

Review

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## Roles of citrus secondary metabolites in tree and fruit defence against pests and pathogens

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**ABSTRACT:** Plants have evolved several mechanisms to protect themselves from different biotic and abiotic challenges, including pest and pathogen attacks. One of the most important mechanisms is the secondary metabolites (SM) (terpenes, phenolics and nitrogen/sulphur-containing compounds). The plants have synthesised diverse compounds in different concentrations (mostly in tiny quantities) and have essential roles in plant defence, survival, adaptation, and reproduction. Citrus crops are among the most essential cultivated fruit groups and are rich in terpenoids and phenolics. Besides the well-known benefits of these compounds on human health, they have a significant role in plant/fruit defence against biotic and abiotic challenges. This review highlights the importance of these compounds (such as limonene, citral, saponin, hesperidin, quercetin, tangeritine, caffeic acid, p-coumaric acid, scoparone, etc.) and discusses their roles in tree and fruit defence against pests and pathogens. In today's world, where there is an essential human impact on nature, a need is raised to reduce pesticides against pests and pathogens. Therefore, understanding the roles of these SM and their induction is believed to have a significant positive impact on the production and/or storage of horticultural crops and may help reduce the use of synthetic agrochemicals. In line with this information, the present review was aimed to provide background information for researchers, farmers, horticulturalists and technology developers about the potential benefits of SM on plant/fruit defence and a guideline about their induction.

## 1. INTRODUCTION

Plants face many challenges in their natural or introduced environments, including pest & pathogen attacks, drought stress, nutrient deficiency, salinity, etc. Plants have evolved some biochemical pathways that help them adapt to these environments (Reymond et al., 2000). Plants synthesize two groups of organic compounds/metabolites. The primary metabolites (produced in large quantities, i.e. carbohydrates, proteins, lipids, amino acids and hormones) mainly involve in regular vital processes including photosynthesis, respiration, growth and development, and the secondary metabolites (produced in small quantities) most commonly have significant roles in the adaptation of plants to different biotic and abiotic environmental conditions (Bhatla & Lal, 2018). One of the essential roles of secondary metabolites (SM) in plants is the plant defence system against pests and pathogens. The two other important roles are attracting beneficial insects (for pollination and seed dispersal) and allelopathy (competition among the plants) (Wink, 2003). Several different characteristics like composition, solubility, pathway, etc., can be used for grouping SM. According to Bhatla and Lal (2018), SM can be grouped as terpenes, phenolics and nitrogen/sulphur-

containing compounds. Terpenes are naturally produced by numerous plants, which are characterized by their volatile nature. Some important subgroups of terpenes are essential oils, pigments, plant hormones, rubber and steroids. They are chemically lipophilic products of 5-carbon isoprene. This is among the most diverse group of SM with more than 30.000 compounds. The volatile characteristic and strong odour (insecticidal property) give terpenes the ability to deter pests (Rohmer, 1999); Bhatla and Lal, 2018). Phenolics are the second important class of SM composed of one or more phenolic groups (with 6-carbon). The polyphenols can be simple molecules (such as flavonoids and phenolic acid) or complex molecules (i.e. lignin, coumarin and tannin) (Bhatla & Lal, 2018; Treutter, 2006). Nitrogen/sulphur-containing compounds are the third groups of SM that contain nitrogen or sulphur in their structure, including alkaloids (caffeine, nicotine, morphine, etc.), glycosides (saponins and cyanogenic glycosides) and some non-protein amino acids (Crozier & Clifford, 2008; Zenk & Juenger, 2007).

