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Chapter

Using Biostimulants Containing Phytohormones to Recover Hail-Damaged Essential Oil Plants

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Abstract

Hail can cause significant damage to aromatic and medicinal plants; however, this has never been investigated scientifically on most of aromatic and medicinal plants. Globally, essential oil crop producers primarily make use of agricultural crop insurance and costly mitigation strategies to recover lost production costs and alleviate hail-damaged plants. However, most aromatic and medicinal plants are not covered under agricultural crop insurance, and many commercial farmers are not able to regularly employ expensive alternative strategies. Therefore, hail damage may present a challenge to essential oil growers. The use of natural and synthetic phytohormones in a form of biostimulants, as an alternative biological mitigation strategy against hail damage in essential oil crops, has not received much attention, and there is no information on this topic. Exogenous applications of natural and synthetic biostimulants have consistently demonstrated growth enhancement, nutrient acquisition, yield and quality optimization, as well as physiological efficiency in plants. Biostimulants in a form of phytohormones are involved in diverse plant physiological processes, including the regulation of gene expression for adaptive responses to biotic and abiotic stresses. Using biostimulants, this chapter will detail the potential recovery response of aromatic and medicinal plants to hail damage, and the response of plants treated with biostimulants.

Keywords: biostimulants, phytohormones, post hail damage, recovery, secondary metabolites

1. Introduction

Prolonged droughts, increased floods and frequent extreme weather events are evidence of climate change, as a consequence of global warming [1]. Agriculture is adapting to the variability in global climatic conditions, with farmers continually developing strategies to respond to changing weather patterns [2]. Aromatic and medicinal plants are among those plants which are negatively affected by climate

change [3]. In addition, there is a concern over climate change affecting the secondary metabolites of many medicinal and aromatic plants [4]. Hailstorms are one of the most common global natural disasters [5], and temperate zones seem especially prone to hailstorm events [6]. To date, there is no recorded data for the impact of hail damage on essential oil plants; however, it was reported that hail causes substantial damage to aromatic plants [7, 8].

Changes in the secondary metabolites of essential oil plants vary depending on the type of damage incurred by the plant [9]. Hail wounding on these plants affect specific aromatic and therapeutic attributes that make these plants economically important [10]. It has also been shown that hail damage, mechanical damage, and insect herbivory cause essential oil compound changes [10]. For example, hail damage simulation through leaf puncturing resulted in reduced menthone levels and increased pulegone concentrations in muña (*Minthostachys mollis* [Kunth] Griseb.). This subsequently altered the composition of the volatiles released from the damaged leaves [9].

A common mitigation strategy for the loss in yield caused by hail damage is crop insurance [11]. Globally, crop insurance against hail damage can be purchased for most commercial plants, but not for essential oil crops [12]. Other alternative strategies include the construction of hail nets as a preventative measure against hail damage. However, this strategy is often unfeasible as the high construction and maintenance costs require more herbage material to produce sufficient essential oil to recover these costs. This, in turn, requires more land for production. Some farmers increase the application of nitrogen after hail to facilitate the formation of new leaves and buds [13]. It has been reported that increased nitrogen fertilization increases rose geranium herbage material [14]; however, the essential oil quality is reduced (based on the ISO standard) [15]. In temperate regions where hail frequencies are high, agro-meteorologists implement strategies, such as hail forecasting and cloud seeding, to reduce the extent of hail damage [11].

Hail is a natural hazard that can cause significant loss to crop yields [16]. Hailstones larger than 8.4 mm in diameter can result in defoliation, which, in turn, initiates cell division and the synthesis of cellular components [6]. Such wounding can also lead to stress that affects plant growth and metabolic activities [10]. To produce a stress-response and recover metabolic functions, plants rely on the crosstalk between phytohormones [9]. Biostimulants are also used in the agricultural industry to mitigate against these types of biotic and abiotic stresses [17].

Plants perform unique functions in plant development and stress repair, as well as improving the primary and secondary metabolite content of plants, which directly affects the essential oil biosynthesis and quality [18]. Exogenous applications of natural and synthetic biostimulants have consistently demonstrated growth enhancement, yield and quality optimization, as well as physiological efficiency in plants [19, 20]. Phytohormones are involved in diverse plant physiological processes, including the regulation of gene expression for adaptive responses to biotic and abiotic stresses [21]. Primary biostimulants include auxins, abscisic acid (ABA), cytokinins (CKs), gibberellic acids (GAs) and ethylene [22]. Secondary biostimulants include jasmonates and its analogues (methyl jasmonate, MeJA), brassinosteroids (BRs), salicylic acid, polyamines, sterols, and dehydrodiconiferyl alcohol glucosides [22]. There is currently no specific hail-mitigation strategy for most medicinal and aromatic crops, and the effects of potential hailstorm damage on essential oil and aromatic plants, as well as mitigation and control mechanisms, require further investigation by researchers.

2. Extent of defoliation, and hail damage on plants

Extreme climatic conditions can lead to significant losses in the agricultural sector [2]. These losses have drastically increased, by at least 400% from 1960 to 2005 [5, 23, 24]. Hailstorms are one of the most common global natural disasters [5], and temperate zones seem especially prone to hailstorm events [6]. The following review focusses on hailstorm as one of the natural disasters responsible for crop loss and damage.

Hail is defined as precipitation in the form of small pellets, or pieces of ice, which vary in size from 0.5 mm to 100 mm [25]. Hail can cause extensive damage to growing crops and other vegetation [26]. Hail formation takes place in elongated convective cumulonimbus clouds, which are often associated with thunderstorms [6]. Severe hail-related losses result from hailstones above H2 size [27]. Hailstones above H2 cause defoliation, tearing, bruising, breaking, and the loss of stems and flowers [26]. Such wounding can also lead to plant stress, which affects growth and metabolic activities [28]. This can further predispose plants to disease outbreaks since wounds provide an entry point for plant pathogens [28].

