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**Advances in biology through
agronomy, aquaculture, coastal and
environmental sciences**
Volume II



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Advances in Biology through Agronomy, Aquaculture, Coastal and Environmental Sciences, Volume II, is an e-book that continues the work of the first version (<https://editorapantanal.com.br/ebooks/2023/advances-in-biology-through-agronomy-aquaculture-coastal-and-environmental-sciences/ebook.pdf>), published in 2023 by Leandris Argente-Martínez and Ofelda Peñuelas-Rubio.

Our e-book compiles 25 manuscripts that present scientific results and reviews based on biological aspects. All of them contribute to explaining the responses of living organisms to agricultural, aquaculture, and coastal ecosystems, as well as those facing fragility or threat of climate change. This e-book was edited by Leandris Argente-Martínez, Ofelda Peñuelas-Rubio, and Joe Luis Arias-Moscato, members of the Consolidated Academic Group ITVAYA-CA-3.

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Genomic Reprogramming and Epigenetic Memory: Transforming Somaclonal Variation into a Tool for Climate Resilience

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ABSTRACT

This chapter examines the conceptual transition of somaclonal variation from “biological noise” to an adaptive breeding tool during the Agricultural Anthropocene. Given the increase in abiotic stress, particularly soil salinity, which affects 10.7% of the global land surface, and the structural bottlenecks associated with conventional breeding in perennial crops, plant biotechnology has emerged as a critical solution. Somatic embryogenesis (SE) is characterized by the ultimate expression of totipotency, unlocked through extensive chromatin remodeling mediated by the BRAHMA ATPase and the hierarchical activation of master genes such as BABY BOOM (BBM) and WUSCHEL (WUS). Experimental evidence in blackberry (*Rubus* spp.) has demonstrated that overcoming biological recalcitrance requires specific strategies, such as substituting 2,4-D with thidiazuron (TDZ) and organic nitrogen (L-glutamine), to transition from disorganized proliferation to morphogenetic autonomy. This process is governed by a critical “oxidative window” of reactive oxygen species (ROS) signaling that act as a master switch for cell fate. Furthermore, this chapter explores the phenomenon of “epigenetic memory” or priming, which allows for the generation of “epitypes” with constitutive tolerance to future stressors without exogenous gene introgression. Finally, the implementation of high-precision aeroponic systems under LED lighting is discussed as an indispensable technological bridge for validating adaptive vigor under ex vitro conditions. By integrating cellular biotechnology with advanced cultivation systems, this work provides a framework for engineering plant resilience and ensuring global food security under environmental volatility.

Keywords: Somatic embryogenesis, Abiotic stress, Totipotency. Aeroponic culture

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INTRODUCTION: THE CONVERGENCE OF CAUSES IN THE AGRICULTURAL ANTHROPOCENE

During the early expansion of the commercial micropropagation industry, somaclonal variation was universally perceived as a technical failure—a form of “biological noise” that needed to be silenced. The promise of *in vitro* cloning rested on the exponential multiplication of elite genotypes identical to those of the original donor. In this context, any deviation from the desired phenotype represented an unacceptable economic risk (Karp, 1994; Bairu et al., 2011).

This negative perception was not unfounded; it was grounded in large-scale agronomic disasters that traumatized entire sectors of tropical agribusiness. The most emblematic and devastating case involved the oil palm (*Elaeis guineensis*) in Southeast Asia and West Africa. The massive introduction of clones propagated via somatic embryogenesis resulted in a 30% increase in yield because of the heterosis of the tenera hybrid (Corley; Law, 1997). However, upon reaching the productive phase, millions of palms exhibited a “mantled” floral anomaly. This condition is characterized by the homeotic transformation of stamens into carpeloid structures, resulting in partial sterility or fruit abortion (Jaligot et al., 2000; Ong-Abdullah et al., 2015). This phenomenon, which affected thousands of hectares, led to catastrophic financial losses and lasting distrust of tissue culture products among farmers and corporate planters (Rival et al., 2013).

Historically, plant breeding has prioritized pest resistance and yield under optimal conditions, a focus that has inadvertently eroded genetic diversity; for instance, modern wheat has lost a significant portion of the diversity found in its wild relatives, such as wild emmer. Climate change has shifted the risk landscape, elevating abiotic stresses—drought, heat, and salinity—to primary threats. The scientific literature indicates that developing crops capable of withstanding these stressors by utilizing biological models of extremophile and halophytic plants is the most promising path to securing the future food supply (Razzaq et al., 2021; Zhang et al., 2018).

Soil salinization represents one of the most insidious threats to sustainable agriculture, as it can compromise soil fertility, ecosystem health, and the economic stability of key producing regions. The Food and Agriculture Organization (FAO) of the United Nations recently presented a global assessment of salt-affected soils. The report, *Global Status of Salt-Affected Soils* (2024), reveals that approximately 1.4 billion hectares (1,381 Mha) of land are affected by salinity, constituting 10.7% of the total land surface. Critically, 10% of both irrigated and rainfed croplands are already compromised. This distribution is asymmetric, with ten countries—including major producers such as the United States, China, Australia, and Argentina—accounting for 70% of these soils. The economic impact is devastating, with estimated annual losses to global agricultural productivity totaling \$27.3 billion USD (FAO, 2024; Qadir et al., 2014).

Climate change acts as a threat multiplier, potentially expanding the area affected by salinity to encompass between 24% and 32% of the total land surface by the end of the century. The primary mechanisms include increased evapotranspiration in arid zones, which concentrates salts at the surface; seawater intrusion into fertile deltas because of rising sea levels; and the forced use of marginal or wastewater for irrigation during droughts, which accelerates secondary salinization (Corwin, 2021; FAO, 2024; Tarolli et al., 2023).

Understanding why current crops fail is fundamental to developing new varieties. The plant response to salinity is complex and occurs in two phases: rapid osmotic stress that limits water uptake, and slow ionic toxicity caused by sodium (Na⁺) accumulation in the tissues.

