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REVIEW ARTICLE

Essential oils and their bioactive compounds as eco-friendly novel green pesticides for management of storage insect pests: prospects and retrospects

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Abstract

The control of storage insect pests is largely based on synthetic pesticides. However, due to fast growing resistance in the targeted insects, negative impact on humans and non-target organisms as well as the environment, there is an urgent need to search some safer alternatives of these xenobiotics. Many essential oils (EOs) and their bioactive compounds have received particular attention for application as botanical pesticides, since they exhibited high insecticidal efficacy, diverse mode of action, and favourable safety profiles on mammalian system as well as to the non-target organisms. Data collected from scientific articles show that these EOs and their bioactive compounds exhibited insecticidal activity via fumigant, contact, repellent, antifeedant, ovicidal, oviposition deterrent and larvicidal activity, and by inhibiting/altering important neurotransmitters such as acetylcholine esterase (AChE) and octopamine or neurotransmitter inhibitor γ-amino butyric acid (GABA), as well as by altering the enzymatic [superoxide dismutase (SOD), catalase (CAT), peroxidases (POx), glutathione-S-transferase (GST) and glutathione reductase (GR)] and non-enzymatic [glutathione (GSH)] antioxidant defence systems. However, in spite of promising pesticidal efficacy against storage pests, the practical application of EOs and their bioactive compounds in real food systems remain rather limited because of their high volatility, poor water solubility and susceptibility towards degradation. Nanoencapsulation/nanoemulsion of EOs is currently considered as a promising tool that improved water solubility, enhanced bio-efficacy, stability and controlled release, thereby expanding their applicability.

Keywords Essential oils · Bioactive compounds · Storage pests · Synthetic pesticides · Mechanism of action · Nanoencapsulation

Introduction

Stored food commodities are prone to postharvest loss (up to 30%) in quality as well as quantity due to infestation by different groups of insects. The most common storage insect pests causing considerable loss include *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae), *C. chinensis* (L.) (Coleoptera: Bruchidae), *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae), *S. zeamais* (Motsch.) (Coleoptera: Curculionidae), *S. granarius* (L.) (Coleoptera: Curculionidae), *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae), *T. confusum* (du Val) (Coleoptera: Tenebrionidae), *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), *Acanthoscelides obtectus* (Say) (Coleoptera: Bruchidae), *Lasioderma serricorne* (L.) (Coleoptera: Anobiidae), *Liposcelis bostrychophila* (Badonnel) (Psocoptera: Liposcelididae), *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae) and *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). These cosmopolitan primary pests of stored food commodities have been reported to pose a threat to agricultural products during their storage not only by damaging the stored cereals by feeding on them, but also by providing suitable medium for other contaminants such as fungi and bacteria (Kłyś et al. 2017).

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C. maculatus (pulse beetle) is a cosmopolitan pest of legume seeds and is among the most serious pest of stored food products in tropical and subtropical countries (Viteri Jumbo et al. 2018). It initiates attack in the field and causes substantial losses (both qualitative and quantitative) during storage, resulting in weight and germination loss of seeds (Matos et al. 2020). *C. chinensis* commonly known as 'adzuki bean beetle' is one of the major field-to-storage insect pest of pulses with broad host range including adzuki beans. After an initial invasion in the field, the pest completes its life cycle by continuous feeding and causing up to 100% destruction of seeds within 3–4 months (Shukla et al. 2016). The genus *Sitophilus* is the most common and destructive pests comprising the species *S. oryzae* (rice weevil), *S. zeamais* (maize weevil) and *S. granarius* (granary/wheat weevil). They are found abundantly in tropical and subtropical as well as temperate belts of the world. These species can infest multiple grains, but *S. oryzae* show marked tendency for wheat, *S. zeamais* for maize and *S. granarius* for wheat and barley (Plata-Rueda et al. 2018). The infestation of these weevils can cause both quantitative (weight loss) and qualitative loss (increase in free fatty acids) and might facilitate the colonization of other pests including mites and fungi (Devi et al. 2017). *T. castaneum* (red flour beetle) and *T. confusum* (confused flour beetle) are among the most widespread and destructive insect pest causing significant damage and weigh loss of stored grains especially in the tropical and warm temperate regions of the world (Ismail 2018). In addition, they generally feed on broken kernels or grain dusts rather than intact grains/kernels. *R. dominica* also known as 'lesser grain borer' is one of the notable insect causing attacks during storage on a large number of cereals grains, including wheat, barley, triticale, paddy and oats, and causes their weight loss by consuming endosperms (Filomeno et al. 2020). *A. obtectus* (bean weevil) is a widespread pest that uses the seeds of the common bean (*Phaseolus vulgaris*) as its primary host. The growth of the larvae is restricted inside the mature seeds, since it is the only source of reserve food used for survival during the developmental stage of the insect (Haddi et al. 2018). *L. serricorne* (the cigarette beetle) is an important storage pest of cereals and tobacco in different regions of the world (Cao et al. 2018). Adult beetle chews on these food materials and create holes to mate and lay eggs and after hatching, the developing larvae feed on them causing significant damages (Zhou et al. 2018). Likewise, *L. bostrychophila* (booklouse) is an important insect pest commonly found in processed and unprocessed dry food products in household, granaries and warehouses, especially in tropical and humid countries (Dou et al. 2009). *O. surinamensis* (saw toothed grain beetle) is cosmopolitan in distribution and is likely to be found in cereals, dried fruits and nuts and almost every products of vegetable origin (Abd El-Salam et al. 2019; Gautam et al. 2020). The other important stored product insect, the invasive pest *P. truncatus* (the larger grain borer), is a major pest of stored maize and dried cassava. The host specificity of this pest is quite unclear; however, in a recent study, Athanassiou et al. (2017) documented that *P. truncatus* might found on grain commodities like triticale, rice, barley, oats, wheat and rye. It is also reported that this species was introduced from the Central America to Africa about four decades ago, and expanded rapidly in different regions of Africa, Asia and Americas (Kavallieratos et al. 2020). In addition, this species has been reported abundantly outside of the storage system, such as in forests, where it feeds on woods (Kavallieratos et al. 2018). Considering the above facts from the available literature, these insects were selected as target pests in the current review.

To control these losses, different synthetic pesticides frequently known as 'grey chemicals' have been widely used throughout the world (Athanassiou et al. 2018; Rajkumar et al. 2019). However, the massive application of some of these synthetic pesticides has resulted in an adverse effects on non-target organisms and to the environment (e.g. ozone depletion by methyl bromide) as well as resistance development among pests (as in the case of phosphine), which have stirred the need for search of some safer alternatives, especially of botanical origin. Over the past decades, plant-derived compounds and extracts have been investigated for their potential to control insect pests. As for example, some plant products such as pyrethrins, rotenones, azadirachtin, nicotine and gedunin have already been used as natural pesticides to control insect pests (Isman 2006). In recent years, essential oils (EOs) and their bioactive compounds are preferred as safer alternatives of synthetic pesticides in view of their negligible persistence in the environment (eco-friendly), varied modes of action, low toxicity, large-scale availability, renewable nature of source materials and minimum chances of resistance generation due to multiple components mixture that cause toxicity by interfering with many aspects of insect's physiology and biochemistry (Kiran et al. 2017). Although many of them have also been reported to act as natural toxicants against various arthropods, our focus here is on those which are efficient in controlling the threat of storage insect pests.

EOs are the complex blend of different bioactive compounds with the dominance of monoterpenes, sesquiterpenes and their oxygenated derivatives (Carson et al. 2006; Silvestre et al. 2019). Many EOs/bioactive compound-based formulations like 'DMC base natural' carvone and eugenol under the trade name 'TALENT' and 'EcoPCOR', respectively, have already been introduced in the market for commercial purposes (Dwivedy et al. 2016). Generally, it is assumed that the major compounds present in EOs are responsible for their insecticidal action; however, certain evidences suggested that besides their least per cent occurrence, minor compounds also contribute significant role in bioactivities via acting synergistically with major ones (Grande-Tovar et al. 2016; González et al. 2017). However, despite of having noteworthy insecticidal activities against different storage pests, the practical application of EOs and their bioactive compounds in food systems remain restricted due to poor solubility, susceptibility towards oxidation and negative impact on organoleptic properties of the foods due to aromatic profile (Chaudhari et al. 2019).

Among different strategies used to overcome these issues, the currently employed nanoencapsulation and/or nanoemulsion technology has attracted increasing attention as they will optimize the pest control system by enhancing the insecticidal activity of EOs/bioactive compounds and improving their practical applicability through controlled release and stability leading to considerable increase in shelf-life (Ziaee et al. 2014a; Upadhyay et al. 2019; Adak et al. 2020). Although a plethora of research and review articles have been published reporting the insecticidal activity of EOs and their bioactive compounds, however, most of them have focused only on one or two insect pests. For instance, the investigations of Campolo et al. (2018) have mentioned the application of only EOs against stored product insect pests; only EO components against stored grain insects (Kanda et al. 2017); only nanoparticles for insect pest control (Athanassiou et al. 2018); and studies focusing solely on mode of action against insect pests (Jankowska et al. 2017). Diverse insecticidal potential of both EOs and their bioactive compounds along with different mode of action and strategies to improve their bioactivity and stability through nanoencapsulation have not been reported earlier in a single review.

The present review differs from the earlier published reviews on the subject by providing (1) updated information not only on application of EOs but also on major bioactive compounds as novel plant-based eco-friendly pesticides for the management of most important insect pests causing deterioration of stored food commodities; (2) comprehensive discussion on different pesticidal mode of action of EOs and their bioactive compounds in terms of acetylcholinesterase (AChE) inhibition, alteration in octopamine and γ-amino butyric acid (GABA) receptors, and alteration in enzymatic and non-enzymatic antioxidant defence system, currently lacking in single review article; (3) offering recent information concerned with the application of EOs and their bioactive compounds against wide range of storage insect pests in contrast to previously published reviews oriented towards one or two insect pests; (4) highlighting important information pertaining to current limitations/challenges associated with commercialization of EOs and bioactive compounds for insect pest management including (a) the lack of efficacy in real food system, (b) availability of the EOs, (c) standardization and toxicological evaluation of EOs/bioactive compounds, (d) toxicological evaluation on non-target organisms, and (e) low persistence of the effect and the regulatory approval: and finally (5) including the emerging nanotechnological interventions in application of EOs and bioactive compounds for eco-friendly management of broad range of insect pests with an objective to improve the stability of developed formulation and target specific release of EOs and bioactive compounds for industrial scale application in insect pests control. To the best of our knowledge, this is the first review article towards this direction that aims to gather diverse scattered information on the subject.

