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Review Article

Elicitation-Driven Enhancement of Bioactive Secondary Metabolites in *Aegle marmelos* (L.) Correa: Mechanisms, Methods, and Translational Prospects - A Review

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Abstract

Aegle marmelos (L.) Correa, commonly known as bael, is a multipurpose medicinal tree valued for its diverse repertoire of secondary metabolites, including alkaloids, flavonoids, coumarins, terpenoids, and phenolic compounds. These metabolites exhibit a wide range of pharmacological activities, yet their accumulation in plant is typically low and strongly influenced by environmental variability. Elicitation, the application of biotic, abiotic, physical, or nanomaterial triggers, has emerged as a promising strategy to enhance metabolite biosynthesis under controlled in vitro conditions. Recent advances demonstrate the ability of yeast extract, chitosan, microbial elicitors, salicylic acid, jasmonates, nanoparticles, and light modulation to activate defence pathways and redirect carbon flux toward specialised metabolism. Mechanistic insights highlight the roles of reactive oxygen species, MAPK cascades, and hormone crosstalk in regulating key biosynthetic genes. Emerging technologies, including bioreactor-based scale-up, nanoparticle optimisation, and controlled light-spectrum manipulation, offer new avenues for the sustainable production of bioactive compounds. Future progress will depend on integrating elicitation with omics-guided pathway discovery and bioprocess engineering to realise the commercial potential of *A. marmelos* as a renewable source of high-value natural products.

INTRODUCTION

Aegle marmelos (Rutaceae), commonly called bael or bel, is a medium-sized tree valued in traditional medicine (Ayurveda, Unani) across South and Southeast Asia. Virtually every part of the plant – including fruits, leaves, bark, and roots – contains bioactive secondary metabolites (SMs) used to treat dysentery, diabetes, inflammation, and other conditions (Sankirtha et al., 2024). The major SM classes include coumarins (e.g. imperatorin, marmesin, marmelosin), alkaloids (skimmianine, aegeline, fagarine), flavonoids, tannins and terpenoids (Kumar, 2023; Tiwari et al., 2023). For example, Fonseka and Aluthgamage (2021) list skimmianine, aegeline, lupeol, cineole, citral, eugenol, marmin, marmelosin, and others as metabolites of *Aegle marmelos* (Fonseka & Aluthgamage, 2021). These compounds exhibit antioxidant, anti-inflammatory, antibacterial, and antidiabetic activities. Despite this richness, SM yields are typically low and variable due to limited biomass and environmental factors(Erb & Kliebenstein, 2020). Biotechnological approaches, including in vitro culture and elicitation, are therefore pursued to enhance the production of these valuable metabolites (Zhao et al., 2023).

1. Major Secondary Metabolite Classes in *Aegle marmelos*

A. marmelos contains a broad spectrum of SMs (Table 1). The alkaloids include furoquinoline and phenethylamine derivatives; typical examples are skimmianine, aegeline and fagarine, which often possess anti-inflammatory and insecticidal properties (Ibrahim et al., 2018).

Table 1: Representative Secondary Metabolites in *Aegle marmelos* and Their Classes

Sec. Metabolites	Examples (Representative)	Bioactivities / Applications
Alkaloids	Aegeline, Skimmianine (furoquinoline), Fragarine, Halfordinol, Marmelide	Anti-inflammatory, antimalarial, anti-insecticidal, antioxidant (Jagetia, 2023; Monika et al., 2023).
Flavonoids	Quercetin, Rutin, Luteolin, Esculetin, Scopoletin	Antioxidant, anti-ulcer, cardioprotective, anti-inflammatory(Janarthanan et al., 2012; Kumar, 2023)
Coumarins	Marmelosin, Marmesin, Marmin, Psoralen, Scopoletin, Imperatorin, Auraptene, Xanthotoxol, Bergapten	Hepatoprotective, anti-inflammatory, antidiarrheal(Dahiya et al., 2025; Pathirana et al., 2020)
Phenolics/Tannins	Gallic acid, Ellagic acid, Tannic acid, Total polyphenols	Antioxidant, antimicrobial, antidiabetic, gastroprotective (Pynam & Dharmesh, 2018; Sharma et al., 2022)
Terpenoids & Essential Oils	Lupeol, Citral, Eugenol, Limonene, β-Sitosterol, Caryophyllene, Other monoterpenes, seselin	Anti-inflammatory, antimicrobial, antidiabetic (Kasinathan et al., 2014; Kumar, 2023)
Other Classes	Saponins, Glycosides, Fatty acids, Vitamins (e.g. β-sitosterol glucosides), Carotenoids, Sterols	Immunomodulatory, hepatoprotective, antioxidant. (Gc, 2024; Sahu et al., 2019)

Flavonoids and other phenolics (e.g. quercetin, rutin, gallic and ferulic acids) contribute antioxidant and anti-ulcer activities (Sahu et al., 2019).