There is a fundamental physiological trade-off in plants. Modern elite crops have been selected to maximize yield traits, such as high stomatal conductance, thereby losing the plasticity required to downregulate their metabolism under adverse conditions. Often, tolerance mechanisms—such as active salt exclusion or the synthesis of compatible osmolytes—are so energetically expensive that they compete directly with biomass and grain production, resulting in what is known as a “yield penalty” in tolerant varieties (Dalal et al., 2017; Munns; Tester, 2008; Razzaq et al., 2021).

In the banana industry (*Musa* spp.), the situation was analogous. Micropropagation, which is essential for obtaining disease-free planting material, frequently generates “off-type” variants with undesirable traits, such as dwarfism, leaf variegation, deformed bunches, or changes in fruit hand orientation (Israeli et al., 1991). The export industry, governed by the strict aesthetic standards of European and North American supermarkets, severely penalized these deviations. Consequently, the scientific literature from the late 20th century focused obsessively on protocols to minimize somaclonal variation, optimize plant growth regulators (PGRs) and reduce the number of subculture cycles to ensure genetic stability (Sahijram et al., 2003).

Limitations of Conventional Plant Breeding: Critical Biological and Economic Barriers to Conventional Breeding

Modern agriculture exhibits a sharp technological dichotomy. While annual field crops have accelerated their genetic gains through rapid cycling and hybrid vigor, fruit production remains hindered by structural barriers inherent to the biology of perennial species. Conventional breeding in fruit trees—based on sexual hybridization and phenotypic selection—faces an innovation bottleneck defined by the complex interaction between protracted life cycles, a highly heterozygous genetic architecture, and restrictive reproductive mechanisms. These limitations not only extend varietal development timelines to decades but also impose an economic burden that threatens the viability of breeding programs in the face of urgent climate change and emerging phytosanitary pressures (Flachowsky et al., 2011; Migicovsky; Myles, 2017; van Nocker; Gardiner, 2014).

Physiological and Reproductive Barriers: The “Time Wall” and Genetic Complexity

The most formidable restriction for fruit breeders is juvenility, a mandatory ontogenetic phase during which the plant is physiologically incapable of flowering, regardless of environmental stimuli. Unlike annual crops that complete their cycle in months, woody species require extensive periods of vegetative growth before fruit quality can be evaluated. This juvenile period varies drastically across species: in apple (*Malus domestica*) and pear (*Pyrus communis*), seedlings typically take 4 to 8 years to flower; in citrus (*Citrus* spp.), this span often extends from 5 to 12 years and is accompanied by undesirable juvenile traits such as large thorns; and in avocado (*Persea americana*), the wait can exceed 15 years. This biological latency implies that the introgression of a single trait through six generations of backcrossing would theoretically require more than half a century, rendering the development of pure lines practically unfeasible (Hackett, 1985; Hanke et al., 2007; Lahav et al., 1986; Peña et al., 2007).

In addition to the temporal barrier, the genetic architecture of fruit trees prevents the fixation of traits through conventional inbreeding strategies. Most fruit species are obligate outcrossers and maintain extreme levels of heterozygosity. Unlike in maize or rice, where it is possible to create homozygous inbred lines to exploit heterosis in the F1 generation, self-fertilization in fruit trees triggers severe inbreeding depression. Attempts to “purify” the genome in species such as apple, cherry, or almond result in a drastic loss of vigor, low fertility, and the frequent appearance of lethal or sublethal phenotypes—such as albinism or extreme dwarfism—due to the historical accumulation of deleterious recessive alleles that were masked in the heterozygous state. This forces breeders to work with genetically “noisy” parents, where offspring segregate unpredictably. Consequently, the probability of recovering a superior genotype that combines all desired quality attributes is infinitesimally low, necessitating massive selection (Brown, 1973; McClure et al., 2014; Rahemi et al., 2011; Wu et al., 2016).

Reproductive biology imposes further constraints through self-incompatibility (SI) systems that prevent self-pollination and limit possible crosses. In the Rosaceae (apple, cherry, almond) and Solanaceae families, gametophytic self-incompatibility, which is dominated by the S-locus, prevails. In this mechanism, S-RNases (ribonucleases) in the style arrest pollen tube growth if the pollen has an allele identical to that of the maternal tissue. This not only restricts the breeder’s crossing designs but also complicates agronomic management by necessitating the planting of compatible pollinator varieties. Furthermore, in genera such as *Citrus* and *Mangifera* (mango), nucellar polyembryony and apomixis add a layer of logistical difficulty: seeds produce multiple clonal embryos from the mother that compete with and often eliminate the sexual hybrid embryo. This necessitates the use of costly molecular markers or delayed morphological evaluations to distinguish true hybrids from unwanted maternal clones (De Franceschi et al., 2012; Fujii et al., 2016; Koltunow et al., 1996; Sassa et al., 1997).

Global Food Security and Environmental Pressures

Contemporary agriculture stands at an existential crossroads, defined by the convergence of unprecedented demographic pressures, climatic volatility, and the accelerated degradation of basic edaphic resources. This report addresses the critical issue of global food security through the lens of an urgent need for new cultivars capable of thriving in marginal environments, with a specific focus on soil salinization induced and exacerbated by climate change. As the global population increases, the demand for calories and, crucially, quality nutrition will grow exponentially, challenging current production systems that already show signs of exhaustion.

Modern food security is not limited to supply availability; it depends intrinsically on physical and economic access. Accelerated urbanization is a determining factor in this equation; it is estimated that by 2050, two-thirds of the world's population will reside in urban areas, consuming the vast majority of food produced while creating a geographical dissociation between production and consumption. This dynamic, coupled with water scarcity, constitutes a formidable barrier to sustainable development goals (SDGs). Given that agriculture already occupies 38% of global land and utilizes 70% of freshwater, the expansion of the agricultural frontier is unsustainable; the necessary increases must stem from efficiency and resilience (Tuffrey; Espeut, 2015; van Zutphen et al., 2023; Zhang et al., 2018).

