription factor activity
				Quiescent center (QC) specification and stem cell activity, DNA binding
	BBM	AZ07G0145330	AT5G17430	Cell population proliferation, DNA-binding transcription factor activity

Table 3. Cont.

SE Development Stage	Gene	Coconut Dwarf Accession	Gene Accession	Molecular and Biological Function
Totipotent potential acquisition	CDK	AZ04G0076960 AZ13G0236040	AT1G73690	Involved in cell cycle regulation and cell differentiation, protein binding,
	WUS	AZ11G0210850	AT2G17950	Stem cell population maintenance, DNA-binding transcription factor activity, protein binding
	LEC1	AZ07G0152850 AZ05G0112880	AT1G21970	Somatic embryogenesis, DNA binding
Meristem maintenance	KNOX	AZ10G0201430 AZ02G0037220	AT1G62990 AT1G14760	Leaf proximal/distal pattern formation, DNA binding
	STM	AZ07G0160530	AT1G75410 AT2G23760 AT2G35940 AT3G54220	DNA binding, regulation of timing of the transition from vegetative to reproductive phase
	AS2	AZ14G0257890	AT1G65620	Protein binding, proximal/distal pattern formation
Somatic embryo	WUS	AZ11G0210850	AT2G17950	Stem cell population maintenance, DNA-binding transcription factor activity, protein binding
	SERK	AZ15G0264500	AT1G71830	Protein phosphorylation and protein kinase binding, hormonal signaling pathway, brassinosteroid homeostasis

### 2.1.2. Genetic Component for Dedifferentiation and Totipotency

Cell dedifferentiation is a process in which a differentiated mature cell develops competency for a different developmental fate (Figure 1). Single somatic cells proliferate, change cell destiny to totipotency acquisition, and advance into morphologically recognizable somatic embryos [82]. Embryonic cells do obtain totipotency to progress into somatic embryos. The *WUS* gene involves cell fate transition and the dedication of somatic cells and somatic embryos in tree species such as *Coffea canephora* [83]. *WUS* acts as a marker gene of dedifferentiation after SE induction in *Medicago truncatula* [84].

Other *WUSCHEL-related homeobox* (WOX) transcription factor members are crucial in early embryonic patterning and other signaling networks that control plant growth and SE induction [78,85]. WOX5 is also involved in the dedifferentiation of the somatic embryo and showed high expression after two days of induction and is used as a marker of dedifferentiation [84].

The genes *WUS* and *LEC2* are involved in totipotency and behave similarly during SE [25,86–88]. The *miR156*-regulated *SPL9/SPL10*, which controls the quantity of mature *miR172* in an embryogenic culture, may be one of the upstream regulatory components of the *miR172-AP2-WUS* pathway [89]. The SE of *C. canephora* also revealed the modulation of *WUS* and *LEC1* expression by DNA and histone methylation during early somatic embryogenesis [90]. The *BABY BOOM (BBM)* gene encodes an *APETALA2/ethylene-responsive element-binding factor (AP2/ERF)* and is involved in cell division [91,92]. Moreover, the expression patterns of *LEC1* and *BBM1* were suppressed by 5-AzaC (azacitidine) during SE [90].

### 2.1.3. Release/Induction of Embryogenic Program

A set of proteins known as the subgroup II receptor kinases includes the *SERK* gene that controls somatic embryo development and is famous as a marker gene for SE induction [70,93]. All embryogenic cells and emerging embryos up to the heart stage during *Arabidopsis* SE show upregulation of the *SERK* gene [93]. Furthermore, PGRs are crucial in regulating *SERK* gene expression during SE. *SERK1* expression controls by IAA and CK in *M. truncatula* embryogenic cultures [94]. *SERK2* and *SERK3* produce an IAA-specific

response, while *SERK1* and *SERK5* interrelate with brassinosteroid (BRs) signaling [95]. *SERK*-like genes in *C. nucifera* were sequenced and are known as *CnSERK*. *CnSERK* encodes the *SERK* protein domain similarly to the typical *SERK* (Serine-Proline-Proline domain) protein reported in other plant species. In non-embryogenic tissue, *SERK* genes show no or less relative expression, revealing the role of *CnSERK* in coconut SE. On the other hand, *CnSERK* could be used as a marker for competent cells during the in vitro development of somatic embryos in *C. nucifera* tissue culture [70].