Coumarins are abundant – notably marmelosin, marmin, luvangetin, umbelliferone and imperatorin – imparting characteristic medicinal qualities (e.g. hepatoprotective and anti-inflammatory effects) (Tiwari et al., 2023). Tannins and glycosides are also present. Collectively, alkaloids, flavonoids, coumarins and terpenoids in bael underpin its pharmacological effects. For example, marmelide and marmin (coumarins) are under investigation for anti-cancer activity, while lupeol and eugenol contribute to anti-inflammatory efficacy (Akhouri et al., 2020).

These classes form the core of *A. marmelos'* phytochemical profile. The medicinal uses of bael derive primarily from these SMs. For instance, the coumarin marmelosin (7-geranyloxycoumarin) has demonstrated cytotoxic activity in vitro, and lupeol and eugenol are recognised as anti-inflammatory agents (Jagetia, 2023; Monika et al., 2023).

1.2. Elicitors: Types and Effects on *A. marmelos* SM Production

Elicitors are biotic or abiotic agents that trigger plant defence responses and thus upregulate SM biosynthesis (Moreno-Perez et al., 2020; Selwal et al., 2025). Biotic elicitors encompass microbial or plant-derived molecules, including yeast extract, fungal or bacterial cell wall fragments (e.g., chitin, peptidoglycan), polysaccharides, proteins, and glycoproteins from pathogens or symbionts (Humbal & Pathak, 2023; Kumar et al., 2017). For instance, **chitosan**, a deacetylated derivative of chitin, is widely recognised as a fungal elicitor in plant tissue cultures. It mimics a pathogen attack, inducing defence proteins and the accumulation of pathogenesis-related secondary metabolites (Chowdhury et al., 2025; Kim et al., 2023). Moreover, chitosan activates signal transduction cascades that trigger the production of phytoalexins, secondary metabolism, and antioxidant defence pathways (Mukarram et al., 2023). Treatment of plant cultures with **microbial filtrates** also enhances the production of metabolites. Endophytic fungal filtrates, such as those from *Fusarium solani*, have been reported to significantly increase alkaloid content, including vinblastine, in *Catharanthus roseus* suspension cultures (Morán-Diez et al., 2021). Classic studies demonstrated that fungal elicitors stimulate terpenoid indole alkaloid (TIA) pathways in *C. roseus*; Zhao et al. (2001) showed that fungal extracts rapidly increased the production of ajmalicine and catharanthine (Zhao et al., 2001). More recently, Liang et al. (2018) reported that an elicitor derived from *Aspergillus flavus* increased vindoline, catharanthine, and ajmaline up to 3.29-fold in cambial meristematic cell cultures of *C. roseus* (Liang et al., 2018). Similarly, **bacterial elicitors** are potent inducers of plant secondary metabolism. Plant growth-promoting rhizobacteria (PGPR) such as *Bacillus*, *Pseudomonas*, and *Azospirillum* secrete elicitor molecules that activate phenylpropanoid pathways and stimulate the biosynthesis of flavonoids, phenolic acids, and alkaloids in several crops (Pecher et al., 2020; Rocha & Vivas, 2020). PGPR elicit induced systemic resistance (ISR), which strengthens plant cell walls and promotes the accumulation of phenolics (Prsic & Ongena, 2020). Notably, PGPR treatments have been shown to increase phenolic content by 9–200%, with corresponding improvements in antioxidant activity (Jakubowska et al., 2025).