Plant Biotechnology as a Breeding Tool: Tissue Culture Beyond Clonal Micropropagation

Plant breeding has evolved from conventional phenotypic selection toward integration with advanced biotechnological tools. *In vitro* tissue culture has transitioned from being merely a method for mass multiplication to becoming a critical experimental platform. This platform enables the induction of genetic variability, the selection of resilient genotypes, and the circumvention of biological barriers inherent to traditional sexual hybridization (Gulzar et al., 2024).

Somaclonal variation is not a purely stochastic event; rather, it is a genomic adaptive response to culture-induced stress. This response encompasses point mutations, changes in ploidy, and, fundamentally, epigenetic alterations such as DNA hypomethylation and the activation of transposable elements (Ramos-Sánchez; Dela-Peña, 2025). In species characterized by obligate vegetative propagation or protracted life cycles—such as pineapple (*Ananas comosus*) or species within the *Rubus* genus—the selection of somaclonal variants has facilitated the development of genotypes with superior agronomic traits. These include resistance to fungal pathogens, modified plant architecture, and enhanced secondary metabolite profiles, all of which are achieved without the need for exogenous gene introgression (Ramos-Sánchez; Dela-Peña, 2025).

Historical Context and Paradigm Shift

Historically, the micropropagation industry perceived somaclonal variation as a technical failure and a source of unacceptable economic risk due to undesirable phenotypic deviations (Karp, 1994; Bairu et al., 2011). This stigma was reinforced by agronomic disasters, such as the “mantled” floral anomaly in oil palm (*Elaeis guineensis*), where the homeotic transformation of stamens resulted in partial sterility, and the emergence of “off-type” variants in banana (*Musa* spp.) exhibiting dwarfism and deformed bunches (Israeli et al., 1991; Jaligot et al., 2000).

Today, this paradigm has shifted toward the deliberate exploitation of somaclonal variation as an adaptive genomic response to culture stress. In long-lived species such as pineapple and *Rubus*, this induced variability enables the identification of genotypes with improved resilience and biochemical profiles, thereby consolidating tissue culture as a vital tool to overcome the bottlenecks of conventional breeding (Gulzar et al., 2024; Ramos-Sánchez; Dela-Peña, 2025).

Cell Selection: Capitalizing Induced Variability

This induced variability is harnessed through cell selection, a technique that involves subjecting cell cultures to specific selective pressures that mimic environmental stress.

Biotic and Heavy Metal Stress: Pathogen culture filtrates or sublethal concentrations of heavy metals have been utilized to isolate resistant cell lines. Recent studies emphasize the use of *in vitro* cellular models to select genotypes possessing mechanisms for the exclusion or vacuolar sequestration of toxic metals such as cadmium (Cd) and lead (Pb), thereby contributing to food safety (Nik Yusoff et al., 2024).

Abiotic Stress (Salinity and Drought): The addition of osmotic agents, such as polyethylene glycol (PEG) or NaCl, to the culture medium enables the recovery of drought- and salinity-tolerant variants. These phenotypes, selected at the cellular level, frequently maintain their tolerance following the regeneration of the whole plant, validating the physiological correlation between *in vitro* and *ex vitro* performance (Turfan, 2025).

Physiological and molecular bases of SE

SE represents the ultimate expression of plant totipotency, a potential that is unlocked through dedifferentiation and extensive chromatin remodeling (Fehér, 2019; Ishiuchi; Sakamoto, 2023). Although SE morphologically recapitulates the stages of zygotic embryogenesis, phylotranscriptomic studies suggest that SE activates a primordial developmental program. In species such as the grapevine (*Vitis vinifera*), the heart stage of somatic embryos expresses the phylogenetically oldest transcriptome of the lineage (Tikhonova et al., 2024).

Table 1. SEQ Table * ARABIC 1. Documented cases of somaclonal variation-mediated induction of abiotic stress tolerance: Selection criteria and metabolic-genomic findings in diverse plant species.

Author(s)	Species	Selection Criteria or Detected Variable	Metabolic, fenotypic and Genomic Findings
Marček et al. (2018)	<i>Rubus</i> spp.	Chlorophyll fluorescence and ionic leakage	Somaclones selected under NaCl showed stabilized Photosystem II and reduced membrane damage.
Rai et al. (2011)	<i>Citrus sinensis</i>	Free proline accumulation	Cell lines showed enhanced Na ⁺ exclusion and osmoprotectant synthesis via the glutamate pathway.
Lutts et al. (1998)	<i>Oryza sativa</i>	K ⁺ /Na ⁺ selectivity ratio	Somaclones exhibited higher affinity for K ⁺ uptake, mitigating ionic toxicity in the cytoplasm.
Patade et al. (2008)	<i>Saccharum</i> spp.	Antioxidant enzyme activity (APX, CAT)	Upregulation of the ascorbate-glutathione cycle to neutralize ROS generated by salt and drought stress.
Morpurgo (1991)	<i>Solanum tuberosum</i>	Cellular osmotic adjustment	Stable tolerance to 150 mM NaCl was linked to increased intracellular solute concentration.
Cano et al. (1996)	<i>Lycopersicon esculentum</i>	Polyamine biosynthetic levels	Increased putrescine and spermidine levels served as protective agents against saline-induced protein degradation.
Wimicov (1991)	<i>Medicago sativa</i>	Alfin1 transcription factor expression	Identification of a specific somaclonal mutation leading to over-expression of genes regulating root growth under stress.
Troncoso et al. (1999)	<i>Vitis vinifera</i>	Vacuolar chloride compartmentation	Somaclonal variants demonstrated enhanced Cl ⁻ sequestration, preventing leaf tissue necrosis.
D'Onofrio et al. (2016)	<i>Fragaria x ananassa</i>	Photosynthetic pigment stability	High-temperature selection yielded somaclones with thermally stable light-harvesting complexes.
Badawy et al. (2021)	<i>Musa</i> spp.	NHX1 gene upregulation	Enhanced activity of vacuolar Na ⁺ /H ⁺ antiporters, essential for maintaining cytoplasmic ionic balance.
Ben-Hayyim (1987)	<i>Citrus aurantium</i>	Intracellular K ⁺ concentration	Confirmed that somaclonal salt tolerance is primarily a function of maintaining high potassium levels.
Rahman et al. (2018)	<i>Solanum tuberosum</i>	Stomatal density and root biomass	Selection using PEG-induced osmotic stress led to variants with optimized water-use efficiency.
Gurel et al. (2008)	<i>Beta vulgaris</i>	BADH enzyme synthesis	Increased betaine aldehyde dehydrogenase activity, crucial for the synthesis of glycine-betaine.