The SM in plants constitute a diverse group of compounds produced in tiny quantities and have no direct role in primary metabolism but have a vital role in plant defence, survival, adaptation, and reproduction (Berini et al., 2018; Kroymann,

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2011). Some terpenes, i.e. carotenoids, was reported to protect tissues from photoprotection and extend the range of light used in photosynthesis, which improves the adaptation of such plants to extreme light and temperatures (Strzałka et al., 2003). Moreover, it was noted that the saponins concentration of some plants increase under hot and cold weather conditions and play an important role in adaptation (Szakiel et al., 2011). A triterpene saponin, the glycyrrhizin, was reported to enhance the UV protection of the plants (Afreen et al., 2005). On the other hand, tannins are reported to improve the adaptability of plants to climatic stresses conditions, such as drought, high heat and light (L. Yang et al., 2018). Additional to abiotic stress conditions, the biotic stress conditions can also induce defence response in plants with the help of specific recognition and signalling systems (Schaller & Ryan, 1996). Most of these SM of the plants are accepted as natural insecticides, which help their survival and defence in natural environments. Such as, nicotine deters herbivores which have also been commercially used as an insecticide (Soloway, 1976).

Similarly, pyrethrins, azadirachtin and limonoids have strong insect deterrent ability and are commercially produced and used in agricultural systems (Clemensen et al., 2020). Besides the functions of these SM in plants in their natural environments, thanks to science, most of these SM are being induced in plants by external applications or used in industry to produce insecticides, herbicides, aromas, gums, cosmetics, flavour enhancers, etc. (Caputi & Aprea, 2011; Freeman & Beattie, 2008; Zillich et al., 2015). Moreover, most of these SM has been used in the pharmaceutical industry due to their scientifically confirmed health benefits (Mendoza & Silva, 2018). Clemensen et al. (2020) identify SM as agents responsible for communication among plants and their environment. They also reported that a better understanding of SM and their roles in agroecology would be beneficial for reducing the negative environmental impacts.

Citrus crops (oranges, mandarins, tangerines, grapefruits, pomelos, lemons and limes) are among the most important fruit groups, with a total of 143 M tonnes of production globally 2019 (FAOSTAT, 2021). Citrus trees/fruits are rich in terpenoids (mostly essential oils and carotenoids) and phenolics (mostly flavonoids). These SM of citrus fruits have an important role in plant/fruit defence against biotic and abiotic stress conditions. Moreover, they have important benefits on human health and have been used in traditional medicine and the food industry (M'hiri et al., 2017). The primary hypothesis of this study is that citrus trees/fruits contain a diverse and essential amount of SM and these phytochemicals have an essential role in plant defence. Moreover, this research aims to provide background information for researchers, farmers, horticulturalists and technology developers about the potential benefits of SM on plant/fruit defence and a guideline about their induction. It is believed that the induction of the SM in plants or their external applications would have a tremendous positive impact on the production and/or storage of horticultural crops, mainly by reducing the need for synthetic agrochemicals and

better management of the lands.

## 2. RESEARCH METHODOLOGY

This is a literature review study that was conducted by collecting literature from several databases. First of all, some keywords were identified for the literature search. The identified keywords are citrus phytochemicals, SM of citrus plants, SM of citrus fruits, citrus phytochemicals and plant defence, citrus phytochemicals and fruit defence, plant defence and citrus SM, fruit defence and citrus SM, citrus terpenes, citrus phenolics, citrus limonene, citrus saponin, citrus citral, citrus quercetin and citrus scoparone. Then, these words were searched on Web of Science, ScienceDirect and Google Scholar. The First 20 papers of these databases (for each keyword) were downloaded and analysed in terms of the suitability of the contents. Finally, the remaining suitable papers were read, reviewed, discussed, and used to prepare the present paper.

## 3. ROLES OF MAIN CITRUS SM IN PLANT/FRUIT DEFENCE

Citrus trees/fruits (including orange, lemon, mandarin, grapefruit and lime) synthesize and accumulate a great diversity of SM, which verifies the research hypothesis (Table 1.), including alkaloids, flavonoids, phenols, tannins and saponins (Okwu, 2008). The most abundant and known SM in citrus trees are the limonoids, with the most common limonene, limonin and nomilin (Craig, 1997). Limonene is very abundant in lemon (*Citrus limon*) trees. It is primarily responsible for the bitterness of lemon fruits and leaves too. It is reported to be immediately realized after the attack of pests as a repellent and attract natural predators, like wasps (Bhatla & Lal, 2018).