Insecticidal activity of EOs and their bioactive compounds

Fumigant and contact toxicity

Fumigants are mostly preferred to control the insects' mediated losses of stored food commodities because they act in the vapour or gaseous phase on the target pests, while the contact toxicants kill the pests upon contact with them. Since long, many synthetic chemicals like methyl bromide and phosphine have been widely applied in foods as efficient fumigants; however, the rising concerns like environmental pollution and resistance development among pests as well as toxic effects on mammalian system restrict their incorporation into food system. Different EOs and their bioactive compounds have been highly recommended as potential fumigants and contact toxicants due to their volatile nature as they leave no significant residual impact. Tables 1 and 2 summarize fumigant and contact toxicities of EOs and their compounds, respectively against target stored product insect pests. In a study, Negahban et al. (2007) investigated the fumigant toxicity of *Artemisia sieberi* EO against *C. maculatus*, *S. oryzae* and *T. castaneum* and achieved complete mortality of all at 37 μL/L concentration after 24 h of exposure. However, the EO was found more sensitive to *C. maculatus* (LC_{50} = 1.45 μL/L air) than *S. oryzae* (LC_{50} = 3.86 μL/L air) and *T. castaneum* (LC_{50} = 16.75 μL/L air). The toxicity of EO can be attributed to the presence of major monoterpene camphor and others like camphene, 1,8-ceneol and α-pinene. A similar study also indicated that camphor, as a pure compound exhibited fumigant and contact toxicity against some important storage pests like *S. oryzae* and *R. dominica* (Rozman et al. 2007). Monoterpenoids, due to their volatility and rather lipophilic properties, can penetrate insect's body easily and interfere with their physiological functions.

Bittner et al. (2008) assessed the contact toxicity of *Gomortega keule* and *Laurelia sempervirens* EOs against *A. obtectus* and recorded 100% mortality of the test insect by both EOs at 8 μL/L air concentration after 3-day exposure. The authors reported that such strong efficacy of EOs against tested insect might be due to the presence of monoterpenes like safrol, 1,8-cineol, terpinene, thymol and carene. Similarly, Liu et al. (2013) tested the toxicity of two important

Table 1 Some essential oils (EOs) with remarkable toxicity against storage insect pests

Essential oils	Target pests	Mode of toxicity	Findings	References
Artemisia herba-alba, *A. campestris*, *A. absinthium*	*C. maculatus*	Fumigant	• *A. herba-alba*, *A. campestris* and *A. absinthium* caused complete mortality of test insect at 24.2, 139.8 and 609.8 μL/L air doses, respectively, after 24 h of exposure in Petri dishes • The highest toxicity of *A. herba-alba* attributed to the presence of major components α-thujone, norboran-2-one and chrysanthenone	Titouhi et al. (2017)
Haplophyllum dauricum (five different EOs viz. OF: EO from fruits in October; O (S + L): EO from stems and leaves in October; NF: EO from fruits in November; NL: EO from leaves in November and NS: EO from stems in November)	*T. castaneum*, *L. serricorne*	Fumigant, contact	• O (S + L) showed strongest contact toxicity on *T. castaneum* (LD_{50} = 20.21 μg/adult), as well as both fumigant and contact toxicity on *L. serricorne* (LC_{50} = 17.17 mg/L air and LD_{50} = 25.46 μg/adult). • The insecticidal activity of EO is related to the presence of oxygenated monoterpenes (44.54%) • The variation in insecticidal activity might be attributed to the differences in body texture, levels of susceptibility, biochemical changes and behavioural responses of the insects	Cao et al. (2019)
Schinus molle, *Aloysia polystachya*, *A. citriodora*	*R. dominica*	Fumigant, contact, repellent	• The EO of *S. molle* exhibited highest fumigant toxicity at concentrations ranging between 0.6 and 0.8 mg/cm^2. The EOs of *S. molle* and *A. polystachya* showed highest contact toxicity having LD_{50} values 0.88 and 0.61 mg cm^{-2}, respectively. The EO of *A. citriodora* showed the highest repellent activity at 120 and 314 μg/cm^2. • The EOs caused toxicity by penetrating the body of test insect through the spiracles and the integument	Benzi et al. (2009)
Pistacia atlantica, *P. khinjuk* (EOs isolated from fruit, gum and leaves)	*C. maculatus*	Fumigant, contact, repellent	• All EOs exhibited strong insecticidal activity with varying LC_{50} values following exposure of 24 and 48 h. • *P. khinjuk* fruit EO and *P. atlantica* gum EO had the strongest fumigant toxicity. *P. khinjuk* fruit and leaf EOs and *P. atlantica* gum EO had the strongest contact toxicity. *P. atlantica* gum and leaf EOs and *P. khinjuk* leaves EO had the strongest repellent activity • The strongest toxicity (fumigant, contact and repellent) of these EOs is related to the presence of a high concentrations of monoterpenes (such as α-pinene, β-pinene) and sesquiterpene (spathulenol). These monoterpenes are lipophilic and can quickly penetrate the body and cause physiological damage to the insects	Pourya et al. (2018)
Eucalytus saligna, *Cupressus sempervirens*	*S. zeamais*, *T. confusum*	Contact, repellent	• *E. saligna* EO exhibited more toxic effect on *S. zeamais* than *C. sempervirens* EO, since total mortality of both insects were achieved at 100 μL/40 g in maize.While both EOs were highly repellent and exhibited more than 70% repellent efficacy against tested insects • The toxicity could be attributed to the presence of major components of these EO such as 1,8-cineole, terpineol and α-pinene as well as due to the synergistic effect of minor component (e.g. limonene) with major ones	Tapondjou et al. (2005)
Curcuma longa	*S. oryzae*, *T. castaneum*, *R. dominica*	Fumigant, contact, antifeedant,	• *R. dominica* adults were more susceptible towards contact toxicity of EO than *S. oryzae* and *T. castaneum*. However, *S. oryzae* adults were more susceptible towards	Tripathi et al. (2002)

Table 1 (continued)

Essential oils	Target pests	Mode of toxicity	Findings	References
		oviposition, larvicidal	fumigant toxicity of EO than *R. dominica* and *T. castaneum*. EO was almost equally effective as an antifeedant against all tested insects adults and larvae and also prevented eggs hatching and larvae survival of all insects	
Eucalyptus dundasii	*R. dominica*, *O. surinamensis*	Fumigant, repellent, antifeedant	• EO was equally effective as fumigant against both the insects. EO acted stronger in *O. surinamensis* and shows a more repellent effect. EO had the highest inhibitory effect as antifeedant against both insects • The toxicity of EO against the mentioned pests is related to their major component i.e. 1,8-cineole	Aref et al. (2015)
Artemisia annua	*T. castaneum*, *L. serricorne*	Repellent	• EO showed either the same or higher level of repellent activity against the tested insects than the positive control (DEET) at all of the concentrations • The repellent activity of EO is related to their major compounds such as α-caryophyllene and α-pinene	Liu et al. (2019)
Artemisia princeps, *Cinnamomum camphora*	*S. oryzae*	Repellent	• The EOs from *A. princeps* and *C. camphora* exhibited good repellent activities against the stored grain pests *S. oryzae* at the tested concentration. However, when tested against mixture, the repellency was found far better than the individual EO • The high repellency of the mixture resulted from the synergetic action between the major compounds in the EOs	Liu et al. (2006)
Carum copticum, *Vitex pseudo-negundo*	*C. maculatus*	Fumigant, ovicidal, larvicidal	• Both EOs exhibited potent fumigant toxicity against eggs, larvae and adults of *C. maculatus*; however, the *C. copticum* EO showed far better efficacy than *V. pseudo-negundo* • The abundance of monoterpenoids in the EOs may act as neurotoxins, and the toxicity might be apparent when the nervous system begins to develop	Sahaf and Moharramipour (2008)
Alpinia katsumadai	*T. castaneum*, *L. bostrychophila*, *L. serricorne*	Contact, repellent	• The EO showed remarkable contact toxicity and repellent activity against all tested insects at lower concentrations • The toxicity is due to major component of EO, methyl cinnamate	Chen et al. (2019)
Cymbopogon citratus	*P. truncatus*	Contact, fumigant	• The dosages of 2.75 mg cm^{-2} of EO gave 90 and 95% mortality rates after 24 and 48 h, respectively, during contact and fumigant toxicity	Masamba et al. (2003)

Table 2 Some bioactive compounds of EOs with remarkable toxicity against storage insect pests