Abiotic elicitors include chemical and physical stimuli. Canonical examples are phytohormones and their analogues—salicylic acid (SA), jasmonic acid (JA), methyl jasmonate (MeJA), ethylene, and abscisic acid (ABA)—as well as heavy-metal/salt ions, UV light, and temperature stress; these are widely used in plant cell/organ cultures to stimulate secondary metabolism (Ramirez-Estrada et al., 2016). SA and JA are central defence hormones that modulate phenylpropanoid and alkaloid pathways; in plant cultures, exogenous SA frequently elevates total phenolics while also driving PR-gene/PR-protein responses, and MeJA repeatedly enhances flavonoid and terpenoid biosynthesis across species (J. Wang et al., 2015; Woch et al., 2023; X. Zhao et al., 2024). A broad review of elicitation in plant cell factories likewise highlights MeJA, SA (and chitosan) among the most effective inducers of secondary metabolites in undifferentiated cultures (Ramirez-Estrada et al., 2016). Nanoparticle elicitors (e.g., Ag, CuO, ZnO) can induce mild oxidative stress and activate defensive secondary-metabolite pathways; this trend is documented in multiple reviews and case studies (Rivero-Montejo et al., 2021; Rohela et al., 2024). For example, silver nanoparticles (AgNPs) applied to *Caralluma tuberculata* callus significantly increased biomass and antioxidant secondary metabolites (A. Ali et al., 2019a). *In vitro*, ZnO nanoparticles boosted medicinal metabolite production in *Nigella sativa* cell cultures, and nanoparticle treatments have also increased secondary-metabolite outputs (e.g., essential oils, phenolics) in *Salvia* species cultures (Ambreen et al., 2024; El-Mahrouk et al., 2024; Ridha Obayes & Fadhil Naji, 2020). Physical elicitors such as UV radiation and temperature shocks also trigger SM pathways. Notably, moderate UV-B irradiation elevates flavonoid biosynthesis in leafy vegetables, and UV exposure influences coumarin accumulation in guaco (*Mikania glomerata*) (Hao et al., 2022). Biotic and abiotic elicitors tend to produce similar downstream effects (reactive oxygen species burst, Ca^{2+} influx, MAP kinase cascades) but differ in their initial perception (Mubeen et al., 2025). Table 2 summarises common elicitor types, examples, and reported effects on SMs in plant cultures (drawn from analogous medicinal plants, as specific studies on *A. marmelos* are limited).

1.3. Signalling Mechanisms Underlying Elicitation

Elicitors trigger a cascade of signalling events that culminate in the activation of secondary-metabolite (SM) genes. Perception typically begins at the plasma membrane, where pattern-recognition receptors (PRRs) or specific hormone receptors bind the elicitor molecule. This binding rapidly initiates downstream signals—including calcium influx, an oxidative burst of reactive oxygen species (ROS), and mitogen-activated protein kinase (MAPK) phosphorylation—which propagate the defence signal (Atanasov et al., 2021; Stapleton et al., 2018).

Pathogen-derived elicitors commonly induce an immediate Ca^{2+} spike followed by an apoplastic burst of superoxide (O_2^-) and hydrogen peroxide (H_2O_2) (Biswas et al., 2023; Samota et al., 2017; Zielińska et al., 2010). These early ionic and redox events activate stress-responsive transcription factors that regulate genes involved in metabolism and defence (Samota et al., 2017). As illustrated in Figure 2, this generalised signal-transduction scheme connects elicitor perception to secondary metabolism. In particular, elicitors frequently upregulate phenylpropanoid pathway genes such as *phenylalanine ammonia-lyase* (PAL) and *chalcone synthase* (CHS) within hours of treatment, leading to the accumulation of flavonoids and other phenolic compounds (Udawat et al., 2017; Wang et al., 2025).

Table 2: Elicitor types, examples, and reported effects on secondary metabolism (from various medicinal plant studies)

Elicitor Type	Examples	Effects on Secondary Metabolites (SMs)	Proposed Mechanism	Representative References
Biotic (Microbial)	Yeast extract; Fungal filtrate (e.g. *Fusarium* broth); Chitosan	Phytoalexins (isoflavonoids), phenolics, alkaloids	Mimics pathogen attack; binds PRRs, triggers ROS burst & defence gene expression	Chitosan induces SMs via defence pathways (Mukarram et al., 2023); Fungal filtrates stimulate alkaloids in *Catharanthus roseus* (Morán-Diez et al., 2021; Zhao et al., 2001)
Biotic (PGPR)	*Bacillus, Pseudomonas* (rhizobacteria)	Alkaloids, flavonoids (e.g., in legumes, soybeans)	Induces ISR signals; JA/SA hormone crosstalk activates key biosynthetic enzymes	PGPR triggers phenolic and flavonoid accumulation (Jakubowska et al., 2025; Pršić & Ongena, 2020)
Abiotic (Hormones)	Salicylic acid (SA); Methyl jasmonate (MeJA); Abscisic acid (ABA)	Phenolics/flavonoids (SA); Terpenoids/alkaloids (MeJA)	Hormone signalling (SA→NPR1; JA→MYC2) upregulates defence genes and enzyme transcripts	SA and JA roles in SM pathways (Mendoza et al., 2018)
Abiotic (Physical)	UV-B light; Wounding; Cold or heat shock	Coumarins, phenolics, anthocyanins	Stress-induced ROS and UV-specific receptors (UVR8) activate phenylpropanoid pathway genes.	UV-B increases flavonoids (Hao et al., 2022)
Abiotic (Nanomaterial)	Ag, ZnO, or CuO nanoparticles	Total phenolics, flavonoids, terpenoids	Nanoparticle stress (ROS generation, ion release) triggers defence responses and SM gene upregulation	AgNPs increased metabolites in *Caralluma tuberculata* (A. Ali et al., 2019b); ZnO NPs boosted metabolites in *Nigella sativ*a (Ambreen et al., 2024); ZnO/SiO_2 NPs enhanced *Salvia officinalis* oils (El-Mahrouk et al., 2024)