The extent of hail damage depends on several factors, such as the number of hailstones per unit area, wind velocity [6], and hailstone size [29]. Changnon [29] and Fernandes et al. [24], reported that hail damage differs extensively among plant species, and is influenced by several factors, such as plant height, and leaf and stem morphology. Certain plant species, e.g. soybean (*Glycine max* [L.] Merr.), tea (*Camellia sinensis* [L.] Kuntze), and tobacco (*Nicotiana tabacum* L.), are susceptible to damage by hailstones of any size (>H0), due to their leaf and stem morphology [29, 30]. In contrast, crops such as maize and wheat are mostly damaged by larger, windblown hailstones (>H3) because of their height, and differences in leaf area, the stem sizes and morphology [29, 30].

Plants also respond differently to wounding stress following hail damage. Physical wounding of plant tissue resulting from hail damage and defoliation initiates a cascade of biochemical or physiological processes, which results in the repair of damaged tissue and resistance to opportunistic pests and pathogens [31]. Such alterations occur both in the tissue immediately surrounding the wound, and in distal tissue not directly in contact with the damaged tissue [31]. At the wound site, cell division and the synthesis of cellular components that are required to isolate the damaged tissue, reduce water loss, and restore tissue integrity, is initiated [31]. In leaves, wounding also induces the synthesis and accumulation of anti-microbial compounds, and in the specific case of damage caused by herbivory, volatile metabolites are released to deter pests and attract their predators and parasitoids [31].

Hail damage hinders plant growth, and affects the yield and quality by changing the cellular metabolic processes [4]. Defoliation and wounding stress in plants results in a knock-back effect that reduces the assimilation of carbon, ultimately affecting the rate of photosynthesis [4]. This stress stimulates the production of bio-inhibitors, reactive oxygen species levels, transient Ca^{2+} influxes into the cytoplasm, and protein phosphorylation. It also causes irreversible injury to cells and tissue that eventually slows growth [32]. This has been reported in potato plants (*Solanum tuberosum* L.), where ribonucleic acid (RNA) homology changed as a result of wounding [33]. Christopher et al. [34] identified a suite of wound-regulated genes, indicating the diversity and multiplicity of the induced defense response in systemically wounded leaves of hybrid poplars (*Populus trichocarpa* × *P. deltoides*). In lettuce (*Lactuca sativa* L.), plant wounding induced the synthesis of phenylalanine ammonia-lyase compounds [35].

The local and systemic plant responses activate and regulate defense mechanisms for localized tissue damage, such as those resulting from hail damage [36]. Plants can also positively adapt with altered growth habits to contradict the damaging effects of hail [4]. Thus, the responses are both reversible and irreversible modifications, such as cell division, alterations of membrane channels, and a change in the structure of the cell wall [4]. This has been demonstrated with muña (*Minthostachys mollis* [Kunth] Griseb.), where leaf puncturing resulted in reduced menthone levels, while the pulegone concentration increased during the first 48 h of the experiment [9]. Furthermore, an increased pulegone level and diminishing menthone emissions also altered the composition of volatiles released from damaged leaves. Depending on the phytohormonal crosstalk and proteins released, wound-inducible genes may either repair damaged plant tissue or produce inhibitory system [36].

3. Biostimulants as a mitigating strategy for hail damaged essential oil plants

Phytohormones are molecules that influence the growth and development of plants, even at low concentrations. There are phytohormones which are produced naturally by plants, as well as synthetic regulators, which have been produced in biotechnology research as biostimulants [9]. Biostimulants are used in global crop production to improve field competitiveness, nutrient use efficiency, and stress resistance in plants [37]. Most biostimulants and their products are extracted from algae, arbuscular mycorrhizal fungi, chitin and chitosan derivatives, fulvic and humic acids, synthetic phytohormones, natural plant extracts and the magnetic field as a growth stimulant for plant species [37, 38]. Exogenous applications of natural and synthetic biostimulants enhance growth, increase oil yield and quality, as well as improving physiological efficiency in plants [37]. This section focuses on the use of biostimulants to recover defoliated, wounded, and hail-damaged plants.

Plant metabolic activities are regulated by phytohormones [39]. Phytohormones are produced naturally by plants and are small organic molecules which, at low endogenous concentrations (10^{-6} M to 10^{-9} M), induce metabolic activities within plant cells to modify growth and development [22]. However, synthetic chemicals, with the same properties and effects as natural phytohormones, can be produced [9]. A key research objective in plant biotechnology is to recognize the mechanism used by plants to respond to and overcome different environmental stressors [4]. Phytohormones are classified as either plant growth regulators (CK, GA, BRs, and auxins) or as bio-inhibitors (ABA, jasmonates, and salicylic acid) [20]. Phytohormones are involved in a number of diverse plant physiological processes, including the regulation of gene expression for adaptive responses to biotic and abiotic stress [21] and in wound healing [4, 17].

Primary phytohormones include auxins, ABA, CK, GA, and ethylene [40]. Other naturally occurring phytohormonal-like molecules include jasmonates, BRs, salicylic acid, polyamines, sterols, and dehydrodiconiferyl alcohol glucosides [40]. Phytohormones alter metabolic activities associated with cell division, cell enlargement, flowering, fruiting, and seed formation. Nemhauser et al. [19] found that exogenous applications of phytohormones regulate plant growth, and greatly influence plant stature and organ size. Bio-inhibitors are involved in the alleviation of biotic and abiotic stress that results from wounding, moisture stress, and temperature stress [20].

3.1 Effects of phytohormones, biostimulants and magnetic field on plant growth and development, refoliation and wounding

Phytohormones promote growth and development, the production of secondary metabolites, as well as bio-inhibition, due to the extensive crosstalk and signal integration which affects the plants physio-morphological chemistry [9]. The recovery mechanism of defoliated, wounded, and hail-damaged plants has provided the rationale for investigating the potential of phytohormone application in this chapter. The following section examines the effects of natural and synthetic ABA, jasmonates, BRs, CK and GA on plant growth and development, and changes in primary and secondary metabolite biosynthesis of essential oil plants.

3.1.1 Absciscic acid as a potential growth stimulant for refoliation and wounding recovery

Absciscic acid is a stress-signaling molecule, found to occur in all kingdoms, except Archea. The effect of foliar applications of ABA on plant growth is dependent on the plant species [41]. It is a crucial regulator of important plant processes, including resilience to abiotic stressors, such as wounding, moisture, light, drought, and temperature [42]. Absciscic acid is also involved in primary plant growth development. This includes buffering the day-night alterations of leaf growth rate, and regulating stomatal movement and transpiration rate [43]. It also improves leaf growth by increasing tissue and whole-plant hydraulic conductivity [44]. Dammann et al. [45] found that hail damage, and defoliation causes increased levels of ABA in plants, which in turn activates the biosynthesis of jasmonates.

