Potential use of essential oils to enhance heat tolerance in plants

DE GRUYTER Z. Naturforsch. 2020; 75(7–8)c: 225–231

Review

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https://doi.org/10.1515/znc-2019-0233
Received December 25, 2019; revised February 22, 2020; accepted March 19, 2020

Abstract: Isothiocyanates, monoterpenes, and leaf volatiles that are components of essential oils induce the expression of heat shock protein genes in plant systems. Here, the modes of heat shock responses induced by the essential oil compounds and their heat-tolerance-enhancing activities are described. Traditionally, green manure produced from essential-oil-containing plants has been used because such manure is thought to have beneficial effects in fertilizing, allelopathic, antibacterial, and animal-repellent activities. In addition to these effects, stress (especially heat stress)-tolerance-enhancing activities can be expected. Biostimulants containing such essential oils may be able to maintain the yield and quality of crops under increasing ambient temperatures. In this review, chemicals that enhance the heat tolerance of plants are designated as heat tolerance enhancers (HTLEs). Some essential oil compounds can be categorized as HTLEs available for biostimulants.

Keywords: heat shock protein; heat shock response; heat tolerance enhancers; isothiocyanates; monoterpenes.

1 Introduction

Essential oils are plant specialized metabolites having characteristic odors. They have been used as traditional herbs, perfumes, food seasonings, and beverage flavorings [1–3]. Essential oils have also been used as pharmaceuticals, such as anti-inflammatories, analgesics, sedatives, and spasmolytics [4, 5]. Preservation and repellence are important purposes of essential oils because they have effective antimicrobial, insecticidal, and antifeedant activities [6–8]. In nature, essential oils affect the growth of plants that neighbor essential-oil-producing plants. Some of them are allelochemicals that inhibit seed germination [9, 10]. Conversely, recent studies have proposed that volatile compounds contained in essential oils might provide benefits to plants growing in unfavorable environments [11–13].

Climate changes affect agricultural production in complex ways. It has been projected that yields of major crops may decrease due to local warming if the crops do not adapt to environmental changes [14–16]. Extreme heat waves severely inhibit plant growth and reduce world crop production [17, 18]. Another opinion is that the ancestors of crop species may have had the potential to adapt to high ambient temperatures because angiosperms evolved during the warm climate periods after the Mesozoic era. However, the heat tolerance of present crops may be low because they were bred during the Quaternary ice ages. This may be a reason why the yields and qualities of today’s crops decrease in elevated temperatures. According to physiological experiments, even plants growing at high latitudes can survive in high-temperature environments after they become acclimated [19]. This supports the idea that any crop species can bear high ambient temperatures if their heat tolerance systems are sufficiently activated.

Various countermeasures have been developed to reduce losses of yield and quality during heat waves. Indoor farming systems are available to control growth temperatures [20]. Breeding can produce thermotolerant crops. Although these tactics are effective, they are too costly and time-consuming to easily apply in many cases. Moreover, the cultivation of crops produced by molecular breeding, including genetic transformation and genome editing technologies, has not completely obtained acceptance from society [21]. Recently, biostimulants that can enhance the growth of plants and ameliorate their stress symptoms have been practically used in agriculture [22–24]. However, few biostimulants designed to enhance the heat tolerance of crops have been developed. This review describes the beneficial effects of essential oil compounds to plants, especially activities that enhance

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heat tolerance. Mechanisms for ameliorating heat damage and their possible application to agriculture are also discussed. In this paper, chemicals that increase the heat adaptability of plants are designated as heat tolerance enhancers (HTLEs).

2 HTLEs as biostimulants

It is known that biostimulants consist of biosubstances and microorganisms that enhance crop yield and quality [25, 26]. They are produced from humic substances, protein hydrolysates, seaweeds, land plants, chitosan, inorganic compounds, and beneficial microorganisms [24]. Biostimulants alleviate abiotic stresses in crop production. It has been reported that a large number of biostimulants could enhance the drought, salinity, and cold tolerance of plants [26]. In contrast, limited examples of biostimulants (e.g. *Pseudomonas putida*, protein hydrolysates, and seaweed extracts) have been shown to elevate the heat tolerance of crops [26]. Thus, studies on HTLEs promote the development of efficient biostimulants to reduce heat damage to crops.