This genomic “reset” toward an ancestral state requires the removal of repressive marks, such as histone H3 lysine 27 trimethylation (H3K27me3), from the promoters of regenerative genes (Li et al., 2025). Recent research has demonstrated that this process is mediated by the BRAHMA (BRM) ATPase, which antagonizes Polycomb-mediated repression to facilitate the transcriptional activation necessary for embryo regeneration. This allows somatic cells to bypass the maturation constraints inherent to adult tissues (Li et al., 2025).

The stress applied during induction not only has an immediate effect on embryo formation but can also leave a lasting imprint on the regenerated plant through the phenomenon of priming or epigenetic memory (Yakovlev; Fossdal, 2017; Kvaalen; Johnsen, 2008). In conifers such as *Picea abies* and *Pinus radiata*, it has been demonstrated that stress conditions during somatic embryogenesis modulate the epigenetic machinery, altering DNA methylation patterns and small RNA (sRNA) expression (Yakovlev; Fossdal, 2017; Kvaalen; Johnsen, 2008).

These stable epigenetic changes generate “epitypes” that exhibit enhanced constitutive tolerance to future stressors, allowing somatic embryogenesis to evolve from a mere cloning technique into a sophisticated tool for adaptive breeding (Yakovlev; Fossdal, 2017). These findings validate the utility of *in vitro* culture for the epigenetic engineering of plant resilience, enabling the generation of individuals “primed” to face climate change scenarios and soil salinization without the need for exogenous gene introgression (Ramos-Sánchez; Dea-Peña, 2025).

Cellular plasticity and totipotency

Totipotency is not a constitutive state of all living plant cells but rather a potential state that must be unlocked through drastic shifts in cell fate.

This process begins with dedifferentiation, in which specialized cells lose their tissue identity and re-enter the cell cycle, where they acquire a state of “competence” or transient pluripotency. This phase requires extensive chromatin remodeling to silence tissue-specific genes and activate proliferation genes. Under specific inductive stimuli (generally auxins), redifferentiation subsequently occurs, where competent cells execute the embryonic developmental program (Fehér, 2019). Recent studies suggest that regeneration involves epigenetic reprogramming that restores an “open” chromatin state, similar to that of meristematic cells (Li et al., 2025).

Differences between Zygotic and Somatic Embryogenesis

Although SEs morphologically recapitulate the stages of zygotic embryogenesis (ZE)—globular, heart, and torpedo—there are significant molecular differences. Physiologically, somatic embryos often

lack the natural desiccation and dormancy phase and may exhibit anomalies in nutrient reserve accumulation (Méndez-Hernández et al., 2019).

From an evolutionary perspective, a striking finding from phylotranscriptomics in *Vitis vinifera* revealed that, while ZE follows an “hourglass model” (where the mid-embryonic stage is the most evolutionarily conserved), SE presents the phylogenetically oldest transcriptome during its “heart” stage. These findings suggest that SE may represent a more “ancestral” or primordial developmental program than sexual embryogenesis does (Tikhonova et al., 2024).

TRANSCRIPTIONAL REPROGRAMMING MECHANISMS

The conversion of a somatic cell into an embryo is governed by a hierarchical network of master transcription factors (TFs) that orchestrates a complete overhaul of the cellular transcriptome.

Expression of Master Genes in Induction: WUSCHEL (WUS), BABY BOOM (BBM), and LEAFY COTYLEDON (LEC)

Ectopic overexpression of BABY BOOM (BBM), an AP2/ERF family transcription factor, is sufficient to trigger spontaneous somatic embryogenesis (SE). BBM functions by directly activating the LAFL gene network (*LEC1*, *ABI3*, *FUS3*, and *LEC2*), which is responsible for embryonic identity and maturation (Horstman et al., 2017).

In parallel, WUSCHEL (WUS), a homeobox gene, is critical for maintaining the stem cell niche during initial division and promoting vegetative-to-embryonic transition. Recently, the coexpression of *BBM* and *WUS* has been used to overcome biological recalcitrance in the genetic transformation of cereals such as maize (*Zea mays*). This synergy induces a robust embryogenic response in tissues that typically fail to regenerate under standard conditions (Wu et al., 2025).

Role of the Somatic Embryogenesis Receptor Kinase (SERK) Complex

Embryogenic competence is molecularly marked by the expression of the *SERK1* gene. The *SERK1* protein is a leucine-rich repeat receptor-like kinase (LRR-RLK) that functions as a versatile coreceptor. It forms heterodimeric complexes with the brassinosteroid receptor *BRI1* and other receptors involved in stress and developmental signaling (Albrecht et al., 2008).

Signaling through the SERK complex integrates hormonal and environmental stimuli, acting as a molecular hub. This signaling center is indispensable for the acquisition of the morphogenetic capacity required for embryo formation by somatic cells (Fontes, 2024).

The reprogramming of the transcriptome during SE depends on chromatin remodeling, which allows the transcriptional machinery to access “locked” totipotency genes.

A key mechanism involves the removal of the repressive H3K27me3 mark (trimethylation of histone H3 at lysine 27) from the promoters of regenerative genes. This process is mediated by the ATP-dependent SWI/SNF chromatin-remodeling complex, specifically by the BRAHMA (BRM) ATPase. Recent investigations in *Arabidopsis* have shown that BRM antagonizes polycomb-mediated repression, facilitating the erasure of H3K27me3 and enabling the transcriptional activation of genes necessary for both shoot and embryo regeneration (Li et al., 2025).

