

# Essential Oils and Terpenoids Effects

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Weeds are one of the major constraints in crop production affecting both yield and quality. The excessive and exclusive use of synthetic herbicides for their management is increasing the development of herbicide-resistant weeds and is provoking risks for the environment and human health. Therefore, the development of new herbicides with multitarget-site activity, new modes of action and low impact on the environment and health are badly needed. The study of plant–plant interactions through the release of secondary metabolites could be a starting point for the identification of new molecules with herbicidal activity. Essential oils (EOs) and their components, mainly terpenoids, as pure natural compounds or in mixtures, because of their structural diversity and strong phytotoxic activity, could be good candidates for the development of new bioherbicides or could serve as a basis for the development of new natural-like low impact synthetic herbicides. EOs and terpenoids have been largely studied for their phytotoxicity and several evidences on their modes of action have been highlighted in the last decades through the use of integrated approaches.

essential oils

terpenoids

phytotoxicity

mode of action

natural herbicides

secondary metabolites

weed control

## 1. Introduction

Plants are sessile organisms daily exposed to various biotic and abiotic stress factors and continuously involved in competition with other organisms for edaphic resources. Such necessity to cope with stress and to fight for species survival has pushed these species in evolving defense mechanisms and in increasing the competitive capacity in favor of the single plant or the whole species <sup>[1][2]</sup>.

The only strategy that could be adopted by plants to face these challenges consists in adjusting their physiological state in preparation for and/or in response to these threats in order to improve their well-being and survival <sup>[1]</sup>. In addition to physiological adjustments, plants have evolved the production of secondary metabolites, not necessary for cell survival but pivotal for the survival of the species, mainly involved in plant–organism communication (bacteria, plants, insects, fungi etc.) and often used as chemical weapons, capable of positively/negatively affecting the growth and development of neighboring species <sup>[3]</sup>.

Secondary metabolites such as phenolic compounds, short-chain fatty acids, terpenoids, alkaloids among others, can be constantly produced by the plants or their production could be induced *ex novo*, since it has an energetic

cost for the plant, by several factors such as both biotic and abiotic stresses, kin recognition, climatic changes and phenological stages [3].

Both constitutive and inducible defense system adopted by plants to communicate, compete and cope with stress is the production of volatile organic compounds, VOCs, chemicals that are involved in several plant processes such as (i) attracting beneficial insects and pollinators, (ii) protecting plants from heat, cold and elevated ozone concentration, (iii) defending plants from herbivory and (iv) priming neighboring species against biotic and abiotic stresses [4][5].

Moreover, these chemicals are involved in most complex trophic interactions playing the role of semiochemicals, which highlight the wide specialization of these compounds. For example, a recent detailed review was focused on the microorganisms–plants–insects tritrophic interaction. Authors have been able to document that microorganism-induced volatile communication could significantly influence insect behavior [6]. VOCs are synthesized, accumulated, and then secreted by specialized tissues or cell types and then stored in complex and specialized secretory structures, generally classified into three types: superficial glandular trichomes (Lamiaceae and Asteraceae, e.g., mint, sage, and chamomile); internal resin ducts, common to conifers; and embedded secretory cavities, characteristic of *Eucalyptus* and *Citrus* (schizogenous origin in Myrtaceae and schizolysigenous in Rutaceae). All structural types contain specialized biosynthetic cells. Additionally, in some cases, essential oils (EOs) are stored in undifferentiated cells, like in Lauraceae [7][8]. From the chemical point of view, VOCs belong to two groups (i) terpenes and terpenoids (a terpene containing oxygen) and (ii) aromatic and aliphatic constituents. Regardless, terpenoids are the most representative and abundant compounds released by plants.