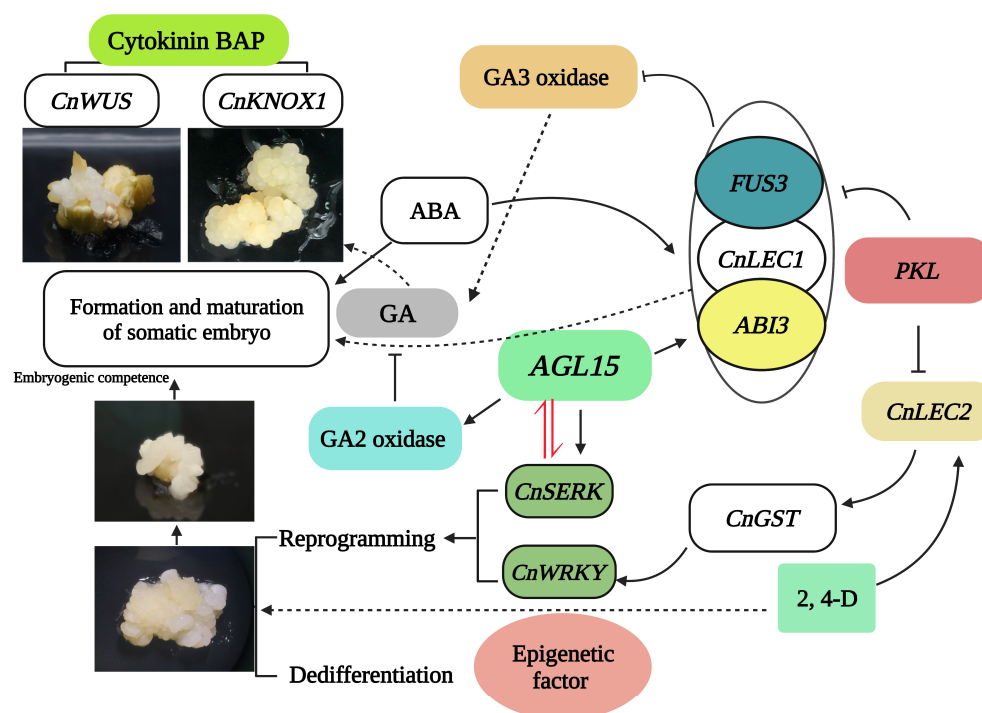
The *CnCDKA* and *CnSERK* genes were isolated from *C. nucifera* and associated with SE induction [96]. *CDK* is involved in embryogenic development, revealing its prominent role in cell division in male gametogenesis [97]. *CDK* expression comparatively increased during the embryogenic callus generation stage after embryogenic competence in coconut. The relative expression pattern of *CnCDK* decreases according to the somatic embryo developmental stages. However, the lowest expression can be observed in the germinated somatic embryo [72]. It is critical to understand that the analysis of *CDK* in *C. nucifera* cells provided more information regarding the embryogenic competence of any in vitro culture. The isolation and characterization of the *AINTEGUMENTA*-like gene in *C. nucifera* revealed the involvement of this gene in somatic embryogenesis (Table 3). It showed a high expression pattern during the callus induction stage, when cells attain somatic embryogenic competence [98,99].