2.1 Physical response to heat shock

Plants respond to heat with various symptoms, such as membrane fluidization, protein denaturation, enzyme inactivation, metabolic disturbances, photosynthesis inhibition, and reactive oxygen species (ROS) generation [27–29]. Heat-exposed plants accumulate compatible solutes, enhance antioxidative activities, and express heat shock proteins (HSPs) [30, 31]. HSP expression is a major response to elevated temperature for many organisms. HSPs are molecular chaperones that can prevent the heat denaturation of proteins. They have different classes, such as HSP60s, HSP70s, HSP90s, HSP100s, and small HSPs characterized according to molecular weight. As HSPs protect proteins from denaturation, organisms including plants can tolerate high temperatures when HSPs are highly expressed [27, 32, 33]. Indeed, heat tolerance has been shown to be enhanced by the overexpression of *HSP* genes in transgenic plants [34–36]. Mutants exhibiting reduced expression of *HSP* genes have been reported to show hypersensitivity to high ambient temperatures [37, 38]. This means that substances enhancing the expression of *HSP* genes are promising biostimulants for ameliorating heat damage to crops.

2.2 HTLEs

Although elevation of ambient temperature is the most effective cue for the induction of *HSP* genes [i.e. heat shock response (HSR)], some phytochemicals also induce apparent HSR in plants. It has been found that salicylic acid [39], benzyl alcohol [40], celastrol [41], isothiocyanates [11], sanguinarine [42], monoterpenes [12], and (*E*)-2-hexenal [13] induce HSR in plants, indicating that these chemicals are HTLEs. Plant-derived HSR inducers that have been identified by using plant systems are summarized in Table 1. In most cases, the mechanisms underlying HSR induction by phytochemical HTLEs have not been elucidated. However, the HSR-inducing mechanism of geldanamycin (GDA) in the *Arabidopsis thaliana* (L.) Heynh. system has been proposed [44]. GDA, a benzoquinone ansamycin antitumor antibiotic, is an inhibitor of HSP90 [45]. In *Arabidopsis* cells under normal conditions, HSP90 holds and inactivates a heat shock factor (HSF), a transcription factor for the induction of HSR. GDA inhibits HSP90 via its ATP-binding pocket and facilitates the release of HSF from HSP90. This can trigger HSF activation, after which HSR occurs. Moreover, various HSP90 inhibitors other than GDA could also induce the

Table 1: Plant-derived HSR inducers in plant systems.

Compound	Chemical group	Tested plant	Reference
Sanguinarine	Alkaloids	*Arabidopsis thaliana* (L.) Heynh.	[42]
Salicylic acid	Aromatics	*Arabidopsis thaliana* (L.) Heynh.	[39]
Benzyl alcohol	Aromatics	*Physcomitrella patens* (Hedw.) B.S.G.	[40]
(*S*)-Perillaldehyde	Monoterpenes	*Arabidopsis thaliana* (L.) Heynh.	[12]
d-Limonene	Monoterpenes	*Arabidopsis thaliana* (L.) Heynh.	[12]
Celastrol	Triterpenes	*Physcomitrella patens* (Hedw.) B.S.G.	[41]
Phenethyl isothiocyanate	Isothiocyanates	*Arabidopsis thaliana* (L.) Heynh.	[11]
Isopropyl isothiocyanate	Isothiocyanates	*Arabidopsis thaliana* (L.) Heynh.	[43]
(*E*)-2-Hexenal	Carbonyls	*Arabidopsis thaliana* (L.) Heynh.	[13]

HSR of *Arabidopsis* [46], suggesting that HSP90 is likely a major regulator of the HSR. Recently, the benzophenanthridine alkaloid sanguinarine was predicted to have a similar mechanism to GDA. When GDA and sanguinarine were added to *Arabidopsis* plants, similar dose and time-course responses were observed in the gene expression and protein accumulation of HSPs [42, 47]. GDA and sanguinarine inhibited luciferase folding by wheat (*Triticum aestivum* L.) germ chaperones at similar efficiencies [47]. This suggests that sanguinarine induces HSR probably via the inhibition of chaperones that hold HSF [48]. However, it is unclear how essential oil HTLEs such as isothiocyanates and monoterpenes promote HSR in plants. In the following section, the features of essential oil HTLEs are described in detail.