Bioactive compounds	Target pests	Mode of toxicity	Findings	References
(*E*)-anethole, estragole, fenchone	*S. oryzae, C. chinensis, L. serricorne*	Fumigant	The compounds caused 100% mortality of all tested insects at 0.42 mg/cm^2 in Petri dish	Kim and Ahn (2001)
1, 8 cineole	*T. castaneum, R. dominica*	Fumigant	Caused 50% mortality of *T. castaneum* and *R. dominica* at 15.3 and 9.5 µL/L air, respectively, in conical flasks	Lee et al. (2004)
Cinnamaldehyde	*C. maculatus*	Contact	Caused complete mortality of test insect at 0.3 mg/cm^2 air after 12 h of exposure in Petri dish	Brari and Thakur (2015)
Methyl cinnamate	*T. castaneum, L. bostrychophila, L. serricorne*	Contact, repellent	Caused 50% contact toxicity of *T. castaneum*, *L. bostrychophila* and *L. serricorne* at 5.0, 2.2 and 23.5 µg/cm^2 air, respectively, and 80% repellent activity of all tested insects at 78.63 nL/cm^2 in glass vials	Chen et al. (2019)
Cymol	*T. confusum, S. zeamais*	Contact	Caused 71% and 100% of *T. confusum* and *S. zeamais* at 1.30 µL/cm^2 after 5 day of exposure in maize grains	Tapondjou et al. (2005)
(R) and (S)-limonene	*S. zeamais*	Contact, repellent	Both (R) and (S)-limonene caused 50% contact toxicity at 49.97 and 52.39 µL/mL air, respectively, and 60–80% repellent activity at 30 and 40 µL/mL air, respectively, after 24 h of exposure in Petri dish	Fouad and da Camara (2017)
1, 8 cineole	*S. granaries*	Contact, repellent	Caused 100% contact toxicity and 70% repellent activity at the dose of 7 and 10 µL/disc, respectively, in glass Petri plates	Obeng-Ofori and Reichmuth (1997)
β-asarone	*P. truncates*	Antifeedant	A strong depression of feeding was observed between 21 and 42 days after treatment	Schmidt and Streloke (1994)
t-anethole, thymol	*T. castaneum*	Larvicidal	Caused 100% mortality of test insect larvae at 0.288 mg/cm^2 dose in screw cap chamber	Mondal and Khalequzzaman (2010)

compounds (methyleugenol and (*E*)-methylisoeugenol) against *L. bostrychophila* and observed remarkable (LD$_{50}$ value of 92.21 µg/L air) mortality. Kiran and Prakash et al. (2015) carried out an assessment on fumigant toxicity of *Rosmarinus officinalis* EO against *S. oryzae* and *O. surinamensis* and reported 100% toxicity at 0.15 µL/mL air concentrations. The authors also observed that the EO was more sensitive towards *O. surinamensis* (LC$_{50}$ = 0.039 µL/mL air) than *S. oryzae* (LC$_{50}$ = 0.057 µL/mL air). The possible reason for the toxicity could be attributed to the increased accumulation of EO bioactive compounds in desiccators during increased period of exposure, while differences in sensitivity may be due to differences in exoskeleton texture, decrease in penetration or the biochemical and physiological adaptations of the insects itself. In addition, the variation in toxicity of EO among different pests at the same concentration might be linked to a number of factors. One important factor is temperature, whose role in regulation of efficacy of the EOs has been well documented by Papachristos and Stamopoulos (2002) during investigating the toxicity of volatiles of three EOs against immature stages of *A. obtectus*. They reported that temperature may have a determinant role on factors such as the rate of vapour release, level of adsorption, rate of insect development, efficacy of detoxification systems and uptake of volatiles by the insects.

In a similar way, Hamdi et al. (2015) demonstrated the fumigant toxicity of *Eucalyptus lehmannii* and *E. astringens* EOs against *T. castaneum*, *R. dominica* and *C. maculatus* from Tunisia and Algeria and found that after 46 h of exposure at 6.5 µL/L air dose, *E. lehmani* EO caused 11.33, 35 and 43.33% toxicity against *T. castaneum, C. maculatus* and *R. dominica*, respectively, which was comparatively higher than the Tunisian region's pest. Similar response has also been recorded for *E. astringens* EO showing 9.5, 27.57 and 39.33% toxicity of Algerian pests at the same dose. The greater efficacy of *E. lehmannii* EO could be attributed to its richness on oxygenated monoterpenes, since these were more toxic to insects than non-oxygenated compounds (Regnault-Roger and Hamraoui 1995). Moreover, as the major components of EOs determine their biological activity, the highest percentage of α-pinene, 1,8-cineole and α-terpineol in *E. lehmani* EO compared to *E. astringens* EO conferred it superior insecticidal activity against the tested insect species. Finally, they concluded that the pests from Algeria were more sensitive towards test EOs than Tunisian region suggesting the variation of insecticidal potency with respect to different tribes in one particular insect species.

Kim et al. (2016) performed a survey on efficacy of *Hyssopus officinalis*, *Origanum majorana* and *Thymus zygis* EOs against adult rice weevil, *S. oryzae*, as fumigant and reported pronounced fumigant toxicity of all EOs against test insect. They also evaluated the potential of some of their major compounds viz. sabinene hydrate, linalool, α-terpineol and terpinen-4-ol and achieved 100% mortality of *S. oryzae* at lower (3.9 mg/L air) dose. In an effort to find out the applicability of EO as fumigant, Kiran et al. (2017) determined the fumigant toxicity of *Boswellia carterii* EO and reported absolute mortality at 0.10 μL/mL air against *C. chinensis* and *C. maculatus* after 24 h of exposure. Further, they observed that the *C. maculatus* adults were more susceptible to EO exposure than *C. chinensis* and clarified that this variation in toxicity can be due to the differences in body texture, levels of susceptibility, biochemical changes and behavioural responses of the insect pest. In addition, they also measured the efficacy of same EO at sublethal concentrations (1/10 and 1/20 of LC_{50}) and found no significant mortality of test insect except few changes in oviposition activity, feeding behaviour and oxidative stress.

In another study, Kamanula et al. (2017) tested the fumigant and contact toxicity of *Lippia javonica* EO and some compounds such as perillaldehyde, limonene, linalool and a mixture of perillaldehyde and linalool against *S. zeamais*. The authors observed that the EO exhibited 60% fumigant toxicity at 370 $\mu g/cm^3$ air concentration after 72 h of exposure. The toxicity was increased to 68% after 120 h of exposure at the same concentration, suggesting exposure duration-dependent fumigant toxicity response. However, in case of contact toxicity, the test EO, linalool, perillaldehyde and a mixture (perillaldehyde + linalool) exhibited 85, 100, 99.5 and 100% toxicity with LC_{50} value equivalent to 6.22, 1.07, 1.82 and 0.85 mg/mL, respectively, in contrast to no toxicity recorded for major component myrcenone, implying differences in biological activity because of chemotypic differences in plant EOs. Cao et al. (2018) measured the fumigant toxicity of *Evodia lenticellata* EO and reported remarkable mortality of *T. castaneum*, *L. serricorne* and *L. bostrychophila* at 103.88, 58.83 and 1.53 mg/L air concentrations, respectively. They also evaluated the contact toxicity of the same EO and obtained 100, 97 and 97% mortality of *T. castaneum*, *L. serricorne* and *L. bostrychophila*, respectively, at the concentrations of 145.26, 22.70 and 71.63 $\mu g/cm^2$ air. The authors observed an excited behaviour and black dead body with unfolded wings of the exposed insects and predicted that the test EO and its bioactive compounds might act as neurotoxicants on insects via blocking the trachea of insects or binding to the target sites on receptors that regulate nervous activity and interrupt normal neurotransmission, leading to paralysis and the death. During contact toxicity assay, they observed tremors and lack of coordination (neurotoxic symptoms) and suggested that the EO might exhibit their insecticidal activity via inhibiting acetylcholinesterase activity or by blocking octopamine receptors. Plata-Rueda et al. (2018) analyzed the fumigant and contact toxicity of *Cinnamomum zeylanicum* and *Syzygium aromaticum* EOs along with their major compound eugenol against *S. granarius* and reported the strongest mortality (LC_{50} = 2.76 μL/mL; LC_{90} = 5.72 μL/mL) of eugenol over the EO of *C. zeylanicum* (LC_{50} = 11.9 μL/mL and LC_{90} = 23.4 μL/mL) and *S. aromaticum* (LC_{50} = 13.8 and LC_{90} = 26.0 μL/mL). The likely explanation for the toxicity differences in this insect is that the efficacy can be affected by the penetration ability of the compounds into the body and the ability of the insect to metabolize these compounds. The role of thickness and the composition of cuticle in determining the insecticidal efficacy of EO/bioactive compound has already been explained by the other (Balabanidou et al. 2018).

In a study, Upadhyay et al. (2019) measured the efficacy of *Melissa officinalis* EO against *T. castaneum* and reported that EO exhibited strong fumigant and contact toxicity against test insect after 48 h of exposure at 0.067 μL/mL and 0.157 $\mu L/cm^2$ air concentrations, respectively. They also explained that the insecticidal activity of the EO might be attributed to the abundance of major compound citral whose biological activity as insecticidal agent has already been reported in literature by several workers (Tak et al. 2016; de Souza et al. 2019; Plata-Rueda et al. 2020). Recently, Zhang et al. (2019) also evaluated the contact toxicity of EO obtained from *Ostericum viridiflorum* and two compounds (α-humulene and β-caryophyllene) against *T. castaneum* and recorded remarkable toxicity at their respective LC_{50} doses. They explained that the EO exhibited toxicity due to the interaction of their major compounds with others present as active ingredients in the EO. More recently, Pang et al. (2020) investigated the insecticidal activity of *Mentha piperita* EO against *T. castaneum*, *L. serricorne* and *L. bostrychophila* and observed significant fumigant and contact toxicity against *T. castaneum* (LC_{50} = 18.1 mg/L air and LD_{50} = 2.9 μg/adult), *L. serricorne* (LC_{50} = 68.4 mg/L air and LD_{50} = 12.6 μg/adult) and *L. bostrychophila* (LC_{50} = 0.6 mg/L air and LD_{50} = 49.8 μg/adult), respectively. They also suggested that the toxicity of EO could be attributed to the absorption of its major component (L-menthone) on the surface of insects due to the presence of specific carbonyl group. The authors also observed some typical neurotoxic behaviours of test insects such as tremors, wings movement and erratic legs, and predicted that such behaviour in insects after exposure to EO might occur due to the inhibition of neurotransmitter acetylcholinesterase.

The detailed mode of action of these botanicals acting on insect pests to exert their fumigant and contact toxicity is still unclear; however, certain line of evidences suggests that EOs due to the richness of highly volatile monoterpenes may cause fumigant and contact toxicity via penetrating the respiratory system and cuticles, respectively (Prates et al. 1998). Sikkema et al. (1995) and Benelli et al. (2019) suggested that some bioactive compounds like thymol and linalool exert their fumigant action by interdicting with plasma membrane lipids resulting into alteration of membrane potential which subsequently causes considerable loss of important metabolites and ions from the cells. Other line of evidence suggested that the lethal activity of EOs or their bioactive compounds might be attributed to lipophlic nature, causing ease in penetration through the exoskeleton leading to cellular lyses (Bennis et al. 2004).