Note: SM = secondary metabolite; PRRs = pattern recognition receptors; ISR = induced systemic resistance.

The salicylic acid (SA) pathway, mediated via NPR1/TGA transcription factors, primarily induces pathogenesis-related proteins and phenolic compounds (Caarls et al., 2015). By contrast, jasmonic acid (JA)/ethylene signalling, mediated via JAZ repressors and MYC2 transcription factors, enhances the expression of biosynthetic genes for alkaloids and terpenoids (Zhao et al., 2024). Crosstalk between SA- and JA-dependent pathways fine-tunes defence responses, enabling plants to distinguish between biotrophic and necrotrophic pathogen attacks (Caarls et al., 2015; Wang et al., 2022). Moreover, abiotic elicitors such as UV radiation and heavy metals act essentially through ROS and MAPK cascades, activating broad-spectrum antioxidant defences (Biswas et al., 2022;

Wang et al., 2025). Downstream of these early events, the hormonal network coordinates the transcriptional response. Typically, biotrophic elicitors activate the SA-dependent route, whereas herbivore or necrotrophic elicitors engage the JA/ethylene-dependent route (Caarls et al., 2015; Kolanchi et al., 2025). This hormonal interplay modulates the diversity of secondary metabolites produced. For instance, SA signalling via NPR1 promotes the biosynthesis of phenolic compounds and PR proteins, while JA signalling via MYC2 (following release from JAZ repression) upregulates the biosynthesis of alkaloids and terpenes (Kaya et al., 2023; Moreno-Perez et al., 2020). Physical elicitors, such as UV-B, act through ROS bursts and photoreceptors like UVR8, broadly activating phenylpropanoid and antioxidant pathways (Chen et al., 2022; Erb & Kliebenstein, 2020).

1.4. Recent Trends and Experimental Evidence

Over the past decade, numerous studies have demonstrated elicitation effects in various medicinal plants using cell, tissue, or hairy root cultures. While direct reports on *Aegle marmelos* are limited, analogies from other species are highly informative. For example, *Catharanthus roseus* cell cultures treated with fungal extracts showed significant increases in indole alkaloid production (Zhao et al., 2001). Similarly, methyl jasmonate (MeJA) elicitation has been shown to enhance taxane (e.g., paclitaxel) accumulation—up to 15-fold—in *Taxus* cell cultures (Kolewe, 2011). In another case, treatments with salicylic acid (SA) or chitosan in medicinal herbs, such as *Ocimum basilicum*, increased total phenolic and flavonoid levels (Kim et al., 2005; Qazizadah et al., 2021). Nanoparticles are also emerging as elicitors: for instance, ZnO nanoparticles significantly enhanced antioxidant activity in *Nigella sativa* cell cultures (Ambreen et al., 2024), and green-synthesised ZnO NPs exhibited strong radical scavenging capacity, reflecting enhanced phenolic/antioxidant content (Alhujaily et al., 2022)