In addition to histone modifications, DNA methylation acts as a stable epigenetic lock that maintains differentiation. The transition toward SEs requires global DNA hypomethylation. In studies of *Coffea canephora* and *Medicago truncatula*, the application of demethylating agents such as 5-azacytidine induced the expression of *LEC1* and *BBM*, promoting embryo formation. These findings demonstrate that a reduction in DNA methylation is a functional prerequisite for unlocking the embryonic genetic program in somatic cells (Nic-Can et al., 2013; Orłowska; Kępczyńska, 2020).

Methodology: Factors Regulating Induction (Herbaceous vs. Woody Species): The Role of Stress as a Developmental Switch

The technical foundation of plant biotechnology rests on the ability to regenerate whole plants from *in vitro*-selected somatic cells. However, the efficiency of these technologies is intrinsically tied to the ability of the plant cell to revert to its differentiated state—a phenomenon that is frequently hindered by biological recalcitrance, particularly in long-cycle woody species.

Contemporary understanding has shifted from a focus solely on hormonal balance to a paradigm in which abiotic stress acts as the master developmental switch. In this context, physical and chemical stress signals, mediated by reactive oxygen species (ROS) such as H₂O₂ and O₂, unlock cellular plasticity. This mechanism contrasts the fluid developmental dynamics of herbaceous models with the complex physiological barriers found in woody species (Fehér, 2015; Guan et al., 2016).

Genotypic Determinants and the Maturation Barrier in Woody Species

The induction of somatic embryogenesis (SE) is a multifactorial process in which the genotype of the explant determines the threshold for responding to inductive signals. In herbaceous model species, such as *Arabidopsis thaliana* or *Brassica napus*, there is broad regenerative plasticity that allows the reprogramming of various types of somatic tissue, even at advanced stages of development. In contrast, woody species—including fruit trees and economically vital forest species such as conifers—exhibit strict genotypic dependence and a rapid loss of embryogenic competence with age, a phenomenon known as phase maturation or cyclophilins.

This biological constraint forces breeders to work almost exclusively with juvenile material, such as immature zygotic embryos. Consequently, the ability to clone and improve elite adult trees that have already demonstrated superior field performance is severely limited. Recalcitrance in woody plants is not merely a failure of culture techniques but also a reflection of a repressive epigenetic architecture and robust cellular stability that evolved to support the longevity of the organism. Therefore, compared with their herbaceous counterparts, dedifferentiation in these species requires much more precise and often aggressive stress stimuli (Isah, 2016; Bonga et al., 2010).

Stress as a Primary Signal: Mechanics of Cellular Reprogramming

The transition from a somatic cell to an embryogenic cell requires a violent disruption of cellular homeostasis to force the abandonment of the current gene expression program.

1. Wounding Stress

Mechanical wounding represents the primary and universal inductive stimulus. The physical damage inflicted during explant preparation triggers instantaneous changes in turgor pressure gradients and systemic ion fluxes, most notably calcium (Ca^{2+}) waves that propagate through the tissue.

In herbaceous species, this signaling rapidly activates key transcription factors, such as *WOUND INDUCED DEDIFFERENTIATION 1 (WIND1)*, which coordinates healing and promotes the dedifferentiation required for callus formation and subsequent regeneration. In woody species, the activation of these regenerative pathways often involves direct competition with conserved defense mechanisms, such as rapid lignification and phenolic compound synthesis. While these responses seal the wound to prevent infection, they paradoxically block the cell proliferation necessary for embryogenesis (Iwase et al., 2011; Isah, 2016).

2. Osmotic Stress and Nutrient Starvation

Osmotic stress and nutrient deprivation act as potent inducers by simulating adverse environmental conditions. Plasmolysis induced by high concentrations of osmotic agents—such as sucrose or polyethylene glycol (PEG)—causes protoplast retraction and the rupture of plasmodesmata (intercellular connections).

This physiological isolation is considered a fundamental prerequisite for the cell to “forget” its original tissue function and acquire the autonomy needed to initiate a new embryogenic program. In microspore systems (e.g., tobacco or barley), sugar and nitrogen starvation induce autophagy, which recycles cytoplasmic components and eliminates proteins associated with the differentiated state, effectively “cleaning” the cellular environment to prepare for totipotency. In conifers, while osmotic stress is primarily used for embryo maturation, its controlled application during induction can modulate endogenous abscisic acid (ABA) levels and promote the formation of embryogenic tissue (Fehér, 2015; Stasolla; Yeung, 2003).

Thermal and Chemical Stress: Catalysts for Cellular Reprogramming

Thermal and chemical stresses are equally relevant, as they disrupt the stability of cellular structures and chromatin architecture. Thermal shock—whether induced by heat or cold—triggers the massive synthesis of heat shock proteins (HSPs) and reorganizes the cytoskeleton. This structural reorganization can reorient the plane of cell division toward an embryogenic pathway, a phenomenon clearly observed during androgenesis in *Brassica* species.

Furthermore, chemical agents such as colchicine, often used in *Vaccinium* breeding to induce polyploidy, act as severe stressors. At sublethal doses, colchicine drastically reprogrammed the cell cycle by disrupting microtubule polymerization. Similarly, the application of high concentrations of synthetic auxins, such as 2,4-D, should not be interpreted merely as a form of hormonal supplementation. Instead, it constitutes a chemical stress (“auxinic shock”) that alters DNA methylation patterns and disrupts endogenous auxin homeostasis, thereby unlocking the expression of master embryogenesis genes such as *WUSCHEL* (*WUS*) and *BABY BOOM* (*BBM*) (Seguí-Simarro, 2010; Hernández et al., 2024).