Absciscic acid is a C₁₅ sesquiterpenoid, formed by the joining of three isoprenoid units [4, 41]. Absciscic acid occurs naturally as (S)-(+)-ABA, which is often called a *cis* isomer; a combination of 1:1 *cis* and *trans* absciscic acids, classed as isoprenoids [44]. The ABA biosynthetic pathway starts from oxidative cleavage of epoxy-carotenoids and 9-*cis* violaxanthin, where xanthoxin is converted to absciscic acid [4, 41]. The early C₅ precursor of ABA, isopentenyl pyrophosphate, is produced primarily in plastids, via 1-deoxy-D-xylulose-5-phosphate from pyruvate and glyceraldehydes-3-phosphate. This is then processed to farnesyl pyrophosphate, geranylgeranyl pyrophosphate, phytoene, carotene, and lycopene [4, 41]. Subsequently, xanthoxin migrates from the plastid to the cytosol, where it is converted to ABA by absciscic aldehyde, xanthosis acid, or absciscic alcohol; clearly, absciscic aldehyde is an intermediary in the conversion of xanthoxin to absciscic acid [4, 41].

Transportation of ABA primarily occurs through the vascular tissues of plants [46]. However, ABA responds to abiotic stress through the cells [41]; this requires translocation from ABA-producing cells, via intercellular transport, to allow rapid distribution to other plant tissue [41]. Absciscic acid is ubiquitous in plants; the endogenous levels in plant cells determine its homeostasis [4]. However, developmental and environmental factors such as light, wounding, salinity, and water stress affect ABA concentration levels [4].

Absciscic acid is sensitive to direct sunlight and high temperatures, and rapidly deteriorates under these conditions [47]. Kong and Zhao [48] found that foliar-applied ABA elevates the aroma content of aromatic rice (*Oryza sativa* L.). Foliar application of ABA on yeba mate (*Ilex paraguariensis* A.St.-Hil.) increases plant growth, by reducing water stress through stomatal closure [49]. It has also been reported that the exogenous application of ABA improves wounding tolerance in

tomatoes and potatoes, and induces jasmonate gene expression in the leaves and roots of potatoes [49]. The exogenous application of ABA should preferably be conducted during cool mornings, before sunrise and increasing temperatures.

As well as direct involvement in plant growth and development, ABA has a significant role in the regulation of environmental stress. [50] reported that there are two distinct pathways responsible for the developmental and environmental stress regulatory processes. Responses to plant wounding includes the local response at the site of the wound, and the systemic response, which occurs throughout the whole plant [36]. The foliar concentrations of ABA applied to wounded plants varies from 0.001 mM to 1.5 mM solution per plant, with the optimal application rate and concentration differing between different crop species [48, 49, 51, 52].

3.1.2 Jasmonates as a potential growth stimulant for refoliation and wounding recovery

Jasmonates and their methyl ester, MeJA, are natural-occurring growth regulators found in higher plants [53]. Jasmonates were first discovered and isolated from a culture of the fungus *Lasiodiplodia theobromae* (Pat.), while MeJA is a component of the essential oils of *Jasminum grandiflorum* (L.) and *Rosmanus officinalis* (L.) [53]. Cyclopentanone-derived jasmonates are widespread in plants [54], while MeJA, and jasmonic acid and its hydroxylated derivatives are commonly used jasmonates for agricultural purposes. In plants, cis-jasmone, jasmonyl-1-aminocyclopropane-1 carboxylic acid, and jasmonoyl isoleucine are also known to act as analogues of jasmonates [54].

Jasmonates are present throughout the plant body, with the highest concentration in growing tissues such as shoot tips, root tips, immature fruits, and young leaves [54]. Jasmonate biosynthesis in plants ranges from 0.01 µg/g to 3 µg/g in fresh mass [54]; however, it has been found to be as high as 95 µg/g in fresh mass of sagebrush (*Artemisia tridentate* [Nutt.]) [53]. Jasmonates are derived from the fatty acid metabolism pathway and are harvested directly from jasmine (*Jasminum grandiflorum* L.) [53]. Huang et al. [55] reported that biosynthesis of jasmonates takes place in three different cell membranes, and is activated by 13-lipoxygenase to form hydroperoxyoctadecatrienoic acid.

Jasmonates, along with their derivatives, control various aspects of plant growth and development, such as stamen development, root development, flowering, and leaf senescence [55]. Jasmonates also induce a variety of physiological processes, such as seed germination, pollen development, ethylene synthesis, tuber formation, fruit ripening, and tendril coiling [56]. However, when applied exogenously, jasmonates can modulate stress by either enhancing or suppressing plant development [57].

Jasmonates also activate a signal transduction pathway in response to different kinds of stress [57]. Plant responses to abiotic stresses, such as wounding, are coordinated both locally and systemically by jasmonate signaling molecules [56]. In addition, there is a causal link between wounding and jasmonates; wounding causes the release of linoleic acid, a jasmonate precursor, from the membrane lipids, in turn forming jasmonate [56]. Thus, the jasmonate signaling pathway involves signal transduction events that are regulated by wounding shock, especially in relation to leaf defoliation [56].

The molecular mechanism of crosstalk between growth and immune-signaling networks are regulated and mediated through biosynthetic pathways of phenylpropanoids, polyketides, terpenoids, and N-containing compounds, which are directly

associated with jasmonates [58]. The effects of exogenously applied jasmonic acid on growth, changes in essential oil biosynthesis, and plants subjected to biotic and abiotic stresses has been tested [59, 60]. In a study conducted by [61], a high concentration of MeJA (1 mM) inhibited primary root growth of soybeans, while a low application concentration (0.01 μ M) slightly stimulated root growth. Anderson [62] also reported that low levels (1 μ M–10 μ M) of MeJA alters protein and mRNA populations, without inducing senescence in cell culture, while a high concentration of jasmonic acid or MeJA (50 μ M) induces senescence in cell culture, and slows the primary root growth of soybeans [61].