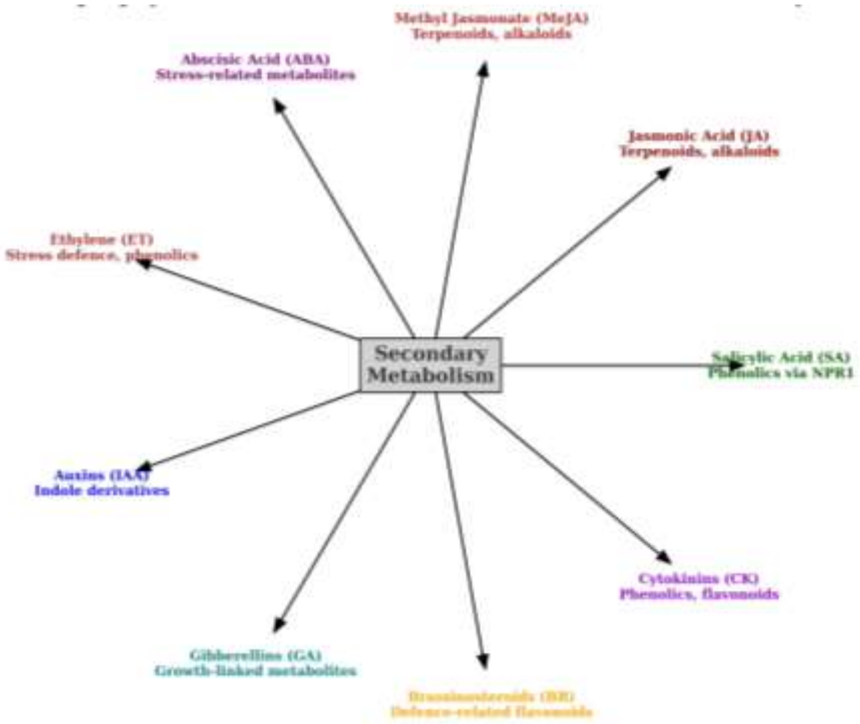

Figure 1: Major phytohormones present in plants that can function as elicitors of secondary metabolism. (These include salicylic acid (SA), jasmonic acid (JA) and methyl jasmonate (MeJA), abscisic acid (ABA), ethylene (ET), auxins (IAA), gibberellins (GA), brassinosteroids (BR), and cytokinins. Each can trigger specific signalling cascades (e.g. SA often induces phenolic phytoalexins via NPR1; JA induces terpenoids and alkaloids via JAZ/MYC transcription factors).

Figure 1 demonstrates some key hormone-type elicitors (SA, JA, etc.) that act as defence signals. In practice, **elicitor studies in *Aegle marmelos*** remain scarce, and most mechanistic insights are inferred from related medicinal plants.

Nevertheless, similar strategies can be proposed. For instance, treating cell or organ cultures with **yeast extract or fungal β-glucan** is known to enhance phenolic and coumarin biosynthesis in various species, and could plausibly stimulate comparable pathways in *A. marmelos* (Morán-Diez et al., 2021; J. Zhao et al., 2001). The application of methyl jasmonate (MeJA) has been repeatedly shown to promote the accumulation of alkaloids and terpenoids (essential oils) in plant suspension cultures (Toppo et al., 2023; Złotek et al., 2020).

Likewise, exogenous treatment of intact plants with **salicylic acid (SA)** or **JA analogues** often elevates soluble phenolics, flavonoids, and defence-related enzymes, confirming their broad role as secondary-metabolism elicitors (Mendoza et al., 2018).