Terpenes are unsaturated hydrocarbons, which have a distinct architectural and chemical relation to the simple isoprene molecule. The simplest terpenes are monoterpenes (molecular formula  $C_{10}H_{16}$ ), which are biosynthesized through the head to tail union of two isoprene units [9]. The general formula used to express their composition is  $(C_5H_8)_n$ . Depending on “ $n$ ” number we can have monoterpenes ( $n = 2$ ), sesquiterpenes ( $n = 3$ ), diterpenes ( $n = 4$ ) etc. [9]. Terpenoids are terpenes that, through an enzymatic-driven biochemical modification, lose a methyl group, which is substituted by oxygen addition [9].

Terpenoids biosynthesis is localized in both cytoplasm and plastids of plant cells via the methyl-d-erythritol-4-phosphate pathway (MEP), which provides the precursors for the biosynthesis of the volatile hemiterpenes (C5), monoterpenes (C10), and diterpenes (C20), via the mevalonic acid pathway (MAV), from which originate the volatile sesquiterpenes (C15) [9][10] and via the shikimic acid pathway, which heads to phenylpropenes [11].

Generally, VOCs are constituted by a few major components at relatively high concentrations (20–70%) and several components that are present in trace amounts. It was generally assumed that the biological properties of VOCs were mainly determined by their major components. However, relatively recent studies have also demonstrated that trace elements can be determinant in plant defense strategies and could play a pivotal role by acting synergistically in improving the biological activity of the major constituents [12].

In the last few years, because of their complex chemical composition, their high biological activity, and being safe compounds for the environment and human health, VOCs gained a renewed interest in several industrial areas, which pushed both researchers and industries in finding strategies to extract and concentrate them. VOCs extraction and concentration are generally achieved by hydrodistillation and/or mechanical means (e.g., cold-press extraction) and the final product is essential oils (EOs) or aetherolea.

EOs are natural, volatile, complex mixtures of compounds, consisting of aromatic liquids, obtained from different plant material, like flowers, roots, bark, leaves, seeds, peel, fruits, wood, or the whole plant [13][14]. They are defined by the International Organization for Standardization (ISO, 2014) [15] as “a product obtained from the natural raw material of plant origin, by steam distillation, by mechanical processes from the epicarp of citrus fruits, or by dry distillation, after separation of the aqueous phase by physical processes.” This definition is common with other prestigious institutions, such as the European Pharmacopoeia (Ph. Eur.) [16], or the Association Française de Normalisation (AFNOR). EOs have great potential in agriculture for crop protection, as they possess antimicrobial [17] and antibacterial [18] properties, as well as insecticidal [19] and herbicidal activity [20][21].

The EO composition, which includes mainly lipophilic and highly volatile, scarcely water-soluble compounds, determines the properties and the biological activities of EOs [22][23][24]. The main compounds of EOs are terpenoids, principally mono- and sesquiterpenes, but also diterpenes can be found, all of them in the form of hydrocarbons, alcohols, aldehydes, ketones, ethers, esters, peroxides, and phenols. Aromatic compounds are less frequent than terpenes but are characteristic of some EOs (e.g., eugenol is the main compound of clove EO (*Zygium aromaticum* (L.) Merr. et L.M.Perry), and the *trans*-cinnamic aldehyde is the major constituent of cinnamon EO (*Cinnamomum verum* J.Presl). Aliphatic compounds (hydrocarbons, alcohols, acids, aldehydes, esters, and lactones) can also be present in the EO composition [24]. Furthermore, other substances, such as fats, coumarins, anthraquinones, and certain alkaloids, which are distillable, have been identified in EOs obtained by distillation. Some compounds are derived from glycosides, which are transformed during the distillation process [7]. In EOs from *Citrus* species, volatile and semivolatile compounds represent 85–99% of the EO composition, with the most frequent compounds being hydrocarbon and derived mono- and sesquiterpenes, followed by aliphatic and olefinic C6–C12 monoterpene aldehydes, alcohols, ketones, esters, and acids, together with several aromatic compounds. The nonvolatile residue is mainly composed of flavonoids, coumarins, diterpenoids, sterols, and fatty acids [25].