#### 2.1.4. Formation of SE Meristem Maintenance and Regulation

Artificial induction and maintenance of cell division are necessary to generate the dedifferentiation of meristematic cells (Figure 2). The knotted-like homeobox (*KNOX*) proteins function as regulators of cell specification, pattern formation, and SE in plants [100]. *KNOX* (*KNOX1* and *KNOX2*) genes show high expression during somatic embryo globular and coleoptile stages. Notably, GA3 regulates the expression of *KNOX* genes. GA3 increases the expression of *KNOX1* and decreases the expression of *KNOX2* [71]. *HBK3*, a class I *KNOX* homeobox overexpression, increases the development and growth of somatic embryos [101]. *SHOOT MERISTEMLESS* (*STM*) encodes the class-1 *KNOX* homeodomain-containing protein and enhances *WUS* expression [100]. These proteins are found in the apical shoot pole and regulate meristematic cell behavior [102]. In *Arabidopsis*, *STM* is first noticed in a few cells of immature embryos and then expands to significant apical dominance. Notably, *STM* suppresses the expression of *MYB*-related genes such as *ASYMMETRIC LEAVES 1* (*AS1*), which are required to start organogenesis [103]. *WUS* is a homeobox gene prominently involved in forming and maintaining the center of the shoot apical meristem [78,104]. The *WUS* gene promotes the transcription of *CLAVATA3* (*CLV3*); the feedback loop between *CLV3* and *WUS* is mandatory for shoot apical maintenance [105].

#### 2.2. Hormonal Regulatory Mechanisms Involved in SE

PGRs are chemical substances produced naturally within plants that control cell differentiation and development (Figure 2). 2,4-D induced many *GLUTATHIONE-S-TRANSFERASE* (*GST*) genes during SE formation [106]. In the later stages of SE, BAP (6-Benzylaminopurine) and ABA (abscisic acid) act as significant regulators for somatic embryo development [34]. According to some earlier studies, stress increased the expression of SE-related genes like *AGAMOUS-15* (*AGL15*), *SERK1*, and *WRKY* [107–110]. ABA synthesis and signaling are significantly involved in the in vitro embryogenic processes. The *ABSCISIC ACID INSENSITIVE 3* (*ABI3*) and *ABI4* transcription factors are relevant in embryo formation [111]. *ABI3* is involved in the regulation of the *LEC1*, *LEC2*, and *AGL15* genes [112]. Overexpression of *LEC2* significantly affects SE in *Theobroma cacao* [113,114]. *LEC2* represses *GA3ox2* and promotes the auxin pathway, whereas *FUSCA3* (*FUS3*) negatively regulates gibberellin (GA) accumulation by suppressing *GA3ox2* and *GA3ox3* [115]. GA also has a positive role during SE, stimulating the expression of *CnKNOX1* [71].



**Figure 2.** Hormonal signal transduction pathway involved in somatic embryogenesis. *WUS*, *WUSCHEL-related homeobox transcription factor*; *SERK*, somatic embryogenesis receptor-like kinase (RLK); *PKL*, *PICKLE*; *GST*, glutathione S-transferase; *LEC*, late embryogenesis abundant protein; *FUS3*, *FUSCA3*; *KNOX1*, *Class I Knotted-Like Homeobox*; *GST*, glutathione S-transferase; *AGL15*, *AGAMOUS-15*; *ABSCISIC ACID INSENSITIVE 3 (ABI3)*; *GA3*, gibberellin 2,4-dichlorophenoxyacetic acid (2,4-D); *ABA*, abscisic acid; *BAP* (6-Benzylaminopurine).

Auxin regulates apical, basal axis, and asymmetry formation during embryo development. Auxin is also crucial in signaling the generation and proliferation of tissue during embryogenesis [116]. Only 16 h in the induction medium showed *PIN1*-mediated auxin movement in *Arabidopsis* explants, which helped to identify the *WUS*-expressing cells that would later serve as the sites of embryo formation [117]. The introduction of SE marker genes (*WUS*, *SERK*, and *BBM*) is facilitated by endogenous auxin concentrations [38]. The expression of *WUS* regulates the auxin-mediated vegetative-to-embryogenic transition. Notably, during the early stages of SE, the induction of *WUS* expression and the establishment of IAA are correlated [118]. In *M. truncatula*, auxins and CK synergistically stimulate *SERK1*. BR signaling is also connected to *SERK1* and *SERK5*, while *SERK2* and *SERK3* elicit auxin-specific responses [119]. CK acts as a critical regulator in the embryogenic system. Many propagation protocols use the idea that a high CK and IAA ratio induces the creation of shoots. In contrast, a low ratio grows roots [120].