Repellent activity

Repellents are the chemicals that deter an organism (in general arthropod) from coming close over the applied surface. Different EOs and their bioactive compounds have been found to exhibit effective long-lasting repellency against a wide range of storage insect pests. They prevent the insects from landing on the surface of foods by providing a vapour barrier and, therefore, many of them viz. clove, citronella, lemon and eucalyptus oil have been fully exempted from the toxicity parameters required by the United Stated-Food and Drug Administration (US-FDA) (Lee 2018). Some of the EOs/bioactive compounds with prominent repellent activities are compiled in Tables 1 and 2. Earlier in a study, Nerio et al. (2009) performed the screening of *Lippia origanoides*, *L. alba*, *Tagetes lucida*, *Rosmarinus officinalis*, *Cananga odorata*, *Eucalyptus citriodora* and *Cymbopogon citratus* EOs from Columbia and observed their repellent activity against *S. zeamais*. Among all tested EOs, *L. origanoides* was found to be the most effective causing 92 ± 3% repellency at 0.503 µL/cm^2 dose followed by *E. citriodora* (91 ± 3%), *C. odorata* (90 ± 8%), *C. citratus* (8 2 ± 5%), *T. lucida* (79 ± 6%), *R. officinalis* (67 ± 8%) and least by *L. alba* (4%) at the same dose. They also predicted that the efficacy of these EOs can be ascribed to the presence of thymol, whose role as plant-based insecticide has already been demonstrated by many authors (Oliveira et al. 2018; Salehi et al. 2019).

Similarly, Caballero-Gallardo et al. (2011) tested the efficacy of four of the above-mentioned EO (*L. alba*, *T. lucida*, *R. officinalis* and *C. odorata*) and one other (*Lepechinia betonicifolia*) along with 12 compounds (benzyl benzoate, citronellol, β-myrcene, carvacrol, citral, geraniol, geranyl acetate, nerol, p-cymene, two carvone (S (+) & R (–) form) and benzyl salycylate) against wheat flour beetle *T. castaneum*. Among all tested EOs, *C. odorata* showed maximum repellent activity accounting 98 ± 2% followed by *L. alba* (96 ± 2%), *L. betonicifolia* (92 ± 4%), *R. officinalis* (92 ± 4%) and *T. lucida* (90 ± 3%) after 4 h of exposure at 0.2 µL/cm^2 threshold concentration. The tested compounds showed following order: benzyl salicylate (99 ± 1%) > citral (98 ± 2%) > citronellal (96 ± 3%) > nerol (95 ± 4%) ≥ geraniol (95 ± 3%) ≥ R (–) carvone (95 ± 2%) >S (+) carvone (94 ± 3%) ≥ geranyl acetate (94 ± 2%) > *β*-myrcene (93 ± 3%) > benzyl benzoate (91 ± 5%) > carvacrol (90 ± 3%) > *p*-cymene (69 ± 5%). Based on findings, they recommended these EOs and the bioactive compounds as potent source of natural repellents to control *T. castaneum* in stored food items. Fogang et al. (2012) demonstrated the biological activity of *Zanthoxylum xanthoxyloides* EO against *A. obtectus* and reported 100% repellency at 0.501 µL/cm^2 air concentration. They concluded that the toxic effects of EO can be attributed to the major components citronellol and limonene or due to the enhancing effect of some of its minor compounds. They also proposed that the EO may exhibit its toxic efficacy via penetrating the body of the insect through the respiratory system, the cuticle or through the digestive system.

Nattudurai et al. (2017) evaluated the efficacy of *Atalantia monophylla* EO at five different concentrations (5, 10, 15, 20 and 25 µL/L air) using a Y-tube glass olfactometer and achieved 85.24 and 75.24% repellency against *C. maculatus* and *S. oryzae*, respectively at highest concentration (25 µL/L air) after 3 h of exposure and reported that the efficacy of EO as a repellent was increased with increasing their concentration and time of exposure. They also explained that the repellent activity of EO is due to the presence of major volatile compounds, especially monoterpenes. Mahdi and Behnam (2018) tested the repellent activity of *Citrus sinensis* EO against two important storage pests *R. dominica* and *L. serricorne* and reported 49.99 and 58.33% repellency, respectively after 3 h of exposure. Wang et al. (2018) described the repellent activity of EO from *Asarum heterotropoides* along with three important compounds (methyleugenol, safrole and 3, 5-dimethoxytoluene) against *L. serricorne* and *L. bostrychophila* and reported more than 80% repellency by EO at 78.63 mL/cm^2 concentration against both the pests. The three compounds showed pronounced repellency at 63.17 mL/cm^2 concentration. They explained that the distance between the side chain double bond and the benzene ring along with the methoxy groups attached to either the aromatic ring or the alkyl side chain of the major compounds are appeared to be determining factors for their insecticidal and repellent activity. Recently, Hu et al. (2019) examined the repellent property of *Artemisia brachyloba* EO and two of its major compounds α-terpineol and davanone against *T. castaneum* using area preference method at three different time intervals (2, 4 and 8 h) and observed 100%

repellency in the case of α-terpineol followed by *A. brachyloba* (96.67%) and moderately (61.67%) by davanone at the concentration of 0.315 μL/cm^2 after 8 h exposure. They concluded that the repellent activity of these tested botanicals was largely influenced by their respective concentrations and time of exposure. According to Wang et al. (2006), the lipophilic nature and volatilization pattern of compounds present in the EOs and dipole interactions along with boiling points are largely associated to their repellent activity. In addition, the presence of mono (linalool, menthol, thymol, borneol, *p*-cimene, geranial and pulegone) and sesquiterpenes (bisabol, cedrol, β-caryophyllene, germacrone and patchoulol) in EOs is also related with their repellent activity (Kiran and Devi 2007; Pavela 2015).

Antifeedant/feeding deterrent activity

The antifeedants usually signal the unsuitability of a product allowing the insect to refuse on contact, and thus avoiding the eating of compounds that could be toxic. On the other hand, more closely related terms 'antixenosis' and 'antibiosis' are used to describe the phenomenon of resistance in plants against pests or herbivores. The term antixenosis (also called as non-preference reaction) is generally used to demonstrate the adverse effect of a plant on pests behaviour in a way that reduce the acceptance of a plant as a host, while antibiosis is used to describe adverse effects of plants on pest's physiology or life history such as growth, development, survival and fecundity (Hondelmann et al. 2020). Despite the amount of research already undertaken on insect selection behaviour, researchers still do not fully understand the taste sensilla that are used by an insect to taste its food and are of primary significance in enabling an insect to detect antifeedants. Generally, it is believed that plant-derived bioactive compounds may stimulate the taste neurons and they produce electrical impulses that transmit the neural code, which can result in the modification of insect behaviour (Simmonds 2006). Currently, a number of EOs and their bioactive compounds have been reported to possess antifeedant activity against different storage pests. Some studies dealing with the antifeedant activity of EOs and their bioactive compounds are shown in the Tables 1 and 2, respectively.

Huang and Ho (1998) using flour disc method tested the efficacy of cinnamaldehyde as potent antifeedant against *S. oryzae* and *T. castaneum* and reported that the compound was more efficacious towards *T. castaneum* larvae than adults as they reduced the growth, food and dietary consumption at concentration of 27.2–54.4 mg/g food. However, in the case of *S. zeamais*, this compound only reduced consumption of food at a concentration of 6.8–13.6 mg/g food and showed no effect on growth and dietary utilization. Using flour disc bioassay, Liu and Ho (1999) also measured the antifeedant activity of *Evodia rutaecarpa* EO against *S. oryzae* and *T. castaneum* and reported that the EO showed a strong antifeedant action against *T. castaneum* larvae than adults with the reduction in their growth and food consumption rate at a concentration of 0.75 and 1.5 mg/disc, respectively, while against *S. zeamais* adults, the rate was 1.5 and 2.2 mg/disc concentration for growth and food consumption, respectively. In conclusion, the authors suggested that the reduction in growth rate of *T. castaneum* larvae and *S. zeamais* adults might be attributed to the behavioural action rather than to post-ingestive toxicity. In a research, Stefanazzi et al. (2011) evaluated the potential of *Tagetus terniflora*, *Cymbopogon citratus* and *Elionurus muticus* EOs against *T. castaneum* and *S. oryzae* and reported that EOs of *T. terniflora* and *C. citratus* at 4 mg/disc and *E. muticus* at 2 and 4 mg/disc concentration showed strong feeding deterrent activity against *S. oryzae*, while, against *T. castaneum*, no effect on the feeding behaviour was observed by these EOs. They explained that the post-ingestive toxicity observed in *T. castaneum* larvae and *S. oryzae* adults could be due to an increase in the gut pH or a reduction in α-amylase activity by the EOs. It is a well-known fact that extreme pH in the insect gut has complex effects on the activity of ingested allelochemicals and hence, high pH favours the oxidation of these chemicals to toxic metabolites (Chown et al. 2004). Another studies carried out on *T. castaneum* showed that larvae fed on treated diet with bioactive compounds (extracts) of different plant species had lower α-amylase activity, probably due to cytotoxic effect of extract on epithelial cells of the midgut that secreted the enzyme α-amylase (Jbilou et al. 2008).

Kiran and Prakash (2015) reported the antifeedant behaviour of *Gaultheria procumbens* EO and their major compound methyl salicylate against *S. oryzae* and *R. dominica* and recorded complete feeding deterrency for both at their respective LC_{50} concentrations (58.62 and 63.49 μL/L air) against *S. oryzae* and 2.71 and 1.90 μL/L air against *R. dominica* for EO and methyl salicylate, respectively. Kanda et al. (2017) compared the feeding deterrent activity of thymol, carvacrol, eugenol, t-anethole and linalool against *T. castaneum*, *R. dominica* and *S. oryzae* in a choice assay and reported significant antifeedant activity at different concentrations. They suggested that the compounds tested in the present study exhibited antifeedant activity via more orientation towards physiological toxicity rather than interaction with gustatory receptors, as has been normally observed in the case of true antifeedants. Recently, Rajkumar et al. (2019) performed extensive investigations on antifeedant activity of *Mentha piperita* EO and their major compounds menthol and menthone against *S. oryzae* and *T. castaneum* and reported that *M. piperita* at 43.19 and 48.68 μL/L, menthol at 49.37 and 54.49 μL/L and menthone at 46.66 and 51.95 μL/L concentration exhibited 100% deterrent activity against *S. oryzae* and *T. castaneum,* respectively.