The qualitative and quantitative composition of EOs determines their quality, value, and price on the market and it is not standard. It is necessary to know the causes of variability in EO composition to control and manage them [26], which can be divided into abiotic and biotic factors. Abiotic factors include growing conditions of the plant from which they are extracted, like climatic conditions (temperature, rainfall, humidity, light intensity, wind), soil conditions, agronomical practices (water supply, fertilization), and harvesting time [26]. The biotic/biological factors are the genetic/biological differences of the source plants and root colonization by symbiotic microorganisms. For example, differences in the EO composition can be found depending on the organ from which the EO is extracted. EO composition in some species is very stable but in others can have great variations, and different chemotypes can be found [26].

Approximately, 3000 different EOs have been described, and 300 of them are commercially important for their applications in the pharmaceutical, agronomic, food, sanitary, cosmetic, and perfume industries [13].

The main botanical families that produce EOs are, according to Vigan [27] and Raut and Karuppayil [28], the Abietaceae, which contains *Pinus pinaster* Aiton, from which turpentine is obtained; the Cupressaceae, including thuja (*Thuja* spp.), cypress (*Cupressus* spp.) and juniper (*Juniperus* spp.); the Lamiaceae, one of the most important, which comprises basil (*Ocimum basilicum* L.), true or hybrid lavender (*Lavandula* spp.), marjoram (*Origanum majorana* L.), lemon balm (*Melissa officinalis* L.), mint (*Mentha* spp.), oregano (*Origanum* spp.), patchouli (*Pogostemon cablin* (Blanco) Benth.), rosemary (*Rosmarinus officinalis* L.) and sage (*Salvia officinalis* L.); the Myrtaceae, containing *Eucalyptus* spp., clove tree (*S. aromaticum*), myrtle (*Myrtus* spp.) and niaouli (*Melaleuca quinquenervia* (Cav.) S.T.Blake); the Lauraceae, covering cinnamon (*C. verum*), laurel (*Laurus nobilis* L.), rosewood (*Aniba rosaeodora* Ducke), clove nutmeg (*Pimenta dioica* (L.) Merr.) and sassafras (*Sassafras albidum* (Nutt.) Nees); the Rutaceae, which is another of the most important families, including a great number of EOs from *Citrus* fruits, that are the most popular natural EOs and account for the largest proportion of commercial natural flavors and fragrances [29], as lemon (*Citrus limon* (L.) Osbeck), lime (*Citrus aurantiifolia* (Christm.) Swingle), mandarin (*Citrus reticulata* Blanco), sweet and bitter orange (*Citrus sinensis* (L.) Osbeck and *Citrus × aurantium* L.) and grapefruit (*Citrus paradisi* Macfad.); the Ericaceae, which contains wintergreen (*Gaultheria procumbens* L.) and Labrador tea (*Ledum palustre* subsp. *groenlandicum* (Oeder) Hultén); the Asteraceae, which includes camomile (*Matricaria chamomilla* L.), tarragon (*Artemisia dracunculus* L.), sweet inula (*Dittrichia graveolens* (L.) Greuter) and gray santolina (*Santolina chamaecyparissus* L.); the Alliaceae, from which *Allium* genera have been the most studied [30][31]; the Apiaceae, which EOs have shown insecticidal properties (*Anethum graveolens* L., *Cuminum cyminum* L., *Foeniculum vulgare* Mill., *Petroselinum crispum* (Mill.) Fuss) [32], and antioxidant and hepatoprotective potential (*Coriandrum sativum* L. and *Carum carvi* L.) [33]; the Poaceae, with lemon grass (*Cymbopogon citratus* (DC.) Stapf) being the most important representative; the Rosaceae, containing rose (*Rosa* spp.), which EO has been widely investigated [34,35]; Geraniaceae, which contains *Pelargonium* spp.; and Santalaceae with *Santalum* spp.