Reactive oxygen species (ROS) signaling and the “oxidative window”

At the molecular core of the stress response lies the generation of reactive oxygen species (ROS). These molecules are no longer viewed solely as toxic metabolic byproducts but are recognized as essential second messengers in developmental signal transduction.

The successful induction of somatic embryogenesis depends on the existence of a critical “oxidative window”: a specific concentration range of ROS—particularly hydrogen peroxide (H_2O_2) needed to modify the redox state of transcription factors and activate the embryogenic gene cascade. While basal ROS levels maintain quiescence or a normal cell cycle, a transient and controlled increase acts as a reprogramming signal.

ROS interact closely with hormone signaling, modulating polar auxin transport and the stability of transcriptional regulators. This interaction creates the morphogenetic gradients necessary for the formation of the new embryo. However, if ROS production exceeds the capacity of cellular antioxidant systems, the signaling threshold is bypassed, leading to lethal oxidative stress, macromolecular damage, and programmed cell death (PCD) (Zhou et al., 2016; Bailly et al., 2008).

Epigenetic Memory: A Bridge toward Climate Adaptation

It is critical to emphasize that the stress applied during induction does not merely have an immediate effect on embryo formation; it can leave a lasting “imprint” on the regenerated plant—a phenomenon with profound implications for the improvement of forest cultivars. In conifers such as Norway spruce (*Picea abies*) and Radiata pine (*Pinus radiata*), temperature and stress conditions during

somatic embryogenesis modulate the epigenetic machinery, altering DNA methylation patterns and the expression of small RNAs (sRNAs).

These stable epigenetic changes generate “epitypes” that exhibit adapted phenologies and enhanced constitutive tolerance to future stressors, a process known as priming or epigenetic memory. These findings increase the use of somatic embryogenesis from a mere cloning technique to a sophisticated tool for adaptive breeding, enabling the generation of trees "primed" to address climate change scenarios. These findings validate the importance of *in vitro* culture not only for genetic selection but also for the epigenetic engineering of plant resilience (Yakovlev; Fossdal, 2017; Kvaalen; Johnsen, 2008).

MECHANISM OF PLANT GROWTH REGULATORS (PGRS)

Auxins: Mechanism of action of 2,4-D, picloram, and Dicamba

The use of synthetic auxins such as 2,4-dichlorophenoxyacetic acid (2,4-D), picloram, and Dicamba is fundamental for inducing cellular dedifferentiation through an “auxinic shock” that reprograms the transcriptome toward totipotency.

At the molecular level, these auxins saturate the receptors of the TIR1/AFB family, triggering the ubiquitination and subsequent degradation of Aux/IAA repressor proteins via the 26S proteasome. Once these repressors are removed, auxin response factors (ARFs) are free to dimerize and activate the expression of master embryogenesis genes, such as *WUSCHEL* (*WUS*) and *BABY BOOM* (*BBM*). Furthermore, these supraphysiological concentrations strongly interfere with polar auxin transport by delocalizing PIN efflux carrier proteins, which disrupts endogenous indole-3-acetic acid (IAA) gradients and forces the establishment of new cellular organizing centers necessary for somatic embryo polarity (Fehér, 2015; Horstman et al., 2017; Seguí-Simarro, 2010; Wu et al., 2025).

Cytokinins: The Importance of TDZ and the SERK Complex

The induction of embryogenic competence depends critically on the auxin/cytokinin ratio, which dictates the transition from a somatic cell to a proembryogenic state. In recalcitrant species, the use of thidiazuron (TDZ) is important because it uniquely inhibits the enzyme cytokinin oxidase (CKX). This inhibition results in a massive accumulation of endogenous cytokinins that are difficult to degrade.

Biochemically, TDZ acts as a potent inductor that facilitates the formation of the SERK1 (Somatic Embryogenesis Receptor Kinase 1) complex. This receptor kinase functions as an indispensable signaling “hub”, allowing somatic cells to acquire morphogenetic competence and execute the embryonic developmental program under stress conditions (Albrecht et al., 2008; Fontes, 2024; Isah, 2016).

The practical application of transcriptional reprogramming concepts is clearly illustrated by the response of blackberry (*Rubus* spp.) anther cultures. Initially, the application of the synthetic auxin 2,4-D induced an “auxinic shock” that promoted massive cellular dedifferentiation; however, in this specific system, the stimulus resulted in spherical, hardened, and vacuolated cells (hollow cells) lacking organized embryonic identity (Figure 2A). In this state, the repressive H3K27me3 marks likely remained prevalent at regenerative loci, preventing the hierarchical activation of master genes and maintaining a state of robust biological recalcitrance where the tissue exhibited a total dependency on exogenous auxins, leading directly to necrosis upon their removal (Chen et al., 2024; Fehér, 2015; Liu et al., 2023; Seguí-Simarro, 2010).

This breakthrough was achieved by substituting 2,4-D with thidiazuron (TDZ) at 1 mg/L for 15 days in MS medium supplemented with 400 mg/L L-glutamine. As shown in Figure 2B, this transition triggered the emergence of organized, chlorophyllous exophytic structures ("green bumps"), marking the transition toward proembryogenic mass formation. This shift is consistent with the role of TDZ as a powerful inducer of morphogenic regulators capable of bypassing the metabolic bottlenecks of conventional auxins in woody species, while L-glutamine acts as a critical signaling molecule, providing the organic nitrogen necessary to stabilize cellular metabolism and enhance embryo quality (Aliu et al., 2024; Ara et al., 2020; Jiang et al., 2024).