Oviposition deterrent and ovicidal activity

Oviposition deterrence is the property of a chemical that do not allow the females to deposit eggs, while ovicidal activity of a substance is the property which kills the eggs by disrupting embryonic development and prevents hatching of such eggs. EOs and their bioactive compounds have been reported to possess satisfactory insecticidal activity via reducing the chances of population emergence against a large number of storage pests. Several research papers have been published about oviposition deterrent and ovicidal activity of EOs and their bioactive compounds, some examples of which are listed in Tables 1 and 2.

Earlier, Tunc et al. (2000) studied the effect of *Pimpinella anisum*, *Cuminum cyminum*, *Eucalyptus camaldulensis*, *Origanum syriacum* and *Rosmarinus officinalis* EOs on *T. confusum* eggs at concentrations of 24.6, 49.2, 98.5 and 196.9 μL/L air and exposure time of 24, 48, 72 and 96 h, respectively, and reported that at highest concentration (196.9 μL/L air), EO from *P. anisum* showed 100% mortality of the eggs (ovicidal) followed by *O. syriacum* (77%), *R. officinalis* (65%) and *E. camaldulensis*. Tripathi et al. (2001) investigated the efficacy of *Anethum sowa* EO and its purified fractions (I, II and III) against *C. maculatus* and recorded 100% oviposition deterrency by EO and its IIIrd fraction at a concentration of 10 μL/mL. However, only IIIrd fraction containing dillapiole showed 100% ovicidal activity at higher (70 μL/mL) concentration. From the obtained results, they predicted that the synergistic action between the d-carvone, dihydro-carvone and dillapiole may be responsible for the complete oviposition deterrency observed in the EO. Papachristos and Stamopoulos (2004) in a study demonstrated the efficacy of EOs isolated from *Lavandula hybrida*, *Rosmarinus officinalis* and *Eucalyptus globulus* against *A. obtectus* and observed significant (27.1–29.9%) oviposition deterrent and ovicidal activity at 197.2 μL/L air concentration. They also observed that the exposure of the eggs to the EO vapours for 1 or 2 days had no effect on their hatching ability, while increasing the exposure period to 3 or 4 days reduced egg hatchability by 26–29%. Most eggs failed to hatch when exposed to EO vapours for 6 days, while 100% inhibition was observed after 7 days in all cases except *E. globulus* EO. It might be possible that the EOs (dominated by monoterpenes) may exhibit their toxic effects on eggs via acting as neurotoxins, since ovicidal activity is merely evident while the neurons begin to develop. Otherwise, changes in the permeability of the vitelline membrane may occur during embryogenesis that may ease the diffusion of vapours into older eggs so that fundamental physiological and biochemical processes are affected.

Shukla et al. (2011) tested the efficacy of *Lippia alba* EO, *Callistemon lanceolatus* EO and their major bioactive compound 1, 8 cineole and recorded 96.03% oviposition deterrency for *C. lanceolatus* followed by *L. alba* (66.86%) and 1, 8 cineole (65.86%) at a dose of 0.1 μL/mL against *C. chinensis*. They also predicted, due to volatile nature, test EOs and their bioactive compounds easily penetrate the chorionic or vitelline membrane of eggs, resulting into alteration in the normal metabolism. Kedia et al. (2014) conducted a research on oviposition deterrency and ovicidal performance of *Mentha spicata* EO against *C. chinensis* and affirmed 98% deterrency at 0.1 μL/mL concentration, which enhanced to 100% in the case of ovicidal activity even at lowest concentration (0.0125 μL/mL). In results, the authors postulated that the EO may exhibit its ovicidal activity via killing the female insects prior to egg laying or preventing them from laying many eggs due to some unknown mechanism. On the other hand, an ovarian alteration following EO exposure (causing sterility effect) might be the likely factor contributing to the ovicidal efficacy. Similarly, Shukla et al. (2016) assessed the efficacy of *Acorus calamus* EO and its major compound β-asarone as a suitable and eco-friendly plant-based candidate molecule for the management of post-harvest losses caused by *C. chinensis*. They further explained that during ovicidal action, EO and β-asarone may enter through the funnel present at posterior pole meant for gaseous exchange and act as neurotoxicants, leading to ovicidal activity especially during early stage of embryonic development when nervous system begins to develop (Papachristos and Stamopoulos 2004).

Kiran et al. (2017) described the deterrent activity of *Boswellia carterii* EO against legume pest *C. chinesis* and *C. maculatus* and recorded a dose-dependent activity. They reported that at their respective LC_{90} concentration (0.096 and 0.075 μL/mL air), the EO showed 100% activity against *C. chinensis* and *C. maculatus*, respectively. The authors also observed that early embryonic stages such as eggs and neonatal larvae were more susceptible to EO exposure than older ones like pupae and adults. The probable reason might be the ease of penetration of volatile components through the respiratory funnel or by changes in the permeability of chorion and vitelline membrane during embryogenesis, affecting vital physiological and biochemical processes. In another study, Nattudurai et al. (2017) measured the efficacy of *Atalantia monophylla* EO against *C. maculatus* and reported 37.62, 44.04 and 100% ovicidal activity at three different sublethal doses $LC_{10} = 4.10$, $LC_{20} = 7.74$ and $LC_{30} = 43.28$ μL/mL, respectively. The EO caused ovicidal activity by diffusion into eggs and affecting their internal physiological and biochemical processes responsible for the development of embryo and emergence of the progeny. In a research recently performed by da Silva et al. (2019), using *Vanillosmopsis arborea* EO and its major compound α-bisabolol against *C. maculatus* demonstrated dose-dependent oviposition deterrency with respect to concentrations. The reduction in the number of eggs per *C. maculatus* female with *V. arborea* EO and its component α-bisabolol in the LC_{50} can be explained by the elevated susceptibility of those mated to monoterpenoids. In addition, the barrier effect of the EO together with the lack of respiratory activity and accumulation of toxic metabolites could explain the mortality of eggs (Credland 1992). Moreover, diffusion of the EO into the eggs can cause a direct toxicity, delaying adult emergence and causing adverse effects on the progeny (Gurusubramanian and Krishna 1996).

Larvicidal activity

Being an internal feeder, larvae are difficult to be controlled and therefore EOs and their bioactive compounds could serve as an ideal strategy to control insect larvae because of volatile nature (Nenaah et al. 2015). Some well-known EOs and their bioactive compounds with reported larvicidal activities are exemplified in Tables 1 and 2. For instance, Mwangi et al. (1992) described the efficacy of five EOs obtained from *Lippia* sp. (*L. somulensis*, *L. grandifolia*, *L. wilmsii*, *L. dauensis* and *L. javanica*) and reported 100% mortality of maize weevil *S. zeamais* larvae at 150 μL/L concentration, which was approximately two-folds more effective than the commercial insecticide DEET. They explained that the larvicidal activity of these EOs might be attributed to the abundance of monoterpene hydrocarbons that has been reported to possess much higher larvicidal activity than their oxygenated counterparts. Huang et al. (1997) examined the effect of *Myristica fragrans* EO on survival of *T. castaneum* larvae exposed to different concentrations and reported loss in survivability of larvae at the concentration range of 1.4–3.2 mg/cm^2. Upadhyay and Jaiswal (2007) evaluated the efficacy of *Piper nigrum* EO against fourth instar larvae of *T. castaneum* and confirmed significant reduction in population at 14.022 μL/L concentration. Similar observation has also been made by Fathi and Shakarami (2014), where they investigated the larvicidal activity of EOs of *Eucalyptus camaldulensis*, *E. viminalis*, *E. microtheca*, *E. grandis* and *E. sargentii* against 3–14 days old larvae of *T. confusum* and *T. castaneum* and reported *E. viminalis* to be the most toxic (LC_{50} = 20.67 and 48.06 μL/L air) among all tested EOs followed by *E. grandis* (26.40 and 71.87 μL/L air) and *E. camaldulensis* (41.52 and 103.27 μL/L air) and the least by *E. sargentii* (110.52 and 155.77 μL/L air) against *T. confusum* and *T. castaneum*, respectively, after 24 h of treatment. They suggested that the abundance of monoterpenes components such as carvacrol, camphor, 1,8-cineole, α-pinene, p-cymene, piperitenone oxide and terpineol in the EOs may contribute to their larvicidal activities.

Kedia et al. (2015) also performed an experiment on *C. chinensis* and *S. oryzae* larvae to test the mortality causing effect of *Cuminum cyminum* seed EO and four of its major compounds (cymene, γ-terpinene, cuminaldehyde and β-pinene). They found that the EO and two of its compounds (β-pinene and γ-terpinene) showed 100% larvicidal activity against *C. chinensis* at the highest concentration (100 μL/mL air). However, against *S. oryzae*, they exhibited the mortality of 74, 89 and 88%, respectively, at the same concentration. They also reported EO and their compounds exerting higher mortality to the neonatal than the adults or pupae and suggested that EO being volatile in nature can easily penetrate the central nervous system and cause neurotoxic effect. In another study, Polatoğlu et al. (2016) reported the larvicidal activity of EO isolated from *Crithimum maritimum* against three storage pests (*O. surinamensis*, *S. granarius* and *S. oryzae*) in Petri plates and observed 100% mortality of all larvae at 100 μL/mL doses.

Pavela (2012) demonstrated the effect of sublethal doses (LD_{30}) of 13 different EOs on the larval development, fecundity, fertility and natality of adults of *S. littoralis*. All EOs caused total mortality (larvae as well as adults) and significant reduction in the number of adults. No significant difference in fecundity (adults mated without any apparent abnormal behaviour) was observed between individual treatments, while only two EOs (*Coriandrum sativum* and *Origanum majorana*) caused significant decrease in fertility as well as natality. Overall, the results indicated that sublethal doses of EOs may cause a significant increase of mortality in the course of their juvenile phase, thereby leading to a significant reduction in the natality of the next adult generation. Similarly, Papachristos and Stamopoulos (2009) also studied the sublethal effect of three EOs (*Lavandula hybrida*, *Rosmarinus officinalis* and *Eucalyptus globules*) on the development, longevity and fecundity of *A. obtectus*. The exposure of larvae and pupae to sublethal doses of EO vapours resulted in increased larval and pupal developmental time and reduced longevity and fecundity of the emerged female adults. Finally, they concluded that an adverse effect on the development (especially fecundity) of test insect surviving the exposure to vapours of tested EOs might be related to their main rapid mortality action. The reduced fecundity upon exposure to EO at sublethal dose was also reported by Nattudurai et al. (2017) during investigation of effect of *Atalantia monophylla* EO on *C. maculatus* and *S. oryzae*. An updated and detailed information on control of insect pests affecting the productivity of vegetable crops through application of eco-friendly insecticides originated from native plants of Mediterranean region is presented by Karkanis and Athanassiou (2020), suggesting the promising potential of plant products in sustainable management of vegetable crop losses resulting from diverse categories of insect pests.