An unsaturated aldehyde, the citral, is among the main components of citrus fruit peel oil and provide a lemon-like pleasant odour. It is mainly used in the food industry to provide lemon aroma and flavour. It has a high antifungal and antimicrobial activity (Tamer et al., 2019). Saponin, a glycoside of both steroids and triterpenes, have been reported to exist in the leaves, peels, root, stem bark, and stem (from high to low) in lime (*Citrus aurantifolia*), pummelo (*C. grandis*), lemon (*C. limon*), grapefruit (*C. paradisi*), mandarin (*C. reticulata*) and sweet orange (*C. sinensis*) (Ezeabara et al., 2014). Another group of SM in citrus trees is the carotenoids. Grapefruits are known to have a high content of  $\beta$ -carotene and lycopene, where other citrus fruits (i.e. orange and tangerines) contain a significant amount of lutein and zeaxanthin (Mangels et al., 1993).

Flavonoids, a subclass of phenolics, are another essential SMSM in citrus trees/fruits. Hesperidin, quercetin, tangeritin, rutin and naringin are among the most common flavonoids in citrus trees/fruits. These flavonoids are primarily responsible for the bitterness of lemons and oranges (Bhatla & Lal, 2018; Okwu, 2005; Okwu & Emenike, 2006).

**Table 1**  
Principal roles and basic information about the most unique/common SM of citrus trees/fruits

No	Class	Compound Name	Molecular Formula	Citrus species	Place on citrus tree	Main role(s) in plants/fruits (not only citrus crops)	References
1	Terpenes	Limonene	C <sub>10</sub> H <sub>16</sub>	• Lemon • Orange • Grapefruit • Mandarin • Lime	• Fruit peel • Fruit • Leaves	• Responsible from bitterness • Protect against pests (insect repellent) • Attract beneficial pests	<a href="#">Bhatla and Lal (2018)</a> ; <a href="#">NCBI (2021)</a>
2	Terpenes	Citral	C <sub>10</sub> H <sub>16</sub> O	• Orange • Lemon • Lime	• Fruit peel	• Show antimicrobial, antifungal, and antiparasitic abilities • Protect fruits against <i>Penicillium digitatum</i> , <i>P. italicum</i> and <i>Aspergillus niger</i>	<a href="#">Chutia et al. (2009)</a> ; <a href="#">Tamer et al. (2019)</a>
3	Terpenes	Saponin	C <sub>58</sub> H <sub>94</sub> O <sub>27</sub>	• Lime • Pummelo • Lemon • Grapefruit • Mandarin • Sweet orange	• Leaves • Peels • Root • Stem bark • Stem	• Toxic to insects and works as feeding deterrents against herbivores • Have an essential impact on pathogens like fungi, molluscs, some bacteria and viruses • Have toxic effects against bacteria, fungi and pests • Reduce development and reproduction of pests	<a href="#">Ezeabara et al. (2014)</a> ; <a href="#">Hussain et al. (2019)</a> ; <a href="#">Zaynab et al. (2021)</a>
4	Terpenes - Carotenoids	β-Carotene	C <sub>40</sub> H <sub>56</sub>	• Grapefruit • Mandarin	• Fruit peel	• Responsible for the orange and yellow colours • Contribute photosynthesis by harvesting light energy • Buffer singlet oxygen and reduce reactive oxygen species (ROS) activity and prevent oxidative damage • Activate cellular defence system of plants	<a href="#">Ahmed and Azmat (2019)</a> ; <a href="#">Mangels et al. (1993)</a> ; <a href="#">Mcelroy and Kopsell (2009)</a> ; <a href="#">Shumbe et al. (2014)</a>
5	Terpenes - Carotenoids	Lycopene	C <sub>40</sub> H <sub>56</sub>	• Grapefruit • Orange	• Fruit peel	• Responsible for the orange, yellow and red colours • Absorb light for photosynthesis and protect plants from photosensitization • Buffer singlet oxygen and reduce reactive oxygen species (ROS) activity and prevent oxidative damage	<a href="#">Ahmed and Azmat (2019)</a> ; <a href="#">Mangels et al. (1993)</a> ; <a href="#">Mcelroy and Kopsell (2009)</a> ; <a href="#">A.V. Rao et al. (2006)</a>