Methyl jasmonate applied at 0.5 mM increases the content of eugenol and linalool in basil plants compared to the control [63]. In another study, MeJA applied to bigleaf marsh-elder (*Iva frutescens* L.) resulted in an increase in volatile compounds (α -pinene, sabinene, and limonene emissions) [64]. The increase in volatile emissions following MeJA treatment was ascribed to terpene synthase activation and de novo synthesis. In these studies, foliar application of MeJA varied between 0.01 mM and 0.5 mM solution, per plant, with the application rate and concentration differing between different crop species, under normal growing conditions [65–68].

3.1.3 Combined cytokinin and gibberellin, and the brassinosteroids as potential growth stimulants for recovery of defoliated and hail-damaged essential oil plants

The effects of phytohormones are based on the synergism to improve the growth and development, as well as the recovery, resistance and survival of stressed plants [60, 69]. Phytohormones rarely function independently; they depend on a cross-talk network between their synergic and antagonistic metabolic processes [40]. Gibberellins primarily controls cell growth and division by stimulating the elongation of internodes [70]. In a study by [71], longer internodes and delayed flowering were observed in tomatoes treated with GA (5 mg/L), while plants treated with only CK (5 mg/L) formed no axillary buds. However, when GA and CK were combined, there was an increase in fresh matter [71]. This demonstrates that there is a possible interaction between the major biostimulants, with antagonistic relations, which improves plant growth and development. The crosstalk between GA and CK involves components from the GA biosynthesis pathways, which plays a central role in the regulation of plant growth and development [72]. Gibberellins and CKs are commonly used in agriculture, viticulture, gardens, and horticulture [73].

Cytokinin was first discovered in the early 1940s when coconut milk was added to aid cell division in tobacco plants [74]. All CKs are adenine derivatives and mostly occur as either free compounds, glucosides, or ribosides in the plant root system, particularly the root apex [44, 75]. According to [44], CK biosynthesis occurs through biochemical modification of dimethylallyl diphosphate, which is initiated through the transference of the isopentenyl moiety from dimethylallyl diphosphate to the N6 position of adenosine triphosphate, catalyzed by isopentenyl transferases. These form the isopentenyl transferases and the isoprene side chain, which is subsequently trans-hydroxylated by cytochrome P450 (CYP450) to yield zeatin ribosides [44]. The metabolic storage and transport of CK is not yet fully understood, however, it is hypothesized that transport takes place via the vascular tissue (particularly the xylem), from the roots to the shoots of the plant [76].

Commonly-used CKs for agricultural purposes include zeatin, kinetin, 6-Benzylaminopurine (BA and BAP), 2-isopentenyl adenine, zeatin riboside, and dihydro-zeatin [40, 77]. The main functional properties of CKs for agricultural use

are the stimulation of cell division, release of lateral bud dormancy, the induction of adventitious bud formation, retarded leaf senescence, and the promotion of chlorophyll synthesis [78]. Exogenous application of CKs is currently used to optimize the internal concentrations of CKs for growth and development, organ regeneration after wounding damage, and changing the chemical compositions of essential oils [78].

Gibberellins were first isolated from the fungus, *Fusarium moniliformae* Sheldon (*Gibberella fujisckuroi* [Swada] Wollenweber), and named gibberellic acid (GA₃) [79]. To date, ca. 126 naturally-occurring GAs have been discovered [73], with each plant species containing at least six to ten GAs [80]. A wise decision was made early in GA research to number the various GAs, rather than naming them separately, as was done with chemical-related sterols. Therefore, GAs are known as GA₁, GA₂, and GA₃, etc. up to more than GA₁₂₆ [81].

Gibberellins are a large group of essential diterpenoid acids [73]. They are biosynthesized in shoot apices, young leaves, and flowers of plants, via the terpenoid pathway [81]. Biosynthesis of GA requires three enzymes viz., terpene synthase, CYP450s, and 2-oxoglutarate [81]. Gibberellins are transported through plants by means of the vascular tissues, xylem, and phloem [81].

The most common molecular mechanisms of GA signaling in plants is through the GA receptor, Gibberellin Insensitive Dwarf 1 (*GID1*) [44, 82]. Upon binding, the receptors undergo conformation changes that favor the binding of *DELLA* proteins, a group of nuclear transcriptional regulators that repress GA signaling and plant growth [44, 82]. Homeostasis and regulation of the GA biosynthetic pathway depends on the developmental and environmental signals, specifically the genes GA₂₀-oxidases, GA₃-oxidase, and GA₂-oxidases [44].

Gibberellins are endogenous hormones functioning as biostimulants that influence a wide range of developmental processes in higher plants [72]. This includes plant growth and development through promoting leaf development, stem elongation, induction of seed germination, promotion of hypocotyls and stem elongation, regulation of pollen development, and flower initiation [81]. Some GA-deficient mutants can cause dwarfism [82]. Different types of GAs are used to achieve specific agronomic objectives, for example, anti-flowering GA₇ and GA₃ are commonly used for promoting germination, seed development, leaf development, and stem elongation [81].

Several studies have revealed a reciprocal developmental dependence between the two hormones, where the ratio between GA and CK affects the developmental processes of the plant [72]. Cato et al. [71] observed positive synergic crosstalk between GA and CK in tomatoes, and [75] reported that a combination of BA and GA induced longer tomato shoots, under different abiotic stress conditions. High CK and low GA signals are required for normal shoot apical meristem functioning [82]. In contrast to these findings, joint applications of GAs and CKs have been shown to exert antagonistic effects on numerous developmental processes, including shoot and root elongation, cell differentiation, shoot regeneration in culture, and meristem activity [83, 84]. Moreover, GA tends to inhibit CK-induced cell differentiation in plants [72]. This inhibition is attributed to the loss of the *SPINDLY* protein function, which results from CK resistance.