The interaction between the lipophilic compounds of EO with proteins and enzymes of insects may play a major role in fatality (Ryan and Byrne 1988; Pavela 2015). The role of double bonds in deciding the larvicidal activity of EOs or their bioactive compounds has been well documented by many investigators. Lomonaco et al. (2009) explained that the hydrogenation of double bonds present in the compounds reduce the lipophilic character, thereby restricting their entry through the cuticle. Perumalsamy et al. (2009) while comparing the larvicidal activity of β-pinene and α-pinene suggested that the endocyclic double bond (as in β-pinene) shows more toxic effect on larvae than exocyclic double bond as in α-pinene.

Mode of action of EOs and their bioactive compounds against storage insect pests

It is believed that the EOs and their bioactive compounds exert their mode of action against insects by causing direct toxicity via inhibiting or altering acetylcholine esterase (AChE), blocking γ-amino butyric acid (GABA) and octopamine receptors or indirect toxicity by altering enzymatic and non-enzymatic antioxidant defence system.

Neurotoxic mode of action

Inhibition of AChE

AChE, the principle enzyme found primarily in synaptic cleft of insects, is responsible for metabolic conversion of 'acetylcholine' which is an important neurotransmitter participating in the transmission of nerve impulse and also acts as the target site for most of the neurotoxic insecticides. Sometimes, the structural modification in AChE is believed to be the main cause of resistance development among pests against synthetic chemical insecticides including organophosphates and carbamates. AChE inhibition is considered as one of the most investigated mechanism and, therefore, many authors have taken them into consideration while demonstrating the insecticidal action of EOs and their bioactive compounds. Because the insect AChE differs from the mammalian system by only a single residue (insect-specific amino acid cysteine), AChE can be an insect selective marker for the development of insecticides, which will be safer to the non-target vertebrates including humans.

Mukherjee et al. (2007) reported that monoterpenes exhibited their insecticidal mode of action by competitively binding in a manner similar to the actual substrate with the catalytic site of AChE, thus reducing its activity and subsequently causing mortality of the target insects. Abdelgaleil et al. (2009) conducted an in vitro experiments on AChE inhibitory activity of four important monoterpenes (cuminaldehyde, 1-8-cineole, limonene and fenchone) against *S. oryzae* and *T. castaneum* and reported among all tested compounds, cuminaldehyde and 1, 8 cineole exhibited AChE enzyme inhibitory (67.35–67.35% and 64.90–70.53%) activity at a concentration of 0.01 to 0.05 M against *S. oryzae* and *T. castaneum*, respectively. Kim et al. (2013) investigated the neurotoxic mode of insecticidal activity of α-pinene, β-pinene and limonene and achieved highest AChE inhibition (97.36%) at a concentration of 1 mg/mL against *S. oryzae* followed by β-pinene (54.96%) and limonene (51.23%). Olmedo et al. (2015) tested an in vitro inhibitory effect of two important phenylpropenes (anethole and estragole) on AChE activity of *T. castaneum* and reported that at 5 mM concentration both the compounds caused 54–63% inhibition in AChE activity. The mortality of the insect in relation to AChE was also explained by Kiran and Prakash et al. (2015), while studying the insecticidal activity of *Rosmarinus officinalis* EO against *S. oryzae* and *O. surinamensis.* Correa et al. (2015) explored the alteration in respiratory and locomotory response of maize weevil *S. zeamais* after treating with *Syzygium aromaticum* and *Cinnamomum zeylanicum* EO and explained such alteration in behaviour due to the inhibitory action of test EOs on AChE activity. Oboh et al. (2017) investigated the insecticidal efficacy of EO isolated from *Citrus sinensis* peels against *T. confusum*, *C. maculatus* and *S. oryzae* and reported that the inhibition of AChE may lead to the accumulation of acetylcholine at neuromuscular junctions which in turn induces neuronal excitation, hyperactivity, paralysis and subsequent mortality of the insect pests. They concluded that besides AChE, the inhibition of Na^+/K^+ ATPase activity (playing important role in transmission of nerve impulse between nerves in insects) by the EO may be strongly related to their insecticidal action.

Abdellaoui et al. (2017) measured the insecticidal activity of *Salvia officinalis* EO against *T. confusum* and observed a significant inhibition of AChE activity in a dose-response relationship. They also explained that, after coming in contact with the insect, EO can easily enter the synaptic cleft of the nerve endings through the cuticle due to volatile nature and cause neurotoxic effect by modifying or inhibiting the activity of AChE resulting into insect mortality. Recently, Bhavya et al. (2018) studied the insecticidal activity of *Ocimum tenuiflorum* EO against *S. oryzae* by measuring the AChE and suggested a positive correlation between anti-AChE and fumigant toxicity. More recently, Hu et al. (2019) demonstrated the insecticidal activity of *Artemisia brachyloba* EO and its major compound α-terpineol and davanone against *T. castaneum* and reported the mortality of the test insect probably occurred due to downregulation of AChE enzyme activity exposed to high concentration of test EO and its respective compounds.

Because AChE has two target sites i.e. catalytic and peripheral, many EOs and the compounds viz. citral, linalool, 1, 8 cineol have been reported to bind competitively (with catalytic site) and others like carvone and camphor bind non competitively (with peripheral domain) to inhibit the action of AChE, resulting into accumulation of acetylcholine, which subsequently caused hyperactivity, paralysis and finally death of the insects (López et al. 2015; Jankowska et al. 2017).

Alteration in octopamine and γ-amino butyric acid receptors

Octopamine and GABA receptors are considered as second important targets next to AChE for EOs and bioactive compound-mediated neurotoxicity among insects. Octopamine acts as a neurotransmitter in insect nervous system, where it influences several physiological events via activating specific G protein receptors, which in turn enable adenylyl cyclase that catalyses conversion of ATP to cAMP (cyclic adenosine monophosphate). Contrary to this, GABA is an inhibitory neurotransmitter distributed throughout the nervous system of almost all the insect species and have attracted a great deal of interest as they are an important site of action of several chemically distinct group of insecticides such as formamidine, dieldrin, lindane and fipronil (Bloomquist 1996; Chen et al. 2007).

Kostyukovsky et al. (2002) tested the insecticidal activity of two natural terpenes (ZP-51 and SEM-76) purified from EO of plants belonging to lamiaceae against *R. dominica* and suggested that the mortality of insects could be attributed to increase in intracellular cAMP concentration due to binding of test compounds with the octopamine receptors. Reports available in the literature also show that the EOs cause neurotoxic mode of action via elevating the level of both cAMP and Ca^{2+} ions in the neurons (Jankowska et al. 2017). Tripathi and Upadhyay (2009) during testing the mode of fumigant toxicity of *Hyptis suaveolens* EO against *C. maculatus*, *R. dominica*, *S. oryzae* and *T. castaneum* suggested that octopamine receptor alteration and respiratory arrest upon treatment can be the possible reason for its insecticidal activity. Some others suggested the blockage of GABA-gated chloride and sodium, tyramine receptors and nicotinic acetylcholine receptors (nAChR, a cholinergic receptor that form ion gated channels in nerve cells of insect's cell membrane) as another targets of EOs and their bioactive compounds mediated toxicity. However, further research is warranted to elucidate the exact mechanism of EOs and their bioactive compounds on insect (especially on storage pests) nervous systems.

Alteration in enzymatic and non-enzymatic antioxidant defence system

Insects hold a range of enzymatic (superoxide dismutase (SOD), catalase (CAT), peroxidases (POx), glutathione-S-transferase (GST) and glutathione reductase (GR)) and non-enzymatic (glutathione (GSH)) antioxidant defence systems that play a leading role in preventing the build up of free radicals which have been generated in cells in response to oxidative burden and other stress such as pesticides exposure and detoxifying xenobiotics as well as maintaining the cellular redox homeostasis (Zhao et al. 2017).

Wu et al. (2014), while testing the insecticidal activity of allyl isothiocyanate (AITC) against adult *S. zeamais*, observed the inhibition of CAT and GST activity at low doses, while at higher dose, AITC caused dual effect (decreased CAT but increased GST), which likely caused the mortality of the test insects. They also explained that the increase in GST activity can be attributed to the binding of –SH group of GST with the test compound. Kiran and Prakash et al. (2015) during their observation on insecticidal activity of *Rosmarinus officinalis* EO against *S. oryzae* and *O. surinamensis* suggested that the EO caused toxicity by significantly increasing the level of SOD and CAT and decreasing GSH/GSSG ratio. Kiran et al. (2017) made an investigation on biochemical mode of action of *Boswellia carterii* EO against *C. chinensis* and *C. maculatus* and reported that the toxicity of EO can be attributed to the elevation of ROS, SOD and CAT and reduction in GSH/GSSG ratio upon treatment. GSH is a non-enzymatic antioxidant and plays an important role in quenching of oxygen radicals and detoxification of xenobiotics as well as maintenance of cellular redox status, thus depletion in their level can cause oxidative burden resulting into damage to nucleic acids and lipoproteins, and ultimately cell death.

In another research, Oni et al. (2019) reported the enhancement in SOD activity as the indicator of ROS accumulation in insect cells, and overproduction of ROS leads to the inability of the endogenous defence system of the cells to neutralize them eventually resulting into damage of important cell constituents, which consequently caused death of the target pests. Rajkumar et al. (2019) tested the biochemical efficacy of *Mentha piperita* EO and its chief compounds (menthone and menthol) against *S. oryzae* and *T. castaneum* and observed an increasing trend for SOD and declining trend for CAT and GSH/GSSG ratio. They explained that the decline in CAT activity can be due to high level of superoxide anions produced by SOD. Recently, Upadhyay et al. (2019) described an increase in ROS, SOD and CAT level and decrease in GSH/GSSG ratio while testing the insecticidal activity of *Melissa officinalis* EO against *T. castaneum*. Petrović et al. (2019) during their investigation on *Carum carvi* EO against *T. castaneum* suggested that the alterations in first line of antioxidant defence (SOD and CAT along with GST) are the significant parameters whose variation would be the key cause responsible for the mortality of the pests.