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Table 1 continued

6	Terpenes - Carotenoids	Lutein	$C_{40}H_{56}O_2$	<ul style="list-style-type: none"> <li>• Grapefruit</li> <li>• Orange</li> <li>• Tangerine</li> <li>• Mandarin</li> </ul>	<ul style="list-style-type: none"> <li>• Fruit peel</li> </ul>	<ul style="list-style-type: none"> <li>• Responsible for the yellow and orange-red colours</li> <li>• Buffer singlet oxygen and reduce reactive oxygen species (ROS) activity and prevent oxidative damage</li> </ul>	<p><a href="#">Ahmed and Azmat (2019)</a>; <a href="#">Mangels et al. (1993)</a>; <a href="#">Mcelroy and Kopsell (2009)</a></p>
7	Terpenes - Carotenoids	Zeaxanthin	$C_{40}H_{56}O_2$	<ul style="list-style-type: none"> <li>• Orange</li> <li>• Tangerine</li> </ul>	<ul style="list-style-type: none"> <li>• Fruit peel</li> </ul>	<ul style="list-style-type: none"> <li>• Responsible for the yellow and bright colours</li> <li>• Protect plants against high-light stress</li> <li>• Protecting lipids of membranes against peroxidative damage</li> </ul>	<p><a href="#">Ahmed and Azmat (2019)</a>; <a href="#">Demmig-Adams et al. (2020)</a>; <a href="#">Mangels et al. (1993)</a></p>
8	Phenolics – Flavonoid glycoside	Hesperidin	$C_{28}H_{34}O_{15}$	<ul style="list-style-type: none"> <li>• Sweet orange</li> <li>• Tangerine</li> <li>• Sour orange</li> <li>• Lime</li> <li>• Lemon</li> <li>• Grapefruit</li> </ul>	<ul style="list-style-type: none"> <li>• Fruits</li> <li>• Fruit juice</li> <li>• Leaves</li> </ul>	<ul style="list-style-type: none"> <li>• Stimulates the oviposition of beneficial insect swallowtail butterfly on young leaves of citrus</li> <li>• Provide bitter taste to the fruits</li> <li>• Protect against microorganisms including fungi, bacteria and viruses</li> <li>• Provide antioxidant activity for the plants</li> </ul>	<p><a href="#">Bhatla and Lal (2018)</a>; <a href="#">Iranshahi et al. (2015)</a>; <a href="#">Yumol and Ward (2018)</a></p>
9	Phenolics – Flavonoid	Quercetin	$C_{15}H_{10}O_7$	<ul style="list-style-type: none"> <li>• Grapefruit</li> <li>• Orange</li> <li>• Limon</li> </ul>	<ul style="list-style-type: none"> <li>• Fruit</li> <li>• Fruit peel</li> <li>• Leaves</li> </ul>	<ul style="list-style-type: none"> <li>• Regulates the activity of antioxidant enzymes and protect against ROS</li> <li>• Act as auxin transport regulator and adjust polar auxin transports</li> <li>• Provides tolerance against several biotic (bacteria, fungi, etc. ) and abiotic stresses (salinity, UV, etc.)</li> <li>• Facilitates pollen growth, seed germination</li> <li>• May promote fruit loosening in oranges</li> <li>• Inhibits nucleic acid synthesis in some bacteria</li> <li>• Stimulates the oviposition of beneficial insect swallowtail butterfly on young leaves of citrus</li> <li>• Prevents egg laying of some pests</li> <li>• Increase the mortality of some parasitic wasps</li> <li>• Act as deterrents against some pests</li> </ul>	<p><a href="#">Ahmed and Azmat (2019)</a>; <a href="#">Kurepa et al. (2016)</a>; <a href="#">Makni et al. (2018)</a>; <a href="#">Mierziak et al. (2014)</a>; <a href="#">Okwu (2005)</a>; <a href="#">Okwu and Emenike (2006)</a>; <a href="#">Singh et al. (2021)</a>; <a href="#">Yuan et al. (2003)</a></p>