Cytokinin activity is highest during early shoot initiation (controlling meristem activity) [85]; in contrast, GAs act at a later stage to regulate plant cell division and shoot elongation [84]. The GA biosynthetic pathway from trans-geranylgeranyl diphosphate to GA₁₂-aldehyde, leads to the identification of positive and negative signaling components [72]. In *Arabidopsis* (*Arabidopsis thaliana* L.), GA and CK signaling regulated the expression of *ARR1* through repression of GA, via

degradation of the *DELLA* protein RGA [86]. This indicates that reducing the GA concentration, 5 days after foliar application, releases *ARR1* from repression, which in turn upregulates *SHY2*. This leads to an increase in cell differentiation, which balances with cell division to control plant growth. In addition, the regulation of *SHY2* by *ARR1* also represents a point of crosstalk with auxin, thus connecting three hormones in a single network [86]. The homeostatic balance of GA and CK in plants may vary between species, and the response of plants to foliar treatments may differ as a result of external factors, such as change in environmental conditions, and stage of development [87].

Changes in the ratios of GAs and CKs to both each other, and to other hormones, often results in distinct and divergent morphological features, such as dwarfism, contorted or twisted growth, weeping forms, or fastigiated and columnar forms [89]. In addition, the ratios may cause extra-large leaves or elongated stems, and extensive shoot proliferation, especially under less favorable environmental conditions. Weeping forms have been observed in spruce (*Picea abies* Mill.), pine (*Pinus densiflora* L.), and sweet viburnum (*Viburnum odoratissimum* Ker Gawl.) treated with combined GA and CK [88, 89]. Therefore, it is evident that under abiotic stress conditions, plants can be treated with combined GA and CK to induce foliage material development. However, it is crucial to plan the application scheduling and ratios for each of these hormones, as shown in studies by [83, 84].

Brassinosteroids were named after the genus *Brassica* during the late 1970s [90], and they were initially extracted from maize pollen [90, 91]: to date, there are more than 70 free BRs and conjugates, described from various plant species [91]. Trace amounts of BRs in a complex plant matrix are classed as polyhydroxylated steroid plant hormones and are widespread among plants [91]. In addition, BRs are structurally classed as C27, C28, or C29 based on the different alkyl-substitution patterns of the side chains [92]. All the BRs isolated from plants are produced through campesterol biosynthesis and belong to the C28-BRs, with a 24 α -methyl group [80].

The most effective BRs, which have been extracted from plants for agricultural use are brassinolide, castasterone, testosterone, and 6-deoxy castasterone [80]. Of all the BRs, brassinolide is biologically the most active [92]; it is ubiquitous in plants and is produced in almost all plant parts, where it controls growth and developmental processes [93]. Plants synthesize excess brassinolide to meet the continuous need for growth and development, while inactive brassinolide is converted into active forms to maintain BRs homeostasis [92].

Brassinosteroids are found in various plant species, including monoplast freshwater algae and brown algae, suggesting that they are ancient ubiquitous plant hormones [92]. Brassinosteroids are also found in pollen, immature seeds, roots, and flowers [91, 92]. They range from 1 to 100 ng/g fresh weight in flowers, while shoots and leaves have lower amounts of 0.01–0.1 ng/g fresh mass [91, 92]. Brassinosteroids are not mobile within plants, they function by paracrine or autocrine signaling; however, long-distance transport of exogenously-applied BRs does occur in plants, particularly from the roots to shoots, but foliar-applied BRs (24-epibrassinolide) are fixed in the leaves [92]. In addition, [94] reported high mobility of BRs in a plant system.

Brassinosteroids are involved in a wide variety of plant physiological activities. They regulate plant growth, at nanomolar to micromolar concentrations, for multiple developmental processes, including cell division, cell elongation, vascular differentiation, reproductive development, and modulation of gene expression [54]. High metabolic activity, associated with growth, has been observed in rape (*Brassica napus* L.) treated with BRs [90]. BRs are also involved in microbial infection recovery,

hypocotyl growth, increased leaf lamina growth, increased shoot apex fresh weight, pollen tube growth, and stress tolerance [80].

The application of BRs enhances plant biomass, secondary metabolites, antioxidant defense activities, and the accumulation of osmoprotectants under biotic and abiotic stress [93]. This has been demonstrated in soybean, where the application of 1 $\mu\text{mol/L}$ BRs led to hypocotyl and epicotyl elongation. However, epicotyl elongation was affected by photoperiod, with no increase in length under dark conditions [95]. Therefore, BRs applied at higher concentrations ($\geq 1 \mu\text{mol/L}$) in dark-grown plants suppress shoot and root development [95]. Mung beans treated with the BR, 28-homobrasinolid, at 10^{-8} M, had increased leaf area, and plant height, as well as fresh and dry mass of shoots and roots over a 21-day growth period. This treatment also increased proline content [96]. The foliar fresh matter of corn mint (*Mentha arvensis* L.f. *Piperascens* Malinv. Ex Holmes) and its menthol content increased when treated with lactonic spirostane-SABS (0.5 ng/L) and ketonic-SABS (0.5 ng/L) [97]. BRs induce chlorophyll synthesis, through the activation of enzyme proteins [98]. [99] demonstrated this, with a foliar application of 0.5 ppm BRs increasing the chlorophyll content of soybean.

In light of these studies, it is evident that BRs can have a significant impact on plant growth and development, and therefore on recovering the yield and essential oil quality parameters of defoliated, wounded, or hail-damaged plants. The role of BRs in the alleviation of various abiotic and biotic stressors, such as temperature, salinity, moisture, and heavy metal exposure has been reported [100].

3.1.4 Natural biostimulants-containing phytohormones as a recovery mechanism for wounded, defoliated and hail-damaged plants

Exogenous applications of synthetic biostimulants have been shown to consistently enhance growth, yield optimization and oil quality [60], as well as physiological efficiency in plants [19]. However, the production and availability of some synthetic phytohormones are expensive and not readily available. In addition, the practical use of these phytohormones is dependent on various environmental factors, such as temperature and light [101]. The use of synthetic biostimulants is a potential ecological hazard as they could pose a threat to the health of non-target organisms, especially when improperly used [90]. As such, the use of less harmful and cheaper bioactive stimulants are preferred over conventional synthetic phytohormones [80].

There are numerous commercially available bio-fertilizers, plant conditioners, allelopathic preparations, biogenic stimulators, elicitors, plant strengtheners, and biostimulants (**Table 1**). Most of these products are considered as biostimulants, containing biostimulants. However, [102] found that some biostimulants contain traces of natural phytohormones, but their biological action should not be attributed to them, unless registered as biostimulants.