Commercial challenges for product development based on EOs and their bioactive compounds

Despite availability of proof of efficacy of EOs and their bioactive compounds against different storage pests, only few pesticides based on EOs and their bioactive compounds have found their way in pesticide market. Some recent examples of this category that demonstrated efficacy in the field are Ecotec™

(EO based), PrevAM^R (orange oil based) and Requiem^R (a mixture of three monoterpenoids) (Isman 2019). The commercialization of EOs and their bioactive compound-based insecticide against stored product insects are limited due to the following reasons:

The lack of efficacy in real food system

Currently, numerous published reports are available in literature on the efficacy of EOs/bioactive compounds against storage pests (Pavela 2015); however, most of the results showed so far have come from laboratory experiments on model systems, where only a small quantity of foods were placed in closed containers and treated with test EOs to observe their pesticidal efficacy (Upadhyay et al. 2019). Such data do not allow predicting the results under natural system as generally observed during conventional storage, while such type of research is noteworthy for understanding of their actual biological activity for the development of botanical pesticides. Hence, efforts should be made to investigate the pesticidal efficacy of EOs and their bioactive compounds in direct food system to ascertain their actual efficiency in protection of stored food commodities from insect's infestation.

Availability of the EOs

Although some EOs might be plentiful and available throughout the year owing to their demand in different sectors, however, their large-scale commercialization as botanical pesticides could require greater production, while in certain cases, the insecticides derived from EOs of rare plants would not be easily produced due to a lack of sufficient quantities of plant materials. The cultivation of plants needed for production of EOs would require large areas, thus posing potential competition with food production in highly arable agricultural lands (Lengai et al. 2020). The lack of plant resources at affordable prices is another constrain that prevents large-scale production of botanical pesticides (Lu et al. 2020). Further, over-exploitation of plants for extraction of effective EOs may lead to loss of their biodiversity, which remains to be a challenging concern regarding commercialization of botanical pesticides. Therefore, the EOs with abundant resources and low cost has become an inevitable choice for the development of botanical pesticides.

Standardization and toxicological evaluation of EOs/bioactive compounds

Formulation of EOs and their bioactive compound-based botanical pesticides is quite challenging because one plant could have several active compounds that differ in chemical compositions depending on geographical condition, climate, seasons, methods of isolation and characterization, and such variation in chemical composition may significantly influence their actual insecticidal activity. This attribute could, however, be explored by combining several plants with related compounds whose synergy is effective against insect pests.

Different regulatory authorities like Food and Drug Administration (FDA), the International Organization of Flavor Industries (IOFI), Food Chemical Codex (FCC), Manufacturers Association (FEMA), Codex Alimentarium and the Council of Europe (CoE) have developed some accurate procedure for chemical and toxicological analyses for the EOs as the synergistic and antagonistic effect may intend for some EOs (Dima and Dima 2015; Falleh et al. 2020). In general, most of the EOs and their bioactive compounds are non-toxic to mammalian systems. The median lethal dose (LD_{50}) for mice/rats ranged from 0.8 to 3.0 g/kg body weight for pure compounds and more than 5.0 g/kg for insecticides formulation (Isman et al. 2011). Additionally, due to the long history of some traditionally used EOs and their bioactive compounds, they can be recommended without toxicological studies, while such type of experimental evaluation is mandatory for registering botanical pesticides for commercial purposes.

Toxicological evaluation on non-target organisms

Despite the safety associated with botanical pesticides, some EOs and their bioactive compounds with insecticidal activity are often associated with toxicity towards a group of non-target organisms (Benelli et al. 2019). Only a least number of researches have been performed dealing with the measurement of toxicity (either acute or chronic) of EOs or their bioactive compounds on non-target organisms, whereas such type of research is crucial for the development of standardized botanical pesticides. Conti et al. (2014) in a study assessed the toxicity of *Melaleuca alternifolia* EO against *Aedes albopictus* larvae and a non-target organism, *Daphnia magna* (water flea), that share the similar ecological niche of *A. albopictus*. They reported that the EO along with causing toxicity to the target mosquito larvae caused remarkable toxicity to adults of the water flea. Similarly, Pino-Otín et al. (2019) evaluated the toxicological effects of *Artemisia absinthium* EO on an aquatic invertebrate, *Daphnia magna*, a marine bacterium, *Vibrio fisheri*, and an unicellular freshwater green alga, *Chlamydomonas reinhardtii*. They reported high toxicity of *A. absinthium* for *D. magna* followed by *V. fisheri* and *C. reinhardtii*. Some other examples like rotenone, extracted from *Derris* and *Lonchocarpus*, is toxic to mammals, fish and insects, and *Tephrosia vogelli*, an effective insecticide against several pests is acutely toxic to farmed clariid, *Clarias gariepinus* (Lengai et al. 2020). Thus, based on available reports, it can be recommended that more studies are required to better understand the mechanisms of action of pesticides developed from EOs and their bioactive compounds as well as more detailed risk assessment on non-target organisms of natural communities including human being in order to ensure their safer implementation in food industry or agricultural practices.

Low persistence of the effect and the regulatory approval

EOs and their bioactive compounds can be considered a broad family of structurally diverse compounds having different insecticidal activities. However, their complete pesticidal potentials have not been reached yet because of their high volatility and a low persistence (with half-lives less than a day) of their actions that remains shortly after their application. Further, EOs containing more hydrogenated bioactive compounds are more susceptible to oxidation. Hence, their efficacy needs to be experienced in more realistic conditions and mostly over longer periods of time in order to test the persistence of their activity. Ilboudo et al. (2010), in a study, tested the biological activity and persistence of four EOs namely *Ocimum americanum*, *Hyptis suaveolens*, *H. spicigera* and *Lippia multiflora* against *C. maculatus* adults. They reported that among all tested EOs, the oil of *O. americanum* was the most persistent, since the target insect was killed even at 14th day of exposure, while the biological activity of remaining EOs gradually decreased with time. The loss of efficacy was possibly due to their high volatility and quick degradation of the bioactive compounds (Ngamo et al. 2007). Such disadvantage of low persistence of EOs and their bioactive compounds can be resolved through using nanoencapsulation technology (discussed in forthcoming section), which could prolong their persistence, while at the same time optimize the dosage to its achievable minimum level.

Finally, once all the above-mentioned issues are addressed, the regulatory approval of the use of EOs and their bioactive compounds remain the main challenge towards the generalization of their use, and consequently towards their commercialization. Although several plants EOs are exempted from registration in the USA, many more are not. The approval for EO-based botanical pesticides has been difficult since pesticide regulatory strategy have been developed previously to appraise synthetic pesticides where there is a single bioactive ingredient with no ambiguity. The European authority is the only known organization planning to circulate criteria for ‘low-risk active substance’ that some EOs may meet, probably enabling a corridor for agreement of more pesticides based on EOs and their bioactive compounds. In this regard, regulatory approval continues to be a fence to commercialization and will probably continue to be a barrier until regulatory systems are adjusted to better accommodate these products.

Nanoencapsulation: a novel approach towards enhancement of efficacy and commercialization of EOs and their bioactive compounds

Although a plenty of research papers published in recent years have claimed the insecticidal efficacy of EOs and their bioactive compounds against storage insect pests, but only few have been attempted to apply EOs and their bioactive compounds directly into real food system. This can be due to the fact that these EOs and their bioactive compounds are highly volatile, poorly soluble in water and undergo rapid oxidation under light, oxygen, moisture and temperature (Hashem et al. 2018; Chaudhari et al. 2019). Many researchers tried to overcome these challenges and tried to enhance EO efficacy by mixing EOs/compounds with other materials like silica and inert materials or by making various formulations using nano-technology. In a study, Bougherra-Nehaoua et al. (2015) showed that the action of inert dusts was higher when used in combination with the EOs of *Pistacia lentiscus* and *Foeniculum vulgare* against *S. zeamais*. In another study, Korunic and Fields (2020) observed that three different formulations of diatomaceous earth along with dill EO were effective in controlling four major stored product insects at lower doses than diatomaceous earth alone. At these lower doses, there was much less reduction of mass density than the diatomaceous earth used alone. More recently, Suresh et al. (2020) documented the insecticidal efficacy as well as longevity and fecundity of *Crithmum maritimum* EO in nanoemulsion and silica nanoparticles against two important insects viz. crop pest *Spodoptera litura* and the dengue vector *Aedes aegypti*. However, the data on the efficacy of formulations based on inert dusts and silica with EOs against storage insect pests are very scarce and more extensive research is needed for control of storage insect pests.

Most of the recent studies focussed on encapsulating the EO/compounds into edible secondary wall materials called nanoencapsulants (chitosan, gelatin, alginate, carrageenan, cyclodextrins etc.) using different nanoencapsulation techniques such as ionic-gelation, spray drying or chilling, coacervation, electrospinning and emulsification (de Souza et al. 2017). The nanoencapsulation can solve, at least partially, the above-mentioned limitations, allowing for a reduction of their degradation and increase of their persistence due to the minimization of the evaporation. Nanoencapsulation is generally performed using two different (top down and bottom up) approaches. Top down approach generally refers to synthesizing nanoparticles from small-sized materials, while bottom up approach applied to preparing nanostructures by self-assembly of atom with atom, molecule with molecule and vice-versa. These fabricated particles can take different forms like nanoemulsion, nanogel and nanocapsule/nanoparticles depending upon the methods adopted, polymers, cross-linking agents and surfactants used as well as environmental conditions existing during operation (El Asbahani et al. 2015; Athanassiou et al. 2018). The encapsulation of EOs and their bioactive compounds in nano-sized delivery system can provide the bases for their controlled release, making their application easy. Further, the increase of their insecticidal activity can be expected due to extremely small size of the particles facilitating their diffusion in insect's body due to their high surface-to-volume ratio (Mossa 2016; Lucia and Guzmán 2020). This may lead to a situation in which nanoformulations are effective even at very low concentration.