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*Table 1 continued*

10	Phenolics – Flavonoid	Kaempferol	$C_{15}H_{10}O_6$	<ul style="list-style-type: none"> <li>• Grapefruit</li> <li>• Orange</li> <li>• Limon</li> </ul>	<ul style="list-style-type: none"> <li>• Fruit peel</li> <li>• Fruit Leaves</li> </ul>	<ul style="list-style-type: none"> <li>• Act as deterrents against some pests</li> <li>• Improve the spore germination of mycorrhizal fungi</li> <li>• It inhibits the growth of some nematodes</li> <li>• Play a role in the auxin-dependent defence response of <i>Arabidopsis thaliana</i> and limits the systemic movement of the Cucumber mosaic virus</li> <li>• Prevents the growth of <i>Fusarium oxysporum</i></li> </ul>	<p>Galeotti et al. (2008); Likić et al. (2014); M'hiri et al. (2017); Mierziak et al. (2014)</p>
11	Phenolics – Flavonoid	Tangeretin	$C_{20}H_{20}O_7$	<ul style="list-style-type: none"> <li>• Grapefruit</li> <li>• Tangerine</li> <li>• Mandarin</li> <li>• Pummelo</li> <li>• Orange</li> </ul>	<ul style="list-style-type: none"> <li>• Fruit peel</li> <li>• Fruit Leaves</li> </ul>	<ul style="list-style-type: none"> <li>• Strengthens cell wall and improves plant defence against pathogens</li> <li>• Provides the antifungal ability to the plants, (i.e. <i>Phytophthora citrophthora</i> in Nova fruits)</li> </ul>	<p>Ahmed and Azmat (2019); Assini et al. (2013); Okwu and Emenike (2006); Sun et al. (2013)</p>
12	Phenolics – Flavonoid	Rutin	$C_{27}H_{30}O_{16}$	<ul style="list-style-type: none"> <li>• Grapefruit</li> <li>• Pummelo</li> <li>• Orange</li> <li>• Mandarin</li> <li>• Lemon</li> </ul>	<ul style="list-style-type: none"> <li>• Fruit</li> <li>• Leaves</li> </ul>	<ul style="list-style-type: none"> <li>• Increase the mortality of some parasitic wasps</li> <li>• Improve the spore germination of mycorrhizal fungi</li> <li>• Improves plant resistance against bacterial pathogens, (i.e. <i>Xanthomonas oryzae</i>, <i>Ralstonia solanacearum</i> and <i>Pseudomonas syringae</i>)</li> <li>• Enhance defence system against abiotic stresses (i.e. cold weather and UV light)</li> </ul>	<p>Mierziak et al. (2014); Okwu and Emenike (2006); Sun et al. (2013); Suzuki et al. (2015); W. Yang et al. (2016)</p>
13	Phenolics – Flavonoid	Naringin	$C_{27}H_{32}O_{14}$	<ul style="list-style-type: none"> <li>• Pummelo</li> <li>• Grapefruit</li> </ul>	<ul style="list-style-type: none"> <li>• Fruit</li> <li>• Leaves</li> </ul>	<ul style="list-style-type: none"> <li>• Inhibits the development of <i>Aphis craccivora</i></li> <li>• Stimulates nodulation in <i>Rhizobium leguminosarum</i></li> <li>• Act as an allelochemical and suppress the growth of some annual plant species</li> <li>• Improves plant tolerance against salinity stress</li> <li>• Induces resistance against some pathogens, i.e. <i>Pseudomonas syringae</i></li> </ul>	<p>An et al. (2021); Harborne and Williams (2000); Hernandez and Bosch (2012); Mierziak et al. (2014); Okwu and Emenike (2006); Sun et al. (2013)</p>