The use of EOs is continually increasing due to the strong demand for pure natural ingredients in many sectors . In the food industry, EOs could be also used as natural antimicrobials for food preservation . In the latest years in Europe, a great number of EOs have been approved for their use in agriculture, especially as biocides, such as *Mentha arvensis* L. and *Mentha spicata* L., *Artemisia alba* Turra and *Citrus × aurantium* L., among others. There are commercial products available, based on EOs, used as fungicides or bactericides (e.g., BIOXEDA, from Xeda International, France, clove oil), as growth regulators (e.g., BIOX-M, from Xeda International, France, *Mentha spicata* EO) and as fungicides and insecticides (LIMOCIDE, from VIVAGRO SARL, France; OROCID, from Idoi Nature, Spain; and PREV-AM, from ORO AGRI INTERNATIONAL LTD, all three sweet orange EO) but there are still not commercial herbicides based on EOs available in the European market, although there is a European patent involving the use of EOs to control weeds [34].

## 2. Effects of EOs on Plant Physiology and Mode of Action of Their Isolated Constituents

EOs are a complex mixture of biologically active compounds, which can synergistically, additively, and/or antagonistically interact among them. Moreover, it should be considered that their composition is extremely variable depending on genotype, ecotype, biotic and abiotic stress, environmental condition, and/or cropping management [35][36]. The complexity of the mixture joined to its high variability makes the identification of their mode of action extremely complex and hardly achievable.

On the contrary, despite the complexity and the necessity of a multidisciplinary approach, the identification of the mode of action of their pure constituents in controlled conditions is a simpler task. This is the main reason why we find many works in the literature focused on the mode of action of individual compounds rather than essential oils. Regardless, it should be highlighted that despite the lack of information concerning the EOs mode of action, several commercial organic herbicides are already available on the market, whereas herbicides based on their pure constituents, which on the contrary have been deeply studied, are barely available.

### 2.1. Effects of EOs on Plant Physiology and Metabolism

To our knowledge, the only manuscript that has tried to hypothesize the mode of action of an EO was published by Araniti et al. [37]. Through an integrated physiological and metabolomic approach they were able to demonstrate that *Origanum vulgare* EOs treatment was able to inhibit the glutamate and aspartate metabolism altering the photorespiratory pathway and the photosynthetic machinery.

On the other hand, the literature reports much research focused on the potential application of EOs as leaf burning herbicides (with selective and/or nonselective activity) and on their effects on plant physiology.

Concerning the selectivity of the EOs, Synowiec et al. [38] reported that caraway EO emulsion was a good candidate for weed management in corn crops. This EO was selective, severely affecting the physiology and metabolism of *E. crus-galli* without damaging the corn. Moreover, the authors demonstrated that the application of this EO severely impacted the plant metabolism by altering several amino acid pathways and the TCA cycle of treated plants. On the contrary, the same authors demonstrated that peppermint EO phytotoxicity was significantly higher than that of caraway EO but with no selectivity.

Concerning the effects of EOs on plant physiology, it was demonstrated that the application of different EOs, as *E. citriodora*, *E. tereticornis* and *S. hortensis*, caused a reduction in the chlorophyll content and the cellular respiration of the treated weeds. These observations indicate that EOs were affecting negatively the photosynthetic system and the energy metabolism of the target plants.

Phytotoxic effects of EOs that can be visible in treated plants, like growth reduction, chlorosis, and burning of leaves, have been attributed to their interference with some processes in the plant cells, like inhibition of mitosis, a decrease of cellular respiration and chlorophyll content, membrane depolarization and ion leakage, removal of the

cuticular waxes, oxidative damages and microtubule polymerization. EOs that alter the membrane integrity (e.g., *E. citriodora* EO), consequently increasing its permeability and enhancing the solute leakage, affect other physiological and biochemical processes linked to membrane functioning.