Biostimulants products are developed based on the synergism between natural phytohormones [86, 87]. However, there are only a few published scientific reports on these products, since most industrial companies withhold information for market confidentiality purposes (examples in **Table 1**). Below are a few of the published reports to highlight the effects of registered biostimulants (containing traces of phytohormones) on plant growth, recovery, and resistance against stressors.

Application of biostimulants (undisclosed brand-name) containing GA (50 mg/L) and CK (90 mg/L) increased the number of leaves, flower heads and the total flavonoid content of marigold plants inflorescences [106]. Peppers (*Capsicum annuum* L.) treated with Megafol® (0.2% 40 mL; GA & CK content) had increased Ca uptake in

Product	Composition	Citation
Lucky Plant®	Gibberellic acid, BRs and traces of CKs	Agraforum, Germany
ComCat®	Brassinosteroids (2,4-epibrassinolide)	Agraforum, Germany
SilCat™	Brassinosteroids (2,4-epibrassinolide)	Agraforum, Germany
AnnGro® EW	Ethyl esters of fatty acids	Agraforum, Germany
Stimplex®	Cytokinin (Kinetin 0.01%)	[102]
Fungicidal	Salicylic acid	Pan African Farms
PanAf®	Salicylic acid	Pan African Farms
Megafol®	Amino acids, betaines, proteins, vitamins, auxin, GA, and cytokinins	[69]
Biozyme®	Algae extract, GAs, auxin and zeatin, and chelated micronutrients	[69]
Slavol	N-fixing, and phosphate-mineralizing bacteria, and auxins	[69]
Algreen, Leili®	Seaweed extract, plant growth regulator, vitamins, free amino acids, and alginic acid	[69]
Agrispon®	Natural plant extract with traces of phytohormones	[103]
Kelpak®	Seaweed extract and traces of plant growth regulators	[103]
Stifun	Complex biologically active substances of natural origin	[104]
Auxym®	Auxins and CK, amino acids, peptides, vitamins, and essential micronutrients	[105]

Table 1.
Examples of commercial biostimulants containing phytohormones as declared on the labels.

the foliage material and fruits. Megafol® also increased the fruiting yield and the level of antioxidants in the same species [69]. Hüster [90] studied the stimulatory effects of ComCat® on wheat, maize, cabbage (*Brassica oleracea* L.), carrots (*Daucus carota* [Hoffm.] Schübl.), onions (*Allium cepa* L.), lettuce, beetroot (*Beta vulgaris* L.), and peas (*Pisum sativum* L.). They demonstrated that an optimum foliar application of 5 mg/L, significantly increased the foliar biomass of these crops. Marjoram (*Majorana hortensis* Moench.) treated with BRs (25 mg/L) was rich in *cis*-sabinene hydrate content [107]. Foliar application of the tropical plant extract, Auxym® (2 ml/L), improved the yield of jute (*Corchorus olitorius* sp.) [105]. Auxym® also increased the chlorophyll content, enhanced the adaptation of jute plants to fluctuating light levels, and positively increased the starch, soluble proteins, and amino acids content when the plants received the full strength of nutrient solution [105]. From these studies, it is evident that phytohormones and biostimulants containing natural phytohormones can increase crop yield, enhance plant phytochemistry and secondary metabolites biosynthesis, and improve the recovery response mechanism of plants following biotic and abiotic stresses.

3.1.5 Magnetic field as a potential growth stimulant

The emission of magnetic fields (MFs) in the ecosystem due to ever changing and advancing technology has brought significant changes in the human and ecological

environment [108]. In the modern days, the use of MFs as a stimulant for plant performance and capability has been far an interesting alternative method to chemical stimulants [109]. Magnetic fields have positively influenced the morphogenesis, showing great modification of seed germination, seedling growth and development in various plants such as cereals, grasses, medicinal plants, horticultural crops and herbs [38]. It is worth noting that MFs constitute non-toxic stimulus resulting in increased food and environmental safety. Application of MFs on crops has been seen to reduce the attack of pathogenic diseases [110]. Many studies have tried to understand the actual mechanism involved on how seeds germinate when exposed to MFs. Vashisth and Joshi [111] exposed seeds of maize to static-MFs for 4 h on strengths ranging from 50, 100, 150, 200 and 250 milliTesla (mT). The results suggested that MFs application enhance the seed percentage-germination, seedling length, dry weight and speed of germination when compared to the referent group. Furthermore, exposure to MFs reduced cellular leakage, improved water absorption and functional root parameters. Kirdan et al. [112] performed an interesting experiment by treating *Pinus Pinea* L. seeds with a MF of 9.42 mT for a different period of time; 0 min (used as a reference), 15, 30, and 40 min. Seeds exposed for 30 and 45 min showed a higher germination energy. There was also an increased root collar diameter, shoot height and tap root length.

Plants are outstanding experimental models compared to animals when conducting MFs exposure and response growth relationship studies. According to Vian et al. [113], they efficiently intercept with electromagnetic fields (EMFs) because of immobility and constant orientation. The benefit of magnetic seed germination has been seen in various biochemical events such as enzymatic stimulation, bioenergetic excitements and protein synthesis [110, 114]. Electrons in various molecules absorbs MF energy and utilize it for accelerating seed metabolism that triggers biochemical and enzyme reactions in the early stages of seed germination [115]. Afzal et al. [110] applied magnetic field strengths of 50, 100 and 150 mT for 5, 10 and 15 min on sunflower seed, and observed an increased α -amylase activity, with reduced sugar in high strength magnetically treated seeds. This confirms that magnetic treatment stimulates the protein synthesis of existing enzymes by producing germination metabolites at required amounts. Vashisth et al. [116] studied the effects of 200 mT for 2 h on crop growth and the yield of sunflower crops raised from magnetically treated seeds sown under different moisture stress conditions. The experimental results showed that plants from magnetically treated seeds had a higher leaf index area, chlorophyll content, 1000-seed mass, shoot length and biomass compared to untreated seeds. Magnetic field exposures in plants act as a stimulant in improving crop growth and yield under different ecological stress conditions.