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Table 1 continued

14	Phenolics – Flavonoid	Anthocyanins (flavylium ion)	$C_{15}H_{11}O^+$	• Oranges • Lemons • Grapefruit	• Fruit • Fruit peel • Leaves	<ul style="list-style-type: none"> <li>• Commonly appear as red in leaf and fruit cells</li> <li>• Assist plants' defence systems against biotic stress and provides antiviral, antibacterial and fungicidal activities</li> <li>• Attract pollinators and seed dispersers</li> <li>• Discourage some of the herbivores (i.e. aphids, by deterring phloem sap)</li> <li>• Adaptation to low temperatures</li> </ul>	<a href="#">Lev-Yadun and Gould (2008)</a> ; <a href="#">Okwu and Emenike (2006)</a> ; <a href="#">Sun et al. (2013)</a> ; <a href="#">Wrolstad (2004)</a>
15	Phenolics – Phenolic acids	Caffeic acid	$C_9H_8O_4$	• Oranges • Mandarin • Lemon • Grapefruit • Bergamot	• Fruit peel • Leaves	<ul style="list-style-type: none"> <li>• Involves in lignin biosynthesis, regulates cell expansion, turgor pressure and phototropism</li> <li>• Provides tolerance against biotic (pathogens) and abiotic stress (low/high temperatures, UV, drought, salinity) conditions</li> <li>• Provides antifungal activity</li> <li>• Modulates the production of ROS in plant cells</li> </ul>	<a href="#">Ignat et al. (2011)</a> ; <a href="#">Lattanzio et al. (2009)</a> ; <a href="#">Martínez (2012)</a> ; <a href="#">M'hiri et al. (2017)</a> ; <a href="#">Riaz et al. (2019)</a>
16	Phenolics – Phenolic acids	p-coumaric acid	$C_9H_8O_3$	• Oranges • Mandarin • Lemon • Grapefruit • Bergamot	• Fruit peel • Leaves	<ul style="list-style-type: none"> <li>• Improves responses against oxidative and osmosis stress</li> <li>• Increase germination of cereal seeds</li> <li>• Have antimicrobial activity against <i>Bacillus cereus</i> and <i>Bacillus subtilis</i></li> </ul>	<a href="#">Boz (2015)</a> ; <a href="#">Ignat et al. (2011)</a> ; <a href="#">M'hiri et al. (2017)</a> ; <a href="#">Yue et al. (2019)</a>
17	Phenolics – Phenolic acids	Ferulic acid	$C_{10}H_{10}O_4$	• Oranges • Mandarin • Lemon • Grapefruit • Bergamot	• Fruit peel • Leaves	<ul style="list-style-type: none"> <li>• Improves plants' tolerance against necrotrophic pathogens</li> <li>• Reduce the chemical reactions of free radicals and prevent cell damage</li> <li>• Improves rigidity of cell wall</li> </ul>	<a href="#">Ignat et al. (2011)</a> ; <a href="#">M'hiri et al. (2017)</a> ; <a href="#">Reem et al. (2016)</a> ; <a href="#">Rosazza et al. (1995)</a>
18	Phenolics – Coumarin (a type of phytoalexin)	Scoparone	$C_{11}H_{10}O_4$	• Lemon • Mandarins • Orange • Grapefruit • Kumquats	• Fruit • Fruit peel	<ul style="list-style-type: none"> <li>• Provide resistance against some fungi and may reduce spore germination (i.e. <i>Penicillium digitatum</i> and <i>P. Expansum</i>)</li> <li>• Improves fruit resistance against some algae (i.e. <i>Phytophthora parasitica</i>)</li> <li>• Prevents fruit decay</li> </ul>	<a href="#">Kim et al. (1991)</a> ; <a href="#">Ladaniya (2008)</a> ; <a href="#">Ortuno et al. (1997)</a>

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Table 1 continued

19	Phenolics – Coumarin	Xanthyletin	$C_{14}H_{12}O_3$	• Orange	• Roots	• Inhibits symbiotic fungus ( <i>Leucoagaricus gongylophorus</i> ) cultivated by leaf-cutting ant ( <i>Atta sexdens rubropilosa</i> )	<a href="#">Cazal et al. (2009)</a>
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Phenolic acids (commonly the hydroxycinnamic acids) are among the essential SM of citrus trees/fruits. The four most common phenolic acids of citrus fruits are caffeic acid, ferulic acid, p-coumaric acid and sinapic acid (Ignat et al., 2011; M'hiri et al., 2017).