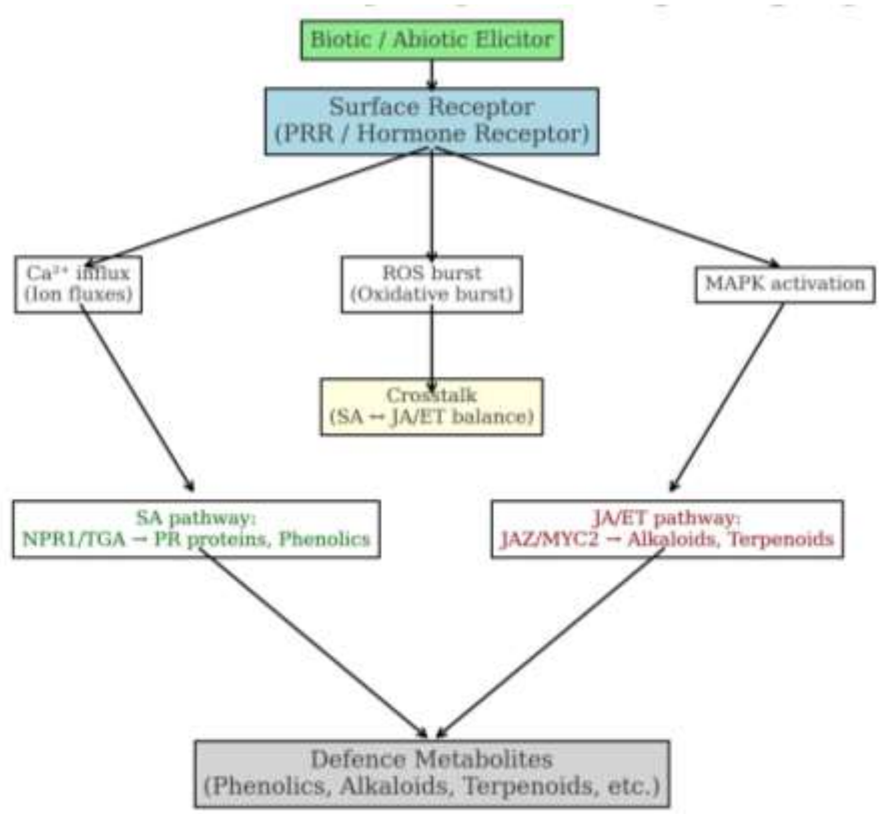

Figure 2. Schematic representation of elicitor perception and signalling in plant cells. (Binding of a biotic or abiotic elicitor to a surface receptor (e.g., PRR or hormone receptor) triggers a signal cascade: **ion fluxes (Ca^{2+} influx), ROS burst, and MAPK activation**. These early events activate transcription factors that induce **biosynthetic enzyme genes** for defence metabolites. **SA signalling** (via NPR1/TGA) upregulates PR proteins and phenolics, whereas **JA/ethylene signalling** (via JAZ–MYC2) promotes alkaloid and terpenoid biosynthesis. **Pathway crosstalk** enables plants to optimise secondary metabolism depending on the type of stress. **Abiotic stressors**, such as UV radiation or heavy metals, primarily signal through ROS/MAPKs, thereby enhancing the production of antioxidant metabolites).

For *Aegle marmelos* itself, one recent study by Fonseka & Aluthgamage (2021) developed a **high-yielding callus culture protocol**, laying the groundwork for future elicitation experiments (Fonseka & Aluthgamage, 2021). Additionally, **ethnobotanical observations** suggest that stressed bael trees—for example, those undergoing **drought or mechanical injury**—often exhibit elevated levels of secondary metabolites, implying inducible in-plant defence pathways (Choudhary et al., 2021; Singh et al., 2019). Future research could systematically elicit *A. marmelos* callus or organ cultures with candidate agents such as **MeJA, yeast polysaccharides, or heavy metal salts**, followed by **metabolite profiling** using HPLC or LC–MS. Comparative **transcriptomics under elicitation** would be especially illuminating, as upregulation of specific SM pathway genes (as demonstrated in other medicinal plants) would confirm pathway activation in bael and provide molecular targets for metabolic engineering.

1.5. Future Directions and Applied Perspectives

1.5.1. Bioreactor-Based Scalable Elicitation Strategies

To translate laboratory-based elicitation to industry, scalable culture systems are essential. Bioreactors offer controlled, high-volume platforms for eliciting and harvesting SMs. Modern designs, such as stirred-tank reactors, airlift reactors, and temporary immersion systems (TIS), enable large-scale in vitro cultivation with uniform exposure to elicitors. *Temporary immersion bioreactors*, such as the Plantform TIS, have shown particular promise. Shoot cultures of Centella asiatica grown in Plantform TIS and treated with MeJA accumulated significantly higher levels of centellosides and phenolic compounds compared to static cultures. Similarly, TIS systems improved the yields of lignans in *Schisandra chinensis* and flavonoids in *Scutellaria lateriflora*, demonstrating the scalability of elicitation approaches (De Carlo et al., 2021; Skrzypczak-Pietraszek et al., 2019).

In addition to immersion systems, fed-batch cultivation with repeated elicitation is a promising strategy. In *Taxus chinensis* cell cultures, fed-batch supplementation of sucrose and a potent jasmonate analogue (DHPJA) through two sequential additions increased taxoid yield to 827 mg/L approximately 5.4-fold higher than batch controls. This process, when transferred from shake flasks to a 1-L airlift bioreactor, achieved substantially elevated volumetric productivity (Qian et al., 2005).

Another advanced strategy is in situ product removal (ISPR) during the elicitation process. Accumulating SMs can inhibit their own biosynthetic machinery or become cytotoxic. In *Tripterygium* root cultures, the addition of an adsorbent resin (Amberlite XAD-7) during MeJA elicitation protected secreted alkaloids from degradation, resulting in 3- to 50-fold increased yields. When implemented in a 10-L bubble-column bioreactor, the elicitation-plus-ISPR process achieved metabolite levels comparable to those of shake-flask controls—validating its scalability (Motolinía-Alcántara et al., 2021).