3 Isothiocyanates

Isothiocyanates are sulfur-containing volatile compounds. The common chemical formula is R–N=C=S, in which N=C=S is the isothiocyanate group. More than 100 isothiocyanates have been identified from Brassicaceae, Capparaceae, and Caricaceae plants, whereas Brassicaceae is the major producing family [49]. Isothiocyanates are produced from thioglucosides (glucosinolates) by a specific thioglucosidase (myrosinase, EC 3.2.3.1). As glucosinolates and myrosinases are localized in different cellular and subcellular compartments, the emission of isothiocyanates by plants is kept at low levels [50, 51]. Once cells are mechanically damaged, glucosinolates and myrosinase can access each other, and then isothiocyanates are produced. This reaction is called the glucosinolate-myrosinase system [52]. As typical isothiocyanates are pungent, plants producing them are used as condiments, including mustard (*Brassica juncea* L.), wasabi (*Wasabia japonica* Matsum.), and watercress (*Nasturtium officinale* R. Br.). Moreover, the physiological functions of isothiocyanates in plants have been studied. The emission of isothiocyanates is thought to be a defense system of plants producing glucosinolates, because isothiocyanates inhibit the growth of microorganisms and repel herbivores [52]. Isothiocyanates also affect the growth of plants: they inhibit seed germination and retard plant growth. Aromatic isothiocyanates show more severe growth inhibition than aliphatic isothiocyanates [53]. Growth inhibition by isothiocyanates might be due to interference with cellular functions. Allyl isothiocyanate inhibits the movement of filaments and actin-dependent intracellular transport in *Arabidopsis* [54].

Traditionally, Brassicaceae plants have been used as green manures to improve crops and inhibit weeds [55]. The effects of Brassicaceae green manures are thought to be based on the antimicrobial, animal-repellent, and allelopathic activities of isothiocyanates. In recent studies, however, isothiocyanates showed positive effects on the stress tolerance of plants at concentrations lower than herbicidal doses. When about 1 mM of isothiocyanates was administered to *Arabidopsis*, the expression of *HSPs* and the heat tolerance of the plants were enhanced [11], suggesting that isothiocyanates acted as HTLEs in the plants. However, isothiocyanates at higher concentrations (10–100 mM) killed the plants by inducing oxidative burst-like responses, such as hydrogen peroxide generation and leaf bleaching [56]. Moreover, the levels of HSR-inducing activities differed among isothiocyanates: the activities of aliphatic isothiocyanates were stronger than those of aromatic isothiocyanates [43]. The strongest inducer of HSR was isopropyl isothiocyanate. This indicates that choosing both the appropriate molecular species and their concentrations is crucial for the use of isothiocyanates as HTLEs. Other studies indicated that allyl isothiocyanate induced stomatal closure and upregulated glutathione *S*-transferases, which are detoxifying enzymes, suggesting that isothiocyanate may protect plants from damage caused by environmental stresses [56, 57]. Brassicaceae green manures are biostimulants from which diverse effects (i.e. antimicrobial, animal-repellent, allelopathic, and stress-ameliorating activities) are expected.

4 Monoterpenes

Monoterpenes consisting of C10-isoprenoid structures are major components of essential oils produced by plants. The basic structures of monoterpenes are biosynthesized from geranyl diphosphate and/or neryl diphosphate [58]. Highly diverse structures are organized by additional rearrangements and oxidations. As monoterpenes have characteristic flavors, they have been used as components of food flavorings, folk medicines, and cosmetics [5]. Monoterpenes have many physiological functions, such as health-protective (e.g. antioxidative, anti-inflammatory, and chemoprotective activities) [4] and chemical-ecological functions (e.g. antibacterial, insecticidal, and repellent activities) [5, 6]. They are known to affect plant growth. Many reports have examined their allelopathic and herbicidal activities. Myrcene and ocimene induce the expression of stress- or defense-related genes of *Arabidopsis* [59]. Some monoterpenes severely damage plant cells by inducing apoptosis-like cell death [60]. Besides such growth-inhibition activities, monoterpenes have been implicated in stress tolerance, especially thermotolerance. The heat tolerance of *Quercus* species is enhanced by exogenous monoterpenes [61, 62], probably due to their membrane stabilization activities and ROS scavenging activities [61, 63]. As the emission of monoterpenes by *Quercus ilex* L. is promoted by heat stress, monoterpenes are likely chemical messengers that transduce heat signals from plants to other plants. Heat-induced monoterpene emission has also been observed in *Solanum lycopersicum* L. [64] and *Musa* species [63]. Recently, it was reported that monoterpenes such as d-limonene, (*S*)-perillaldehyde, d-camphor, (−)-borneol, 1,8-cineol, and α-pinene induce the HSR of *Arabidopsis*. Therefore, these monoterpenes are HTLEs [12]. This suggests that the heat-tolerance-enhancing activities of monoterpenes in plants might be attributable partially to the promotion of HSP accumulation. It is noteworthy that the fumigant used to enhance the heat tolerance of *Q. ilex* contains d-limonene and α-pinene, which were found to induce HSR in the *Arabidopsis* system [61, 65].