3.2 Biostimulants, defoliation and hail damage on the development of leaf trichomes

The production and accumulation of essential oils is restricted to specialized structures (e.g. glandular trichomes, secretory cavities, and idioblasts) since they are toxic to healthy plant cells [9, 60]. The production of these essential oils takes place in closely connected secretory structure formations. It has been shown that biotic and abiotic stress factors affect essential oil production [9, 60]. In addition, plants produce some essential oil compounds in response to physiological stress, pathogen attack, and other ecological factors [60]. Therefore, it has a direct effect on the stimulation of the essential oil biosynthesis, which directly benefits essential oil yield and quality.

The recovery response mechanism of plants to hail damage, defoliation, wounding or grafting is complex, starting from upregulation of plant-stress hormones at the wound site, and later plant growth regulators to recover the lost organs [117, 118]. Therefore, the recovery of leaves following hail damage stress or related climate change affect the essential oil biosynthesis through the specialized structures called glandular trichomes, located on both surfaces of the leaf, and on tender stems and buds [52]. Moreover, [119] claimed that the densification of trichomes occurs as early as during leaf differentiation and continues throughout leaf development of *P. scabrum*.

Trichomes play different roles in plant physiology and ecology, especially with regards to morphological, mechanical and phytochemical characteristics [120]. Trichome density may vary with changes in environmental conditions [120]. These variations may indicate trade-offs between the trichomes, subsequently increasing resistance against trichome production. In defoliated plants, the rate of leaf regeneration is slow, possibly due to the endogenous ratio between CK and GA, and regulated plant bio-inhibitors [45, 121]. In the study conducted by [122], increasing the level of combined CK and GA decreased the density of the non-glandular trichomes on rose geranium, particularly on the adaxial leaf surface. In addition, [119] reported that non-glandular trichomes develop before glandular trichomes in the leaf primordia of *Pelargonium*, and cease development as the leaf expands. Therefore, this process could be ascribed to CK stimulation of the cell division, further regulating the leaf primordia by negatively affecting GA signaling through *IPT7* and *GA₂₀* oxidases, at an early stage of leaf primordia [123]. Zhou et al. [124] demonstrated this on *Arabidopsis*, where the *C2H2* transcriptional factors regulated trichome cell differentiation through CK and GA pathways, suggesting that excess endogenous levels of these biostimulants could be toxic for trichome development. In another study, Zhou et al. [125] further reported that the *ZFP5* transcription factor of GA regulates trichome developmental actions, mainly through cell differentiation. In addition, GA is biosynthesized in young leaves and can translocate freely by diffusing through the plant cell protoplast when applied foliarly.

A combination of endogenous development and external signals regulate the developmental distribution of trichomes on plant leaves [126]. Therefore, under extreme external stimuli, such as complete defoliation, endogenous phytohormones are only synchronized to regenerate lost material. This directly affects leaf expansion and trichome developmental rate. In the study conducted by [122], the development and densities of the asciiform trichome following simulated hail damage was due to high concentration of GA (300 mg/L), applied at a later stage, in contrast to CK (0.64 mg/L) which was used earlier. Zhou et al. [124, 125] reported similar findings in *Arabidopsis*, where GA and CK, at concentrations as low as 100 μ M, increased the density of glandular trichomes. According to the author, this was ascribed to GA and CK molecules, which regulated the development of glandular trichome through the combined action of *ZFP5* and *ZFP6* transcription factors [125]. Thus, in combination, these transcription factors regulate trichome cell differentiation, an important metabolic mechanism associated with trichome development.

Xue et al. [126] also demonstrated that the development of trichomes, and the biosynthesis of essential oil could be influenced by exogenous applications of BRs and jasmonic acid. According to [127], the *dpy* mutant (BR-deficient) is the one which enhances pubescence, while the jasmonic acid *jai1-1* mutant produces the opposite phenotypic effect [127, 128]. The *Arabidopsis bls1* mutant, which is impaired in the BR response, developed fewer trichomes on both the abaxial and adaxial leaf surfaces, indicating the possible involvement of BR in trichome development [129].

Defoliated plants deploy stored resources to rebuild photosynthetic material and regenerate new organs or tissues following defoliation and wounding [118, 130]. During the refoliation, it is possible that the endogenous CK content in defoliated plants is already too high; then GA accumulation occurred at the later stage to regulate growth. According to [89], the amalgamation of CK and GA following hail damage may cause alterations in morphological features, such as increased trichome density. Other than GA and CK, BRs and jasmonic acid directly affect trichome formation through the accumulation of *zgb* and PI-I transcripts, indicating the importance of BRs in leaf recovery following defoliation or wounding [127].

3.3 Biostimulants, defoliation and hail damage on the production of primary and secondary metabolites

Plant chemistry (e.g. the essential oil and phytohormone content) is altered following mechanical damage, as caused by hail and/or animal herbivory [9]. Endogenous phytohormones are the primary inducible defense response for this class of volatiles, signaling to the transduction pathway between wounding stress perception and induction [36, 131]. These physiological response mechanisms occur within matter of minutes to several hours, resulting in the activation of wound-related defense genes [36].

According to [132], increased biomass and essential oil yield was recorded in rose geranium plants when biostimulants such as IAA, IBA, cycocel, cytozyne, biomyze, thephon, mepiquat chloride, triacontanol, and mixtalol were applied. However, the use of most of these natural or synthetic biostimulants as a recovery method for hail-damaged plants has not been tested. In addition, changes in the essential oil yield and quality have been found in most essential oil and medicinal plants, as a result of the exogenous application and endogenous triggering of biostimulants [60]. At least 60 essential oil constituents were identified in elderberry (*Sambucus ebulus* L.), with some of the components significantly increasing in content under different exogenous application of auxin (IAA and NAA) [133]. Treatment with CK increased the total oil yield of peppermint plants by 40% [77].

Jasmonates are directly involved in the mevalonic acid pathway, through the enzyme mevalonate-5-diphosphate carboxylase, which directly affects the biosynthesis of linalool [134]. Linalool levels decreases with increases in excess endogenous MeJA, which mostly accumulated following simulated hail damage [122]. In other studies, [135, 136] demonstrated that applications over 18 μ M (MeJA) may significantly affect the accumulation of linalool content.