### 3. Epigenetic Regulations of Somatic Embryogenesis

The signaling system that results in modifications to the cell's genetic code and the development of SE depends critically on epigenetic modification. Epigenetic modifications such as DNA methylation and chromosome remodeling regulate SE induction in plants [75,121]. The efficiency of cellular differentiation is linked to the methylation profile of DNA [122]. DNA methylation widely occurs in plant cellular dedifferentiation and development. It has been found to be vital for the expansion of SE and zygotic embryogenesis [90,123]. In coconut, DNA methylation is caused by the combined effect of auxin and 2,4 D present in the medium [75,124]. Auxin is also responsible for increasing DNA methylation [125]. The stimulation of SE enhanced DNA methylation in *T. cacao*, and 5-AzaC therapy restored the ability to induce SE in cultures that had grown older [126]. The

DNA methylation inhibitor 5-AzaC can help us better understand the epigenetic changes in coconut [75].

Chromatin remodeling can control totipotency in plant cells [127]. There is proof that chromatin modifications can regulate the totipotency of plant cells [127]. *PICKL* genes are transcriptional regulators containing DNA and chromatin binding domains [128]. *Polycomb repressive complex 2* (*PRC2*) is intricately involved in the methylation of lysine 27 in histone H3 [129]. There are numerous tissue-specific measures linking to H3K27me3. When this mark is lost, the auxin pathway is activated, and as a result, leaf identity is suppressed [130]. In line with the negative effect of *PRC1* on SE, a reduced versus an increased expression of *PRC1* genes (*RING1*, *BMI1*, *LIKE HETEROCHROMATIN PROTEIN1 LHP1*, *EMBRYONIC FLOWER1 EMF1*, and *VERNALIZATION1 VRN1*) has been originated in the embryogenic vs. non-embryogenic genotypes of *M. truncatula* [84]. The *PRC1* complex in *Arabidopsis* contains five proteins, *AtRINGa/b*, and *AtBMI1a-c*, and the *Atbmi1a Atbmi1b* and *Atring1a Atring1b* double mutant seedlings have exposed a spontaneous callus and somatic embryo development [131]. The *microRNAs* regulate the induction of SE, and various *miRNA* expression levels have been seen in *Arabidopsis* embryogenic cells. *miRNAs* regulate the induction of somatic embryogenesis and play a vital role in the epigenetic regulation of some important transcription factors. *Arabidopsis LEC2* and *FUS3* have been controlled by *miRNAs* [132]. In *Arabidopsis*, epigenetic mutants have revealed that DNA methylation and histone modification of regulatory sequences regulate the expression of the *WUS* gene and auxin signaling components, which are important for cell proliferation and shoot initiation and regeneration [133].

Somaclonal variations have been a substantial issue, causing variances in the regenerated plants and, on the other hand, acting as a source of variation to provide agronomically significant traits. The somaclonal variation can be high when the plant comes from the SE. A change in the DNA methylation pattern has been hypothesized to cause this alteration. Multiple species have provided observations of these alterations in the DNA methylation of regenerated plants from somatic embryogenesis. In oil palm (*Elaeis guineensis*), DNA methylation could be involved in the incidence of 5% of somaclonal variation [134]. Somaclonal variations can be limited by using different types of explants and the early detection of mutations in oil palm [135]. The supply of high-quality, mantle-free planting material may be guaranteed by including a detection phase in the propagation strategy [136]. However, the gradual increase in DNA methylation positively regulates the SE process in coconut, whereas changes induced by the pre-treatment of 5-AzaC in explants are becoming a significant alternative for improving the in vitro propagation protocol [75].