Regarding the inhibitory effects on seed germination of EOs, it was demonstrated that the phytochemicals prevent seed germination by the disruption of mitochondrial respiration and oxidative pentose phosphate pathway (OPPP) [39][40][41].

The reduction that EOs cause on seedling root and shoot length can be attributed to the reduced rate of cell division and cell elongation due to the activity of allelochemicals and reduced mitotic index [42].

The main components of EOs are monoterpenes, but oxygenated monoterpenes have shown more phytotoxic effects than monoterpene hydrocarbons [43]. EOs and their components can cause anatomical and physiological changes in plant seedlings, causing accumulation of lipid globules in the cell cytoplasm and reduction in membrane permeability and respiration, possibly due to the inhibition of DNA and RNA syntheses. Phytotoxicity can be increased with the synergistic effects of EO components [44].

## 2.2. Terpenoids Phytotoxicity and Mode of Action

The phytotoxic potential of terpenoids has been largely documented in the last 20 years. Because of their relatively simple structure, as well as their multiple biological activity and ecofriendly characteristics, they have been proposed for the formulation of natural herbicides or as a backbone for the production of synthetic natural-like herbicides [45]. Nevertheless, despite the extensive proof concerning their *in vitro* and *in vivo* (both microcosms and open field) phytotoxicity, only a few experiments have highlighted, or at least have tried to highlight, their mode of action.

In the present review, we tried to focus on those molecules that have been deeply studied, giving proof and/or a hint concerning their potential mode of action.

Amongst terpenoids, cineoles have been the most widely studied, and 1,4 cineole is of particular interest because of its similarity in structure with the synthetic herbicide cinmethylin [46]. This molecule, as well as several other terpenoids, significantly altered the mitotic process affecting the prophase. Moreover, it induced growth abnormalities in shoots, such as helical growth.

Similarly, 1,8-cineole (eucalyptol), a monoterpene largely produced by the allelopathic species *Eucalyptus* sp. [47], is a ubiquitous terpene characterized by a strong inhibition of plant growth affecting mitochondrial respiration and, in onion roots, inducing the formation of swollen root tips and the inhibition of all the mitosis stages [48].

Moreover, a recent publication [49] demonstrated that 1,8-cineole vapors were able to inhibit the tuber sprout growth of *Solanum tuberosum* "Russet Burbank" reducing gibberellin production (in particular GA20 but not GA19). The authors, by supplying exogenous gibberellins (GA1, GA3, and GA20), were able to reverse cineole-induced sprout

growth inhibition. In addition, the expression of genes encoding key gibberellin metabolic enzymes was significantly altered by the treatment, suggesting that this natural monoterpene interferes with plant growth and development by impairing the biosynthesis of gibberellin.

The radial root tip swelling observed after 1,8-cineole treatment and the helical growth of the shoot of plants treated with 1,4-cineole are a clear sign that these molecules are able to interfere with cell division and with the cortical microtubule organization. In fact, Baskin et al. [50] demonstrated that the chemicals oryzalin and colchicine, two tubulin disorganizers, could induce two different effects on the root tip: radial expansion (a phenomenon known as swelling) or root growth inhibition, which can be accompanied by a characteristic anisotropic growth “corkscrew shape” (a phenomenon known as handedness) [51]. In particular, Baskin et al. [50] demonstrated that the root swelling is mainly due to disorganization of cortical microtubules, which stimulated the tangential expansion and reduced the uniformity of cellulose microfibril alignment among cells.

Although no evidence has been provided regarding the effects of 1,8-cineole on microtubules, the ability of terpenoids, in particular, mono- and sesquiterpenes, in altering both cortical and spindle and phragmoplast microtubules, has been largely documented in the last few years.

The first evidence, concerning microtubules as an intracellular target of the terpenoids, was given by Chaimovitch et al. [52] with the monoterpene citral. In a first experiment, they were able to demonstrate that a few minutes exposition of *Arabidopsis* seedlings to citral vapors was sufficient to disrupt the organization and polymerization of the microtubule, leaving intact the actin filaments.