As monoterpenes show antibacterial, insecticidal, and repellent activities, plant extracts rich in monoterpenes can be used as biostimulants to reduce pathogenic and feeding damage to crops. In addition, biostimulants containing monoterpene HTLEs can reduce heat-related crop damage. Although (*S*)-perillaldehyde and d-limonene are potent HSR inducers, they have rather narrow ranges effective for HSR-inducing activities [12], suggesting that these monoterpenes are not suitable for use as biostimulants to enhance heat tolerance. Conversely, d-camphor, (−)-borneol, 1,8-cineol, and α-pinene are possible components of biostimulants as HTLEs because these monoterpenes have wide effective doses for HSR-inducing activities [12].

5 Others

Reactive short-chain leaf volatiles induce the HSP genes of *Arabidopsis* [13]. The effective volatiles are (*E*)-2-hexenal and (*E*)-2-butenal. They are α,β-unsaturated carbonyls, which are produced from polyunsaturated fatty acids by peroxidation. Benzene derivatives (a series of chlorophenols, benzyl alcohol, and salicylate) activate the heat shock promoter of moss *Physcomitrella patens* (Hedw.) B.S.G. [41]. As these chemicals can be categorized as HTLEs, plant residues and extracts containing these chemicals can be used as biostimulants.

6 Action mechanisms of essential oil HTLEs

The comprehensive mechanisms of chemical HSR inducers have not been confirmed. Benzyl alcohol, which has been traditionally used to induce HSR in some organisms, was believed to enhance membrane fluidity in cells [66]. In a previous study, high concentrations of benzyl alcohol (e.g. >10 mM) were needed to induce efficient HSR [67]. However, the effective concentrations of essential oil HTLEs, such as isothiocyanates and monoterpenes, were apparently lower than that of benzyl alcohol, suggesting that the action mechanisms of isothiocyanates and monoterpenes were different from that of benzyl alcohol.

As GDA and sanguinarine efficiently inhibit wheat chaperones at micromolar concentrations, these compounds have been designated as chaperone-inhibition-type HTLEs. However, (*S*)-perillaldehyde is not categorized as a chaperone-inhibition-type HTLE because the monoterpene weakly inhibits wheat chaperones at millimolar levels [12]. Moreover, isothiocyanates also show slight inhibition of wheat chaperones at millimolar concentrations (our unpublished results). Accordingly, (*S*)-perillaldehyde and isothiocyanates should be designated as non-chaperone-inhibition-type HTLEs. As (*S*)-perillaldehyde and isothiocyanates are known to induce ROS production in cells [56, 68], such HTLEs may induce HSR via ROS signaling (Figure 1). Further studies are required to confirm the HSR-inducing mechanisms of non-chaperone-inhibition-type HTLEs.

7 Practical uses of essential oil HTLEs

As essential oils such as isothiocyanates and monoterpenes have allelopathic, antimicrobial, insecticidal, and repellent activities, biostimulants containing these compounds are expected to reduce the damages by weeds, pathogens, and herbivores. In addition, some monoterpenes and isothiocyanates enhance the heat tolerance of plants by inducing the expression of HSP genes. HSPs are related to not only heat tolerance but also diverse stress tolerances, suggesting that the high expression state of HSPs provided by essential oil HTLEs enables plants to tolerate various stresses (Figure 2). If that is the case, biostimulants containing essential oil HTLEs may be able