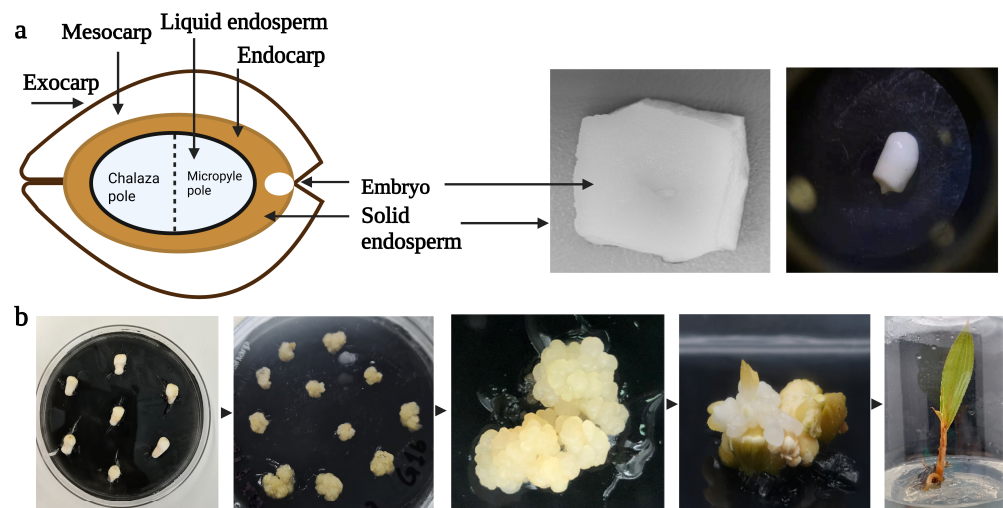
#### 4. Prospects for Using Clonal Propagation to Meet Global Replanting Needs

Market demand for coconut products is increasing, indicating the dire need for an alternative method for rapid and efficient clonal propagation. The genetically defective replanting material used years ago was one of the leading causes of low fruit output. Experts had determined this twenty years earlier, yet the condition has not changed [137]. The international coconut community (ICC, formerly the Asian and Pacific Coconut Community) estimated that at least half of these palms would need to be substituted within the next 20 years. An efficient clonal propagation method would require time to aid the renewal of *C. nucifera* plantations.

Due to the recalcitrant nature of *C. nucifera* tissues in in vitro culture, the importance of developing in vitro culture and the importance of developing a clonal propagation method is well accepted. Therefore, micropropagation methods (plumule explants) are required for the clonal propagation of elite coconut genotypes (Figure 3). The results of efforts to standardize embryogenic callus, medium, and multiplication have been encouraging. Using the most suitable explant is one way of minimizing the genotypic effect on the in vitro response of *C. nucifera* (Figure 3). Various developmental regulators (genes) regulate in vitro regeneration. Remarkably, the SE method did not change the genetic makeup of *C. nucifera* plantlets, and no variation was detected during in vitro propagation [138].