Successively, working on wheat roots, they further demonstrated that citral treatment led to the alteration of root growth and cell ultrastructure (curvature of newly formed cell walls and deformation of microtubule arrays) [108]. They highlighted that mitotic microtubules were more sensitive than cortical and, as a consequence, citral was able to disrupt mitotic microtubules, inhibiting the cell cycle and increasing the frequency of asymmetric cell plates in treated cells by directly interfering on cell plates during their formation . [52][53]

More recently, Graña et al. [54] were able to further confirm the citral-mediated inhibition of cell division and to link for the first time the ultrastructure cellular alteration to a biased hormonal balance (auxin and ethylene), and to a reduction in plasmodesmata-mediated cell-cell communication. In addition, through a staining technique, the authors have been able to histolocalize citral accumulation in *Arabidopsis* roots demonstrated that it accumulates mainly in the differentiation zone [55].

Finally, in 2020, through a transcriptomic and molecular docking approach, Graña et al. [56] demonstrated that just 1 h of exposition to citral was enough to induce inhibition of the single strand DNA-binding proteins, as a consequence, downregulating the transcription of the genes.

A link between cell division, microtubule organization, and the hormonal level was also highlighted by Araniti et al. [57][58] with the sesquiterpene farnesene. This ubiquitous molecule, generally present in low concentrations in



various plant species, has been shown to play a fundamental role in the defense of the plant, and the increase in its production is closely linked to the presence of stress [59][60]. Araniti et al. demonstrated that farnesene was inducing reactive oxygen species (ROS) accumulation, alteration of cell division (bi- and tetranucleated cells), and anisotropic growth of the root (left-handedness and loss of the gravitropic response), mainly due to auxin-mediated microtubule malformations. Further investigating this phenomenon, they were able to demonstrate that the microtubule malformation was a consequence of altered auxin distribution. In fact, during their experiments they observed that farnesene was able to downregulate all the auxin polar transport proteins (PIN proteins) and, through a confocal microscopy approach using GFP (green fluorescent protein) mutant lines, they were able to observe a complete absence of the proteins PIN4 and PIN7, pivotal for auxin redistribution in the root meristem, at the level of the quiescent center. Furthermore, they demonstrated anatomically that the left-handedness phenotype was due to a difference in length between the inner cell of the root meristem and the epidermal cells. In particular, because of farnesene-mediated microtubule malformations, the inner cells were shorter than epidermal cells and the last was characterized by an abnormal shape.

In addition, the sesquiterpene alcohol nerolidol induced in *A. thaliana* an alteration in root morphology, growth, and development, altering the auxin balance and inducing ROS accumulation followed by lipid peroxidation. Moreover, as observed in farnesene, the primary root was characterized by a random corkscrew shape indicating a possible alteration of the cortical microtubules. On the other hand, plants were able to counteract the stress by increasing the activities of the two ROS scavengers, superoxide dismutase, and catalase, as well as inducing the production of metabolites with osmoprotectant activity. The metabolomic pathway analysis highlighted that starch and sucrose metabolism, alanine, aspartate, and glutamate metabolism, and glycine, serine, and threonine metabolism were the most affected pathways [61].

Similar to farnesene, Yan et al. [62] reported that artemisinin, a sesquiterpene endoperoxide, was inducing in lettuce root tips an arrestment of cell division, and the loss of cell viability because of an artemisin-induced ROS burst followed by an increase of lipid peroxidation and damages to the cell membrane. Successively, they also demonstrated that the same molecule altered the root gravitropic responses, as well as root growth, development, and architecture, in seedlings of *Arabidopsis thaliana*. They further demonstrated that the gravitropic alterations observed were mainly due to a reduction in the number of starch grains in the columella cells and to altered auxin lateral distribution (inhibition of the PIN2 carrier) [63].