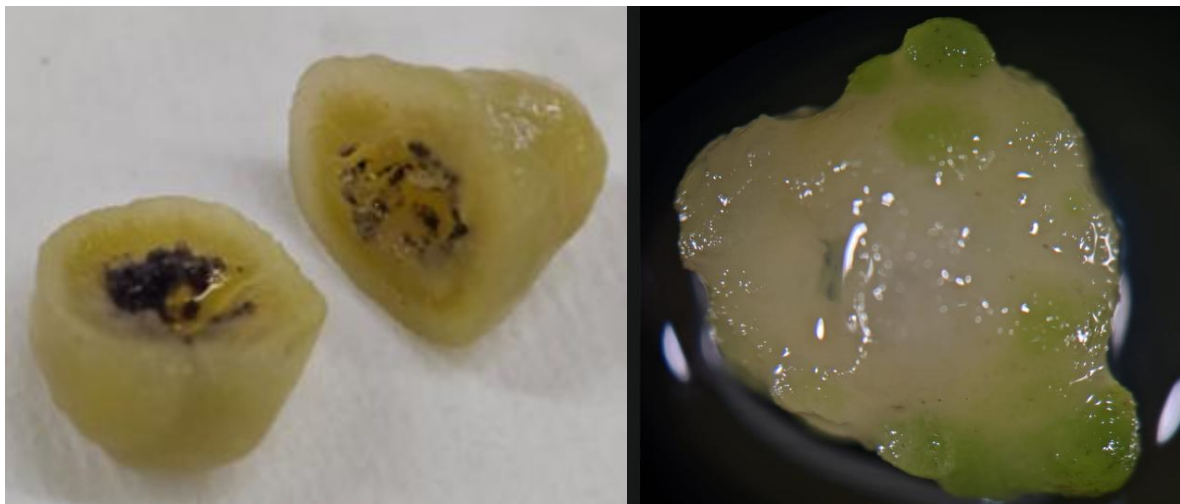


Figure 1. Morphogenetic evolution of blackberry (*Rubus* spp.) anther cultures in suspension. Cellular morphology after prolonged 2,4-D 1 mg/L treatment: round, hardened, and vacuolated cells with no regenerative capacity. (B) Induction of morphogenetic competence after shock with 1 mg/L TDZ and L-glutamine, resulting in the formation of green proembryogenic centers.

Biochemically, the effectiveness of TDZ is attributed to the inhibition of cytokinin oxidase (CKX) activity and the facilitation of the SERK1 complex. This receptor kinase functions as a signaling hub for morphogenetic competence, integrating environmental stress signals into the developmental program.

The current ability of these cultures to maintain growth in hormone-free media validates the achievement of morphogenetic autonomy, suggesting the activation of self-sustaining feedback loops in the LAFL gene network facilitated by reactive oxygen species (ROS) acting as master switches for cell fate (Albrecht et al., 2008; Fontanet-Manzaneque et al., 2024; Fontes, 2024; Horstman et al., 2017; Isah, 2016; Vandeputte et al., 2024; Wu et al., 2025; Zhu et al., 2025).

Comparative Analysis: Herbaceous vs. Woody Models

Recalcitrance in woody species, such as berries, is defined as the inability of tissues to respond to *in vitro* morphogenetic stimuli, acting as a “bottleneck” for biotechnological innovation. Unlike herbaceous models, these species possess a repressive epigenetic architecture and robust cellular stability that evolved to support prolonged life cycles, hindering cellular dedifferentiation.

A critical factor is cyclophysis or phase maturation, a process by which tissue gradually loses its embryogenic competence as the plant ages. This forces researchers to rely almost exclusively on juvenile material, such as immature zygotic embryos or anthers at early developmental stages. Additionally, extreme heterozygosity and self-incompatibility systems complicate the fixation of traits, requiring much more precise and aggressive stress stimuli to unlock the master genes of totipotency (Bonga et al., 2010; Isah, 2016; van Nocker; Gardiner, 2014).

The initial response to culture stress in woody tissues triggers a massive release of secondary metabolites, specifically phenolic compounds, which function as a long-term defense strategy. When the explant is fragmented, the rupture of cellular compartmentalization releases these phenols, which are subsequently oxidized by enzymes such as polyphenol oxidase (PPO) and peroxidase (POD) in the presence of reactive oxygen species (ROS), generating highly reactive and toxic quinones. This process manifests macroscopically as tissue browning, leading to accelerated necrosis. This effectively blocks the constructive ROS signaling required for cellular reprogramming and ultimately triggers programmed cell death (PCD) (Bailly et al., 2008; Isah, 2016; Tang et al., 2004).

To mitigate this impact, the methodology requires the integration of antioxidant strategies and strict control of physical culture conditions. The use of adsorbing agents such as activated charcoal is imperative to sequester quinones and other inhibitors before they affect the explant. Simultaneously, exogenous antioxidants such as ascorbic acid help maintain the redox environment within permissible physiological limits. Additionally, maintaining cultures in initial darkness is a standard practice to prevent the photolytic degradation of synthetic auxins and to inhibit the early synthesis of chlorophyll and other pigments, which could divert the metabolic pathway toward organogenesis rather than somatic embryogenesis (Fehér, 2015; Isah, 2016).

Metabolic Divergence: Herbaceous vs. Woody Species

The management of ROS signaling defines the fundamental difference between the high regenerative capacity of herbaceous plants and the recalcitrance of woody species.

Herbaceous Species: These plants possess dynamic and plastic antioxidant systems (e.g., SOD, CAT, and APX) that allow them to generate the oxidative “peak” required for initial signaling after stress and quickly neutralize it to preserve cell viability.

Woody species are characterized by the constitutive accumulation of secondary metabolites, particularly phenolic compounds, as a long-term defense strategy.

During stress induction in woody tissues, the rupture of cellular compartmentalization releases these phenols. In the presence of ROS, they are oxidized by enzymes such as polyphenol oxidase (PPO) and peroxidase (POD), generating highly reactive and toxic quinones. This process triggers an uncontrollable oxidative stress chain reaction that manifests macroscopically as tissue browning and necrosis.

In this scenario, the constructive signaling function of ROS is overwhelmed by chemical toxicity, effectively blocking the embryogenic pathway. Consequently, the methodology for woody species imperatively requires the use of exogenous antioxidants (e.g., ascorbic acid and citric acid) and adsorbent agents such as activated charcoal to maintain the redox environment within the physiological limits that allow for reprogramming without triggering cell death (Isah, 2016; Tang et al., 2004).