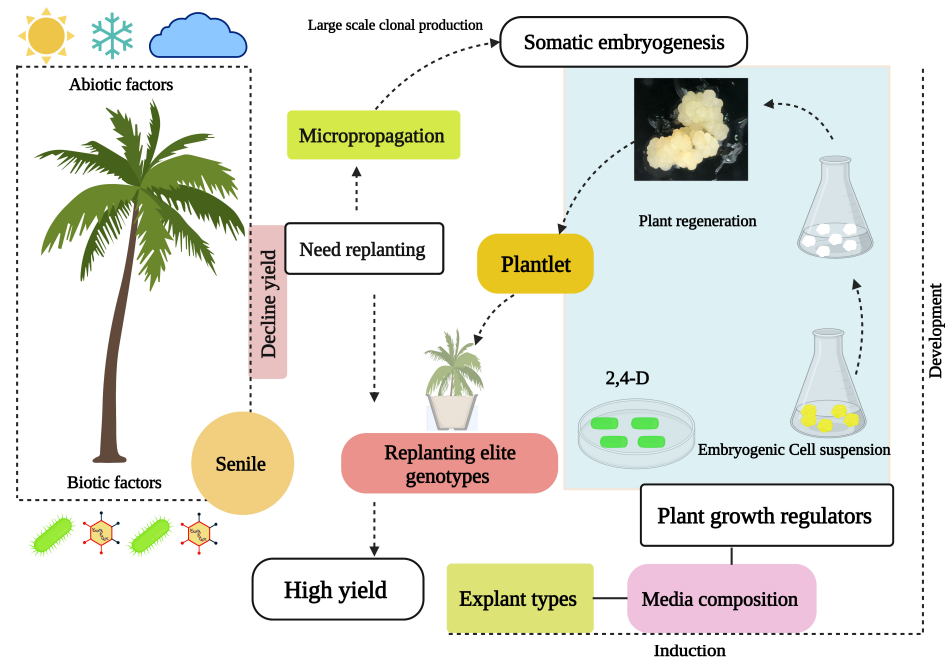
*C. nucifera* plantlets were established via SE and used on a semi-commercial scale in Mexico [14]. After the field trial, the conduction plantlets' performance shows good performance, including acclimatization, growth, and development to the fruit-bearing stage. These SE-derived clonally propagated plants start bearing fruit after six months. Recent biotechnology advancements and genetic transformation could lead to a more efficient regeneration system of SE. Current progress in genome sequencing has identified various candidate genes involved in SE. The availability of draft nuclear genome sequences of dwarf and tall coconut types provides an excellent opportunity to understand the gene regulatory mechanism involved in somatic embryogenesis [139,140]. The Coconut Research Institute at the Chinese Academy of Tropical Agricultural Sciences (CATAS) has been working on the construction of a mutant library via CRISPR/Cas9-based genome editing to reveal gene functioning in coconut [16]. The palm family multiomics database (*Arecaceae*) is available online through Hainan University; *Arecaceae* MDB: *Arecaceae* Multiomics Database (<http://arecaceae-gdb.com/>, accessed on 10 October 2022), provides an authentic source for studying coconut genes' functioning. Furthermore, public-private partnerships could play a key role in achieving a win-win situation in bringing this biotechnology to a commercial scale.



**Figure 3.** Graphic overview of coconut anatomy, (a) somatic embryogenesis induction, (b) plantlet regeneration.

## 5. Conclusions

Coconut markets have been rising abruptly in the past few decades. Unfortunately, along with other major biotic/abiotic factors, coconut cultivation is also threatened by coconut senility (Figure 4). Therefore, efforts need to be commenced globally to replace senile plantations with genetically modified coconut germplasm of high productivity and insect pest/disease resistance. This should include extra insights into the basic knowledge of SE, plantlet development, and embryogenic lines conservation. This review highlighted all the gene regulation and hormonal signaling events that took place during SE induction and development, ultimately leading to new opportunities for understanding the fundamental aspects of SE. Although much more progress has been made in the *in vitro* propagation of coconut in the last few years, some drawbacks still limit its possible application. Considering these contemplations of micropropagation for large-scale replanting in coconut, we could predict the broader scope of progressive coconut production in the future.



**Figure 4.** Schematic overview of somatic embryogenesis and clonal propagation for replanting.

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## Abbreviations

SE	Somatic embryogenesis
2,4-D	2,4-dichlorophenoxyacetic acid
CK	Cytokinin
BAP	6-Benzylaminopurine
BRs	Brassinosteroids
TCPP	Tris(2-chloropropyl) phosphate
GA3	Gibberellins
IAA	Indoleacetic acid
TDZ	Thidiazuron
2-ip	2-isopentenyl adenine

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