All those findings are extremely interesting since the ability of terpenoids to inhibit and/or alter mitosis and cell division is a phenomenon that has been largely reported in the past [64], but only now it is possible to affirm that such alterations are the consequence of the direct effects of these molecules on microtubule organization, suggesting that terpenoids, at least those which are able to affect mitosis, can be considered as a class of mitotic disrupter bioherbicides [65].

However, in vitro experiments are pivotal for rapid and economic screening of molecule phytotoxicity, for the identification of the main target (root and shoot), for the identification of key concentrations (e.g., effective and lethal doses), and for the potential identification of their mode of action under controlled conditions; often the



effects observed in vitro on seedlings do not coincide with those observed on adult plants of the same species [66][67]. Therefore, it is usually necessary to increase the concentrations of the molecules assayed to observe phytotoxicity effects.

For example, the terpenoid citral was extremely active in vitro at concentrations of 194  $\mu\text{M}$  ( $\text{IC}_{50}$ —dose necessary to inhibit the root length by 50%), whereas it was necessary to increase its concentration at least 10 times to see phytotoxic effects on adult plants .

In particular, they observed that the application of citral through irrigation or spraying had completely different effects on plants, suggesting that foliar or root absorption can determine the effectiveness of this compound. Anyway, the sub-irrigation method was the most effective, inducing an alteration of the plant water status followed by oxidative stress and damages to the photosynthetic machinery, which resulted in a strong reduction of plant growth and development. The same authors, further investigating the effects of this molecule on the plant water balance, observed a time-dependent reduction of stomatal conductance accompanied by a reduction of leaf relative water content and its water potential. Moreover, the plant fitness was extremely compromised since treated plants were unable to complete their leaf cycle because of a premature withering of the flowers and the inability to produce silique and develop seeds. These effects are extremely encouraging since citral application, if its effects are reproducible on weed species, could be used as an eco-friendly herbicide able to reduce the fitness of the crop competitors, without completely eradicating them (allowing the maintenance of the biodiversity in the agroecosystem), and to strongly reduce the weed seed bank in the soil.

In addition to mitosis, the alteration of the plant water status is a phenomenon commonly observed in adult plants treated with terpenoids. For example, it was reported that the lipophilic layers of the leaf surface and the stomata are primary targets of menthol and camphor. Full expanded rosettes of *Arabidopsis* exposed for different hours to monoterpenes vapors were characterized by an increase of stomatal aperture, followed by an extreme swelling and a final breakdown of the protoplasts, and alteration of cuticular wax layer, which induced, as a consequence, huge water loss and plant death [68]. They further demonstrated that both compounds, in particular camphor, prevented stomatal closure and inducing changes to stomata cytoskeleton, which plays a pivotal role in stomatal movements. Moreover, the prolonged treatment induced a reduction of the expression of the genes MPK3 and ABF4, which encode for proteins involved in the process of stomatal closure, and a concomitant downregulation of the PEPCase expression, which is an enzyme important for stomatal opening. All these effects were followed by an alteration of the plant water status accompanied by a reduction in growth and development, and final plant death if the exposure to vapors was prolonged for more than 48 h [69].

Araniti et al. [70] observed that adult plants of *Arabidopsis* treated through irrigation with the sesquiterpene *trans*-caryophyllene were characterized by pinwheel-shaped rosettes. In addition, this phenomenon is known as handedness since it could interest both root and shoot organs. Regardless, as for the roots, it is due to a microtubular alteration and a disturbance to their dynamic unstable equilibrium. Such a phenomenon was observed in plants subjected to salinity stress [71]. As for salinity stressed plants, and plants treated with this sesquiterpenoid were characterized by a significant alteration of the plant water status accompanied by an accumulation of reactive

oxygen species and lipid peroxidation, which led to physical damages in the PSII antenna complexes and a consecutive reduction of carbon assimilation [70].

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