Challenges in Maturation and Conversion

Even when somatic embryo induction is successful, the conversion phase into whole plants presents significant challenges because of anomalies in the developmental program. Unlike zygotic embryogenesis, somatic embryos often lack a natural desiccation and dormancy phase, resulting in asynchronous maturation and deficient reserve accumulation. This asynchrony prevents all the embryos from simultaneously reaching the vigor necessary for germination, increasing the incidence of recalcitrant dormancy and reducing survival rates during *ex vitro* acclimatization. Therefore, optimizing embryo quality through the regulation of osmotic potential and the control of abscisic acid (ABA) levels is crucial for ensuring a successful transition toward physiological validation systems (Méndez-Hernández et al., 2019; Stasolla; Yeung, 2003).

Metabolic Divergence in Hormonal Stimulation

There is a marked metabolic dichotomy in how herbaceous and woody models process hormonal signals for regeneration. In herbaceous models (such as *Arabidopsis* or tobacco), the response is rapid and fluid because of the high sensitivity of TIR1/AFB receptors and a more “open” epigenetic architecture that allows for the immediate degradation of Aux/IAA proteins.

Conversely, woody models (such as *Rubus* or *Vaccinium*) exhibit recalcitrance linked to high oxidase activity and the presence of phenolic compounds that act as competitive inhibitors of hormonal perception. While conventional cytokinins (such as BAP or kinetin) are usually sufficient for herbaceous plants, woody species require “supercytokinins” such as thidiazuron to overcome enzymatic degradation by cytokinin oxidase (CKX) and to unlock totipotency loci that are silenced by repressive histone marks (Bonga et al., 2010; Isah, 2016).

Differences in Response Times and Nutritional Requirements

The temporal dynamics of somatic embryogenesis (SE) vary drastically between herbaceous and woody models. Herbaceous species can reach the globular stage within a few days, whereas woody species require prolonged induction periods, often under conditions of total darkness, to prevent the photolytic degradation of synthetic auxins.

From a nutritional perspective, woody species demand more complex media formulations, with a particular emphasis on organic nitrogen sources such as L-glutamine and the strict regulation of osmotic potential to prevent the premature plasmolysis of proembryogenic cells. Furthermore, in woody systems, the use of adsorbing agents such as activated charcoal is imperative to neutralize quinones generated by phenolic oxidation. These quinones directly interfere with the reactive oxygen species (ROS) signaling required for cellular reprogramming (Isah, 2016; Tang et al., 2004).

Influence of Photoperiod and Physical Culture Conditions

The physical environment of the culture acts as a modulator of the redox state and hormonal stability, simultaneously impacting embryogenesis and the emergence of somaclonal variation.

During the induction phase in woody species, the photoperiod is typically eliminated to mimic the endogenous tissue environment and prevent chlorophyll synthesis. Early chlorophyll production can divert the metabolic pathway toward organogenesis rather than somatic embryogenesis. However, once the embryos reach the torpedo or cotyledonary stage, a transition to a light photoperiod (16 h light/8 h dark) is vital:

1. Activate the photosynthetic apparatus.
2. Facilitate the accumulation of nutrient reserves.

This physical alternation is less critical in herbaceous models, which maintain greater plasticity in terms of light variation during the early stages of *in vitro* development (Fehér, 2015; Isah, 2016; Seguí-Simarro, 2010).

Agronomic Validation and the Aeroponic System as a Technological Bridge

The transition from the *in vitro* environment to final establishment is a critical juncture in plant breeding, as the stability of induced somaclonal variations must be rigorously corroborated. Although molecular techniques such as AFLP provide a genomic perspective of variability, *ex vitro* testing is indispensable to validate that these mutations translate into a real physiological advantage, such as tolerance to salinity or sodicity stress. Agronomic evaluation allows for the discarding of genetic instabilities or transient epigenetic effects that would not persist throughout the productive cycle.

In this context, the implementation of aeroponic systems with controlled LED lighting emerges as a superior verification technique compared with conventional field methods. This methodology facilitates precise evaluation by nebulizing the nutrient solution directly onto the root system, eliminating the soil's buffering effect and allowing absolute control over variables such as electrical conductivity and pH. At the metabolic level, the use of LED spectra optimizes the photosynthetic rate and pigment biosynthesis, reducing acclimation stress and accelerating the expression of key morphological traits, such as stem architecture and thorn formation.

The benefits of this technique include real-time monitoring of root kinetics, maximum rhizome oxygenation, and the ability to induce controlled abiotic selection pressures without the risks of substrate contamination. This expertise in managing high-precision aeroponic systems for the validation of micropropagated plants has been successfully documented, demonstrating that the integration of aeroponics and LED light is a robust platform for obtaining genotypes with high genetic fidelity and adaptive vigor (Avila-Avila et al., 2024).

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CONCLUSIONS

The conceptual transition of somaclonal variation, from being perceived as “biological noise” to becoming an adaptive breeding tool, represents an essential paradigm shift for addressing the challenges of the Agricultural Anthropocene. These findings confirm that the success of SE depends on unlocking totipotency through extensive chromatin remodeling and the hierarchical activation of master genes such as *BBM* and *WUS*.

As critical considerations for recalcitrant woody species, the case of *Rubus* spp. demonstrates that overcoming physiological and epigenetic barriers requires specific strategies, such as the use of thidiazuron (TDZ) and the supply of organic nitrogen via L-glutamine, to transition from disorganized proliferation toward morphogenetic autonomy.

With respect to applications, leveraging priming or epigenetic memory enables the generation of “epitypes” with constitutive tolerance to abiotic stresses, particularly soil salinity, without resorting to the introgression of exogenous genes. Finally, the use of high-precision validation systems, such as aeroponics with LED lighting, acts as an indispensable technological bridge to confirm that these variations translate into real adaptive vigor under *ex vitro* conditions. This integration between cellular biotechnology and advanced cultivation systems is the most promising path to ensuring food security and resilience in the face of the global climate crisis.

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