Biosynthesis of isomenthone occurs late in leaf development, when mature oil gland cells are in the post-secretory phase [137]. At this late stage of leaf development, ABA is abundant in the epidermal cells, where it is involved in the abscission process [138]. In the study conducted by [122], the daily application of ABA led to an excess of endogenous ABA content, causing toxicity affecting the biosynthesis of isomenthone. Similarly, [60] stated that the chemical composition of essential oil plants could be influenced by exogenous applications of ABA and methyl jasmonate.

In plants, geraniol and ABA biosynthesis share a similar pathway [41]: the ABA biosynthetic pathway starts from oxidative cleavage of the epoxy-carotenoids and 9-*cis* violaxanthin, where xanthoxin is converted to abscisic acid. The process is then followed by sequential production of farnesyl pyrophosphate, phytoene, carotene, lycopene, and geranyl pyrophosphate [41]. Absciscic acid and geraniol biosynthesis occur at this stage through the isopentenyl diphosphate source [139]. Croteau and

Purkett [140] reported that geranyl pyrophosphate synthase activity is localized in the leaf epidermal glands of sage (*Salvia officinalis* L.), where monoterpenes are biosynthesized, suggesting that geranyl pyrophosphate synthase supplies the C10 precursor for the production of monoterpenes. In this case, any repeated application of ABA can reach a toxic level in the epidermal cells as described by [122, 139], causing disruptions of geraniol biosynthesis through the cytosolic mevalonate pathway.

Geraniol usually undergoes biotransformation into other terpenoids in aromatic plants, which influences the quality of the essential oil [141]. Geranyl formate, geranyl butyrate, geranyl tiglate, and geranyl acetate are some of the acyclic monoterpenes derived from geraniol, which are regarded as geraniol esters [142]. It has been noted in the study conducted by [122] that any prolonged application of a low concentration of MeJA increases the content of geranyl tiglate. This was supported by [143], who described that jasmonates are upregulated by wounding stress and are directly involved in the biosynthesis of these terpenes. In addition, the accumulation of geranyl tiglate can be attributed to simulated hail damage as described by [122], followed by the subsequent daily application of methyl jasmonate. The accumulation of geranyl formate is attributed to the biosynthesis of geraniol, and the effects of subsequent daily use of methyl jasmonate [142].

Plants respond to defoliation and wounding through the induction of phenylpropanoids metabolism to accumulate phenolic compounds [144]. Phenolics provide cytotoxic effects, as well as the building blocks for polyphenolic-based cell wall modifications. Polyphenolic-based cell wall modifications assist with organ regeneration in defoliated or wounded plants [118, 144]. The level of endogenous phenolics in refoliated plants influences plant growth and development, clearly indicating the relation of the leaf refoliation with the leaf ontogeny [97]. The age of the plant is associated with the level of the total phenolics. On wampee (*Clausena lansium* Lour.), [145] reported high total leaf phenolics in early growth stages compared to the later growth stages. A high phenolic content was also observed in the early stages of leaf development of yerba-mate (*Ilex paraguariensis* A.St Hil.), which affected the development and quality of these plants [146]. High phenolics level in young leaves may be associated with defense and refoliation following defoliation [147].

Previous studies have demonstrated that defoliation, wounding and exogenous application of biostimulants on plants may effectively stimulate vegetative growth, improve nutrient acquisition, and increases the antioxidant capacity of plant tissue [69]. Aspects of phenolics accumulation are driven by upregulation of endogenous phytohormones. However, this occurs through crosstalk networks between these phytohormones, for which some commercially available [148]. A combination of spermine, methyl jasmonate, and epibrassinolide was found to induce secondary metabolites, including phenolics, in sweet basil (*Ocimum basilicum* L.) [149]. According to [150], maintenance of minerals is a prerequisite for providing co-factors for many enzymes of the phenolic pathway. The accumulation of caffeic acid, caffeoyl tartaric acid, p-Coumaroyl tyrosine and protocatechuic acid O-hexoside are a typical plant response to defoliation, including wounding stress [118, 151].

Biostimulants stimulate plant growth and terpene biosynthesis in a large number of aromatic plant species, which result in beneficial changes in terpene accumulation [152]. Poyh and Ono [153] recorded higher essential oil content for sage (*S. officinalis* L.) treated with 100 mg/L gibberellic acid. Fraternale et al. [154] reported a higher essential oil yield of Spanish marjoram (*Thimus mastichina* L.) using a medium culture with CK as low as 0.1 mg/L. In the leaves of Spanish marjoram treated with CK, there were a greater number of glandular trichomes recorded

at the later leaf developmental stage, which could be ascribed to increased essential oil yield. Foliar application of a biostilumat-28-homobrassinolide (10^{-6} M) also enhanced the essential oil yield of mint (*M. arvensis* L.) [155].

4. Conclusions

Essential oil plants are mostly grown for essential oil production; therefore, the aerial herbage material is a crucial component of these crops. Environmental stress factors, such as hail damage, can cause significant damage to these plants, reducing this valuable material, and directly affecting the essential oil yield and quality [72]. Natural and synthetic biostimulants have been extensively investigated on plant growth and development, and also on the recovery of plants following stress [60]. Based on [60], it was hypothesized that the application of biostimulants will recover the herbage yield and improve the biosynthesis of essential oil plants subjected to simulated hail damage. This chapter has detailed the potential recovery response of plants to hail damage, the response of plants treated with synthetic biostimulants, and the response of plants treated with natural biostimulants extracted from plants. Therefore, it is evident that the use of natural or synthetic biostimulants, as an alternative mitigation strategy against hail damage, might help in the recovery and improve essential oil plant yield following hail damage. However, future studies should explore;

1. the extents of hail damage on different essential oil plants;
2. determining the effects of root-applied synthetic cytokinin on the recovery of essential oil yield attributes, and the essential oil yield and quality of hail-damaged essential oil plants.
3. determining the effects of cytokinin and the auxin ratio on hail-damaged essential oil plants, *in vivo* study.
4. identifying the effects of synthetic biostimulants as a contaminant of essential oil quality: A perfumery industry study.
5. evaluate the use of combined plant growth regulator as a potential recovery mechanism of the herbage yield, and the essential oil yield and quality of simulated hail-damaged essential oil plants, and,
6. evaluate the use of abscisic acid and methyl jasmonate as a potential mitigating mechanism on simulated hail-damaged rose geranium plants.

Conflict of interest

The authors declare no conflict of interest.

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