#### 4. MODE OF ACTION AND INDUCING BIOSYNTHESIS OF SM IN PLANTS/FRUITS

SM may have a different mode of action on the target pests and diseases. When the pests feed on plants with SM, most of these SM provide toxic characteristics for the herbivores by targeting different parts, including membranes, proteins and nucleic acids (Harborne, 2014). For example, the terpenes suggested blocking chemosensory receptor cells in the mouths of lepidopteran larvae (Gershenson & Dudareva, 2007). The mode of action of the essential oils was then suggested to be the disruption of the endocrinologic balance of pests (Balandrin & Klocke, 1988). A neurotoxic mode of action can also appear on some pests with knockdown due to hyper-excitation of the nerve blockage (Enan, 2001). Nerve poisoning can result in sudden death or paralysis for several days before death. Nicotine is a well-known example of nerve poisoning (Rattan, 2010). Rotenone was reported to disrupt the mitochondria of pest cells by uncoupling ATP synthesis and inhibiting the electron transport system (Rattan, 2010; Storey et al., 1981). Azadirachtin (a limonoid group of the compound from the Neem tree) is among the most important and well-known SM being commercialized against pests. It controls several insects by inhibiting protein synthesis, mainly at the stage from larva to pupa (Ujváry, 2010). It was also noted that azadirachtin inhibits the acetylcholinesterase (AChE has a vital role in the cholinergic system of insects) enzymes activity in some pests, such as *Nilaparvata lugens* (Nathan et al., 2008). To sum up, terpenoids mainly disturb the nervous system of insects by paralysis and mortality (Gershenson & Croteau, 1992), phenolics are generally damaging the gypsy moth (Rossiter et al., 1988), and alkaloid compounds are primarily toxic to vertebrates by damaging acetylcholine receptors in the nervous system (Rattan, 2010).

The SMSM's most common mode of action was noted to interfere with some parts (membranes, proteins and nucleic acids) of the diseases (Engelmeier & Hadacek, 2006). Bostock et al. (1999) suggested that the SM inhibit laccases production by pathogenic fungi. The same study reported that the caffeic acids in the epidermis of peach (*Prunus persica*) fruits improve membrane permeability and increase the resistance to *B. cinerea*. Another study suggested that the citral of plants/fruits penetrates the cell wall of *Aspergillus flavus* and irreversibly damages the membrane and DNA, and inhibit spore germination (Luo et al., 2002). Citral was also noted to have a high ability to form charge transfer complexes with electron donors and damage the fungi (Kurita et al., 1979). Similarly, the saponins have been suggested to produce complex with sterols in cell membranes of fungi and cause loss of membrane integrity (Keukens et al., 1995). Another mode of action for the

SM suggested that the resveratrol can inhibit ATPases in some fungi and damage the fungi (Kindl, 2000).

It has been reported that the concentration of SM in citrus significantly vary (mostly increase) under biotic and abiotic stress conditions. Such as, the infestation of *C. limon* trees with Asian citrus psyllid (ACP) was noted to cause an increase in the total concentration of 15 phenolic compounds (mostly caffeic acid and epicatechin) (Liu et al., 2020). Another study showed that the infestations with Huanglongbing (HLB) pathogen cause an increase in the concentration of secondary metabolites in leaves, fruits and stems of citrus trees (M.J. Rao et al., 2018). Infestation with *Diaphorina citri* was also found to increase the concentrations of citral and limonene from 4- to 20-folds in citrus plants (Hijaz et al., 2013). Eyles et al. (2009) suggested that the plant resistance to insects & pathogens could be explained with different metabolisms as basal resistance (Kiraly et al., 2007), age-dependent resistance (Develey-Rivière & Galiana, 2007), organ-specific resistance (Blodgett et al., 2007) and induced resistance (Agrawal & Tuzun, 1999). In induced resistance, several biotic or abiotic factors (Agrawal & Tuzun, 1999). Herein, the activation can be done by the pest & pathogen itself or by several biotic (polysaccharides, plant hormones, etc.) or abiotic factors (including UV light, drought, hot & cold temperature or external chemicals). It has been reported that acibenzolar-S-methyl can induce resistance in crops by working as a primer/activator and has been widely used as a crop protectant (Leadbeater & Staub, 2007). The site and function of the induced resistance in plants are very important in the success of the resistance. There are two main types as local defence and systemic defence. The main difference is that the local defence is activated at the initial attack or stress site, while the systemic defence occurs throughout the entire tree (Eyles et al., 2009).