Looking ahead, integrating bioprocess intensification techniques such as fed-batch feeding, periodic elicitor addition, ISPR, or even continuous perfusion cultures will be crucial for economically scaling *Aegle marmelos* secondary metabolite production to pilot and industrial levels.

1.5.2. Nanoparticle Elicitors: Comparative Effectiveness and Considerations

Nanoparticles have emerged as a novel class of elicitors, but their effectiveness can vary depending on the material and plant system. Silver nanoparticles (AgNPs) are among the most studied; they tend to induce oxidative stress and defence responses strongly, often leading to enhanced phenolic and flavonoid accumulation. For example, AgNP treatments significantly increased total phenolics, flavonoids, and antioxidant activity in callus cultures of *Melissa officinalis* (*lemon balm*) (Coskun & Kapdan, 2025). Similar effects have been reported in *Salvia officinalis* and other medicinal herbs exposed to silver nanoparticles, where flavonoid and phenolic production rose in parallel with stronger ROS bursts (Ridha Obayes & Fadhil Naji, 2020).

In *Salvia* seedlings subjected to stress, ZnO nanoparticles (ZnONPs) elicited a sharp rise in total phenolics and flavonoids, especially when combined with salicylic acid, indicating a synergistic effect between nanoparticle elicitors and classical chemical elicitors (Alenezi et al., 2022). Other studies confirm that zinc oxide and gold (Au) nanoparticles are also capable of triggering plant defence pathways. However, AgNPs generally show the most substantial elicitation effect on ROS production and secondary metabolism (Selvakesavan et al., 2023). Comparative reports demonstrate that metal oxide nanoparticles (ZnO, CuO) can upregulate antioxidant enzymes and metabolites; however, their effects are typically not as dramatic as those of AgNPs at equivalent concentrations (Coskun & Kapdan, 2025).

It is important to note that the dose and exposure duration of nanoparticle elicitors are critical. Low-to-moderate NP concentrations can boost SM biosynthesis by provoking a mild stress response, whereas higher concentrations become phytotoxic. Prolonged exposure can inhibit culture growth or even cause genetic and cytological damage. For instance, *Vanilla planifolia* cultures continuously exposed to Argovit™ silver nanoparticles over multiple subcultures exhibited cytotoxic and genotoxic effects (DNA polymorphisms, chromosomal abnormalities), even though secondary metabolite levels initially rose (Bello-Bello et al., 2018). This highlights the need to optimise NP elicitor regimens in terms of dose and timing to avoid deleterious effects.

Future research should comparatively evaluate different nanoparticle types (Ag, ZnO, CuO, Au, silica, etc.) in *Aegle marmelos* cultures—not only for their efficacy in boosting specific SMs, but also for potential toxicity or metabolic imbalances. Nanoparticle engineering strategies, such as surface-functionalised nanoparticles or slow-release nanocomposites, may allow more controlled elicitation with reduced toxicity. Nanoparticles, therefore, represent a cutting-edge tool to elicit otherwise “hard-to-induce” compounds, but their application must be carefully calibrated to balance stress and culture viability.