Among different nanoformulation, nanoemulsion-based delivery of EOs and their bioactive compounds are most suitable to be used in food system for the management of different storage pests because of their properties such as kinetic stability, non-toxicity, stiffness, permeability, crystallinity, solubility and biodegradability (Nenaah 2014; Sharma et al. 2020). Many researchers are exploring the EO-based nanoemulsion against various species of insects to encourage the results about the effectiveness of such nanosystems on the prevention of different storage pests. The nanoencapsulation process has a huge opportunity in the food and agriculture field, but little information exists on their use in postharvest protection of food commodities against insects. This is a growing field of research where new informations are regularly added. The prospect of nanoencapsulation of EOs and their bioactive compounds over their free form in management of storage insect pests is diagrammatically illustrated in Fig. 1. Several authors reported the application of EOs and their bioactive compounds in active packaging, aiming to increase the shelf-life of the stored food commodities from insect's infestation.

In a study, Yang et al. (2009) performed the comparative efficacy of free and polyethylene glycol–encapsulated *Allium sativum* EO against *T. castaneum* causing deterioration of stored rice and reported far better (more than 80%) efficacy even after 6 months of storage as compared to free form (11%) at the same concentration (650 mg/kg). The authors suggested that the stronger insecticidal activity of nanoencapsulated EO might be related to the slow release of major bioactive components, leading to increase of persistence to perform its insecticidal activity at lower concentration. Negahban et al. (2012) while assessing the fumigant toxicity of *Cuminum cyminum* EO and its nanoformulation in a glass bottle against *T. castaneum* observed lower LC_{50} value (16.25 μL/L) representing higher toxicity of nanocapsule than free EO (32.12 μL/L). The greater toxicity of encapsulated EO can be demonstrated as a result of controlled released of EO from formulation, allowing the release of only small quantities of EO over a given time interval. González et al. (2014) prepared nanoemulsion containing EOs namely geranium and bergamot into polyethylene glycol (PEG) and tested their efficacy against *T. castaneum* and *R. dominica.* They found a remarkable increase in the toxicity of the EOs by its nanoformulation. This can be achieved due to better mobility of extremely small-sized particles in the nanoemulsion, enabling faster penetration by direct contact through the insect's cuticle or by ingestion through the digestive tract and enhancing insecticidal activity (Margulis-Goshen and Magdassi 2013).

Ziaee et al. (2014b) described the fumigant toxicity of free and myristic acid-chitosan-encapsulated *Carum copticum* EO nanogel against *S. granarius* and *T. confusum* and reported nanogel with higher mortality of both the insects at lower concentration and exposure time as compared to free one. Since, most EOs exhibited insecticidal activity via their fumigant mode of action, they may be toxic by penetrating to the insect body through the respiratory system. The small size of the oil-loaded nanogels can lead to more penetration into the insect body via the respiratory route than the free oil and increased their efficiency. They also explained that the greater persistence of EO due to controlled release of bioactive compounds might be responsible for enhancement of their insecticidal activity. Nenaah (2014) analyzed the toxicity of three EOs (*Achillea biebersteinii*, *A. santolina* and *A. mellifolium*) and their nanoemulsion against *T. castaneum* and reported increased toxicity of oils nanoemulsion over their free forms, where LC_{50} values after 96 h of exposure against larvae and adults were ranged between 11.0–27.5 μL/L air and 8.8–21.3 μL/L air, respectively. Khanahmadi et al. (2017) also reported higher toxicity with low LC_{50} value of EO after nanoencapsulation during testing the contact toxicity of *Artemisia haussknechtii* EO against *S. oryzae* and *T. castaneum*. In a work, Khoobdel et al. (2017) investigated the in vitro fumigant and contact toxicity of free and nanoencapsulated *Rosmarinus officinalis* EO against *T. castaneum* and reported enhanced toxicity after nanoencapsulation. The enhanced efficacy of EO after nanoencapsulation could be attributed to the increased surface area and sustained release. Hashem et al. (2018) developed a nanoemulsion of *Pimpinella anisum* EO containing 81.2% of (*E*)-anethole against *T. castaneum* adults and F_1 progeny and reported that the nanoemulsion caused toxicity of about 81.33% to the adults and suppressed the emergence of its progeny to higher degree ($LC_{50} = 9.3\%$ v/v) when compared with control. They also examined the mode of action of nanoemulsion and stated that the toxicity was caused due to lypophilic nature of (*E*)-anethole and smaller particle size of nanoemulsion, allowing its penetration through cuticle, thereby causing serious injury to different body parts of the insect.

Recently, Upadhyay et al. (2019) encapsulated EO of *Melissa officinalis* into chitosan nanoemulsion and achieved enhanced fumigant activity (0.048 μL/mL air) in contrast to un-encapsulated (0.071 μL/mL air) EO. Based on enhanced efficacy, they suggested that the nanoencapsulated test EO may be recommended as potential plant-based eco-friendly or low-risk pesticide for the protection of stored food against *T. castaneum* infestation. Adak et al. (2020) studied the insecticidal activity of nanoemulsion containing eucalyptus EO stabilized by an emulsifier Tween 80 against *S. oryzae* and *T. castaneum*. They found that the nanoemulsion of EO had better effect against *S. oryzae* and *T. castaneum*. Such results might be attributed to reduced droplet size in nanoemulsion

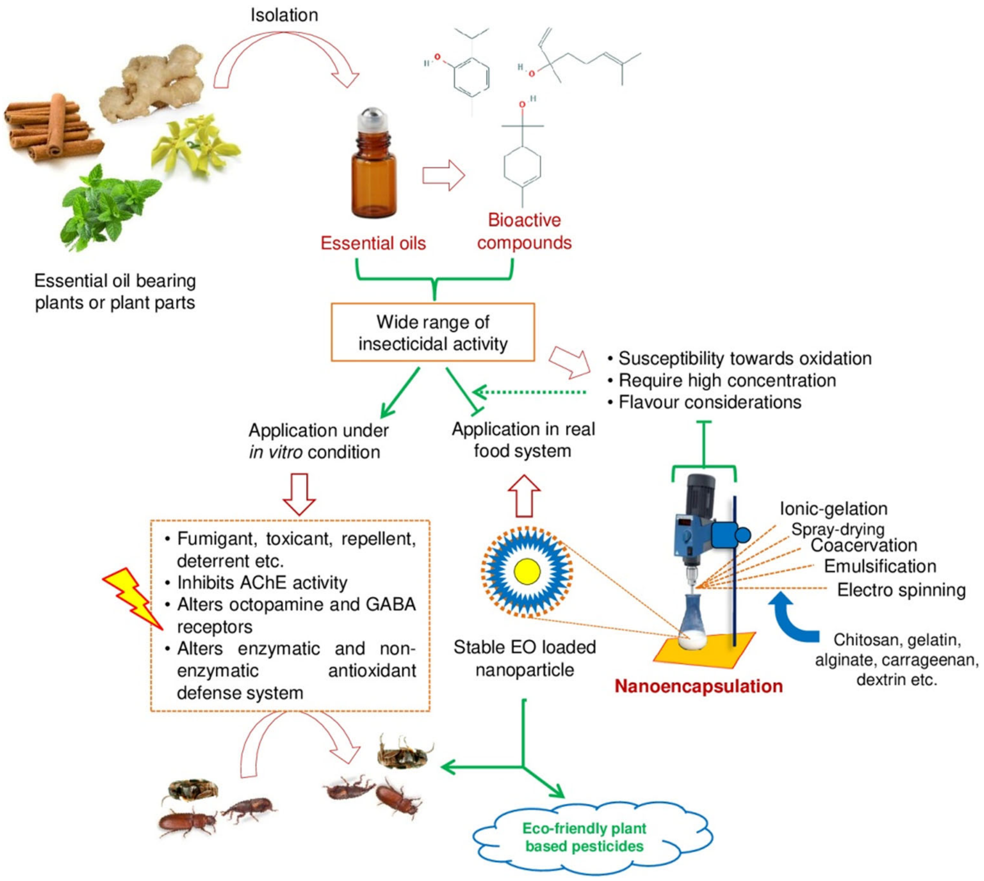

Fig. 1 Prospects of EOs and their bioactive compounds after employment of nanoencapsulation approach in management of storage insect pests at large scale

that have favoured itself to come into contact with insects more closely unlike EO and showed its toxicity effect. Smaller particle sizes of nanoemulsion increased penetration and uptake of active components of EO into the insect body. This may improve the biological activity of nanoemulsion as compared to free EO. Rajkumar et al. (2020) reported that the fumigant toxicity of peppermint EO and chitosan EO nanoparticles to adults of *T. castaneum* and *S. oryzae* increased on increasing the concentration levels of oil nanocapsules, and in comparison, the percentage mortality of EO nanocapsules was higher than EO alone. They suggested that increased mobility of nanoparticles allows better infiltration in insect tissues and eventually enhances insecticidal activity when compared to bulk material. The above examples demonstrate that the EOs after nanoencapsulation could hold great promise and can make a significant contribution to sustainable management of storage insect pest in integrated pest management programmes.

Conclusions

Different EOs and their bioactive compounds have exhibited pronounced insecticidal activity, effectively reducing and/or inhibiting the survival of various stored product insects. Different methods to control storage insects were studied intensively using fumigant toxicity, contact toxicity, repellent, antifeedant, oviposition detterent, ovicidal, larvicidal activities etc. The binding and blocking of nerve regulators such as acetylcholinesterase, octopamine and γ-amino butyric acid as well as alteration in enzymatic and non-enzymatic antioxidant defence systems are found to be the novel mechanisms of their mode of action against storage insects. The main limitations that need to be addressed before commercialization of such products are the issues of availability, stability, standardization, toxicological evaluation and production of cost-effective products for large-scale management of postharvest losses caused by insects. Currently employed nanoencapsulation technology could help in enhancing the stability, functionality and consumer's acceptability and optimizing the performance of EOs and their bioactive compounds, thereby, facilitating their recommendation as potential plant-based eco-friendly pesticides against major insect pests causing deterioration of stored food commodities. Further, detailed investigations are required under in situ conditions in order to accomplish the reproducibility of the research work in the real food system, an area that needs more research insight.

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Data availability All data observed during current study are included in this article.

Declarations

Ethics approval This is an observational study, no ethical approval is required.

Consent to participate All authors participated in this work.

Consent for publication All authors agree to publish this article in the Environmental Science and Pollution Research.

Conflict of interest The authors declare no competing interests.

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