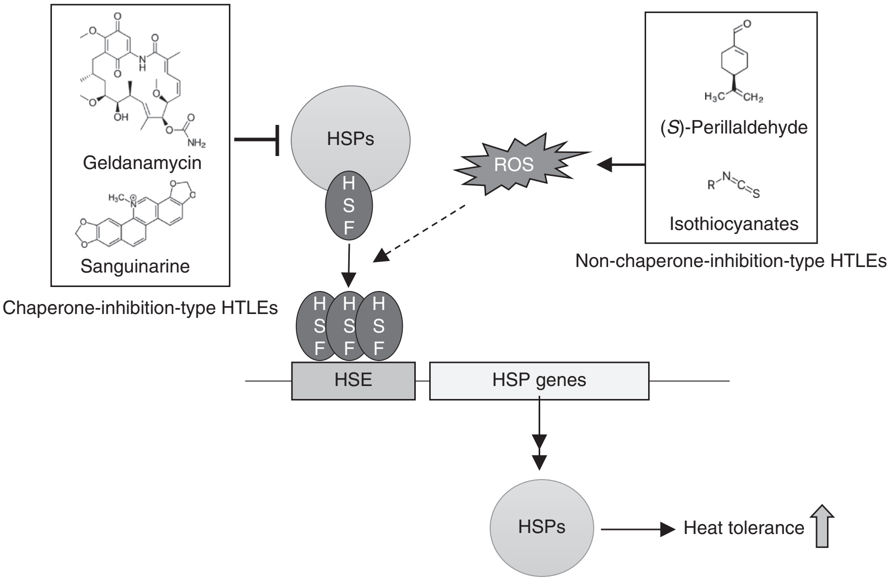

Figure 1: Putative action mechanisms of essential oil HTLEs. Geldanamycin and sanguinarine are chaperone-inhibition-type HTLEs. (*S*)-perillaldehyde and isothiocyanates are thought to be non-chaperone-inhibition-type HTLEs. Chaperone-inhibition-type HTLEs may release HSF by inhibiting HSPs. Non-chaperone-inhibition-type HTLEs may activate HSF via ROS generation. Activated HSFs promote the expression of HSP genes, and then the heat tolerance of plants is enhanced.

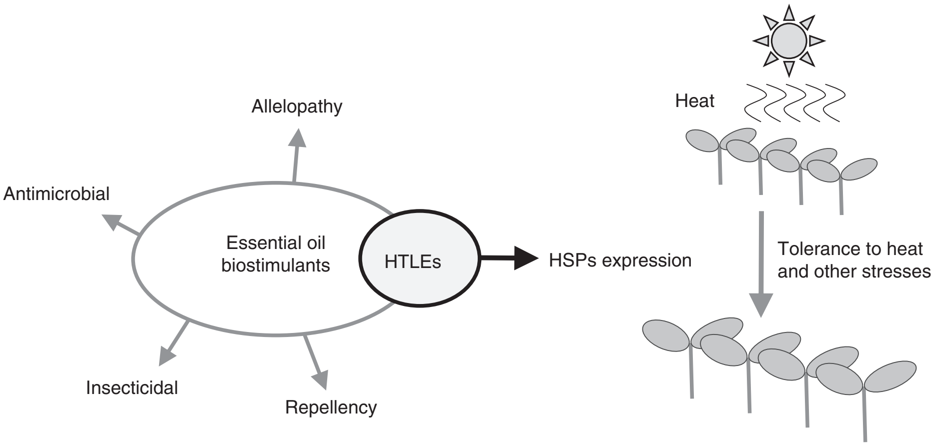

Figure 2: Diverse effects of biostimulants that contain essential oils on the production of crops. Essential oil HTLEs may facilitate the growth of plants under high-temperature conditions.

to ameliorate multiple kinds of damage to crops. Moreover, natural essential oils will be easily accepted by consumers, because essential oils have been used for a long period in human history. If activity, safety, and stability conditions are established, essential oil HTLEs would be widely commercialized in the future. However, it should be noted that quantitative administration to crops would be difficult because most essential oils are composed of volatile compounds. The development of a dose-control system is needed for the practical use of essential oil HTLEs in agriculture.

8 Conclusion

Essential oils such as isothiocyanates and monoterpenes enhance the heat tolerance of plants. Biostimulants containing essential oil HTLEs may be useful for reducing losses of crop yield and quality due to various stresses, especially heat. However, physiological responses for essential oil HTLEs have been tested only in model plants, i.e. *A. thaliana* and *P. patens*. Therefore, practical studies on essential oil HTLEs are needed. Although a great deal of biostimulants have been developed, few have demonstrated heat-tolerance-enhancing activities. Intensive investigations of HSR-inducing activities will uncover biostimulants that can enhance the heat tolerance of crops. Moreover, large-scale screening may provide more effective essential oil HTLEs that are useful for enhancing the functions of biostimulants. For the use of essential oil HTLEs, the chemical species and application methods should be determined according to the species and growth stages of crops. The ecological and environmental influence should be investigated. Further studies will deepen our understanding of essential oil HTLEs and facilitate their practical use as biostimulants.

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