1.5.3. Physical Elicitation via Light Spectrum Modulation

Light is a fundamental environmental signal that functions effectively as a physical elicitor. Advances in LED technology now enable the exposure of plant cultures to specific light wavelengths and intensities, allowing for the precise modulation of secondary metabolism. **UV-B radiation (280–320 nm)** is particularly effective at triggering the production of phenolic compounds, as plants perceive UV-B as a stressor and respond by accumulating UV-absorbing secondary metabolites like flavonoids and coumarins as “sunscreens.” Low doses of UV-B applied intermittently can significantly enhance the production of phytochemicals. For instance, UV-B exposure in red cabbage sprouts resulted in substantial increases in phenolics, flavonoids, and carotenoids—up to +22% (ABTS assay) and +35% (FRAP assay) — compared to controls (Santin et al., 2022). Similarly, controlled UV-B exposure during buckwheat germination notably elevated total flavonoid content, including the flavonol rutin (Xue et al., 2024). **Blue light** (around 450 nm) is another potent elicitor—monochromatic blue LED illumination has been shown to boost phenolic and flavonoid levels in various species. Lettuce grown under continuous blue LEDs accumulated significantly higher rutin and total phenolics compared to white light controls (V. Ali et al., 2025). Blue light also helps stabilise flavonoid profiles following UV-B exposure in Brassicaceae sprouts, particularly by enhancing quercetin and kaempferol glycosides, as reported in the literature (Neugart et al., 2021). For *Aegle marmelos*, manipulating the light spectrum presents an inexpensive and "clean" elicitation method. One could envision using LED panels to deliver enriched UV-B or blue light during targeted stages of bael microshoot or callus culture growth to induce specific SM pathways—phenylpropanoids through UV-B, perhaps terpenoids via other spectra. Studies on Ruta species support this approach; for example, *Ruta graveolens* shoot cultures exposed to particular light conditions showed enhanced accumulation of coumarins and furanocoumarins (Ekiert & Gomolka, 1999; Kawka et al., 2017). Modern controlled-environment agriculture tools (like growth chambers and bioreactors equipped with customised LED lighting) allow precisely tuned control over photoperiod, wavelength, and fluence rate, thereby optimising elicitation regimens. That said, the long-term physiological effects of such light modulation must be carefully evaluated. While short bursts of UV-B can effectively induce the synthesis of secondary metabolites, chronic or high-dose UV exposure may damage DNA and photosystems, leading to growth suppression or cell death. A phased strategy—culturing under optimal light for biomass accumulation and then applying timed UV-B pulses—can mitigate these risks. For example, *Artemisia annua* plants grown under ideal conditions, and then given a UV-B pulse, produced more artemisinin with minimal growth penalty (Rai et al., 2011). Further, combining light elicitation with other stimuli may yield synergistic effects. In Brassicaceae sprouts, exposure to UV-B followed by blue or green light generated additive improvements in antioxidant metabolites (Neugart et al., 2021). Tailoring the light spectrum—using UV-B, blue, red, or combinations thereof—thus represents a highly controllable elicitor strategy for *A. marmelos*. Future experimentation should focus on optimising light quality, intensity, and exposure timing to maximise SM yields while safeguarding culture health.

1.6. Knowledge Gaps and Future Directions

Despite promising lab-scale results, several challenges remain. Elicitor responses are highly dose and time-dependent, and excessive or prolonged stress can inhibit growth or divert metabolic flux away from secondary pathways. This reflects a growth–defence trade-off where resources are redirected from growth to defence. In controlled environments, elicitor dosages are easier to manage; however, the field application of elicitors—such as foliar sprays of SA or JA on *A. marmelos* trees—has yielded inconsistent effects due to environmental variability and difficulty in sustaining consistent dosages (Délano-Frier et al., 2004; Kandoudi et al., 2022). Moreover, the molecular basis of elicitation is incompletely understood in *A. marmelos*, limiting rational design and optimisation. A reference genome or transcriptome for bael is currently lacking; such genomic resources would greatly facilitate the identification of key biosynthetic genes and regulatory transcription factors responsive to elicitors. Another challenge lies in integrating elicitation with downstream bioprocessing in a holistic production pipeline. For instance, combining elicitation with metabolic engineering—such as overexpressing elicitor-responsive genes—or optimising bioreactor conditions can substantially improve yields. On the positive side, omics technologies (genomics, transcriptomics, and metabolomics) and synthetic biology offer powerful tools. Mapping *A. marmelos* SM pathways and their regulatory networks could enable the design of precision elicitors (e.g., customised elicitor combinations or synthetic analogues targeted to activate desired pathways). Nanotechnology also introduces advanced possibilities not just for elicitor formulations, but for precision delivery—such as nano-carriers designed to target elicitors to specific tissues or cells.

Addressing these limitations and leveraging emerging technologies will be crucial for progressing elicitor-based approaches toward innovative breakthroughs in *A. marmelos* metabolite production.

Conclusions

Elicitation offers a robust "booster" for secondary metabolite production in medicinal plants. In *Aegle marmelos*, this strategy remains underexplored. Still, general principles apply: biotic agents (yeast extract, chitosan, microbial elicitors) and abiotic signals (SA, JA, UV, nanoparticles, etc.) can activate defence pathways and increase SM content. To capitalize on this, future work should focus on (1) establishing robust *A. marmelos* cell or organ culture systems amenable to elicitation; (2) systematically testing a spectrum of elicitors (and their combinations or delivery methods) on bael tissues; and (3) unravelling the signalling network (ROS bursts, hormone crosstalk, transcription factors) that drives bael SM biosynthesis under elicitation. Combined with improved cultivation techniques and perhaps metabolic engineering, elicitor-mediated enhancement could substantially boost the yield of bael's valuable natural products for pharmaceutical and nutraceutical applications.

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