Some plant hormones, most commonly jasmonic acid (JA) and salicylic acid (SA) are known to be involved in the induction of plant defence mechanisms by activating the defence-related genes. It was recommended that salicylic acid biosynthesis in fruits induces the accumulation of defence-related SM in citrus fruits and improves their resistance to the fungal pathogen (Zhang et al., 2021). Some researchers suggest that the pest and disease damages firstly increase the accumulation of such hormones, and these hormones activate the defence systems by improving the biosynthesis of some SM (Matsukawa et al., 2017). The gibberellic acid also induces SM, such as caffeic acid in *Echinacea purpurea* (Liang et al., 2013). Several different biotic elicitors had also been noted to induce the biosynthesis of different SM. Some examples are: oligogalacturonic acid increases saponin content in *Panax ginseng* (Hu et al., 2003), chitosan increases the coumarin content in *Ruta graveolens* (Orlita et al., 2008) and resveratrol content in *Vitis vinifera* (Taurino et al., 2015).

Studies also suggested that heat and drought stress can stimulate SM in two important rootstocks of citrus: *Carrizo citrange* and *Cleopatra mandarin* (Zandalinas et al., 2017). Drought causes oxidative stress in plants and enhances the



biosynthesis of SM, mostly flavonoids. Drought was previously noted to increase the concentrations of kaempferol and quercetin in tomato plants (Solíz-Guerrero et al., 2002). High temperature is known to induce the biosynthesis of SM, where the reverse (low temperature) may cause a reduction (Zu et al., 2003). Besides temperature, salinity is also known to impact the biosynthesis of SM. It commonly induces stress in plants and produces defence response pathways ROS production, which is responsible for the biosynthesis of SM (Manuka et al., 2019).

The quality of light (including length, power and repeat) can also play an essential role in the biosynthesis of SM (Zoratti et al., 2014). The biosynthesis of SM under extreme (abnormal) light conditions improves the defence system and improves their adaptations to the changing conditions (Jaakola & Hohtola, 2010). Studies by Camm et al. (1993) suggested that the long sunlight conditions increase the anthocyanins concentrations in *Pinus contorta*. The plants' increase in the red light reception was also noted to increase the important SM of citrus, including caffeic acid and kaempferol (Kliwer, 1997). A study with Citrus aurantium fruits suggested that UV irradiation improves the naringin and tangeretin concentrations and helps to reduce the infection with *Penicillium digitatum* (Arcas et al., 2000). Therefore, the induction of the biosynthesis of suitable SM in plants and/or fruits is an important method to control pests and diseases and reduce the need for synthetic agrochemicals.

## 5. CONCLUSIONS

Plants have evolved indigenous defensive mechanisms to adopt different biotic and abiotic environments, including pest and pathogen attacks. Herein the SM are very important biological tools for combating biotic and abiotic stress. The concentration of these SM in trees/fruits is deficient, and its stimuli are essential for the plant defence system. This review highlighted the importance of some biotic and abiotic factors that can stimulate the biosynthesis of these SM. Among the above-listed biotic and abiotic factors, the polysaccharides, phytohormones, light, hot temperature and drought are thought to be the most important ones, and it is of utmost importance to study their mechanism for inducing the SM. It is believed that the use of these factors can stimulate the biosynthesis of SM in trees/fruits and help to reduce the need for agrochemicals for controlling pests and diseases both in production and postharvest storage. It is strongly recommended that the researchers focus on this topic to improve the plants' /fruits' defence against pests and diseases by increasing the contents of SM.

## CONFLICTS OF INTEREST

The authors declare no conflict of interest in the submission and publication of this research.

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## AUTHOR CONTRIBUTIONS

IK and SU - Research concept and design, IK and SU - Collection and/or assembly of data, IK - Data analysis and interpretation, IK - Writing the article, IK and SU - Critical revision of the article, IK and SU - Final approval of the article.

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