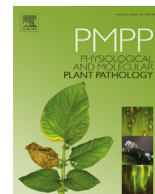




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journal homepage: www.elsevier.com/locate/pmppRole of kairomone in biological control of crop pests-A review[☆]

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ABSTRACT

Kairomones are inter-specific semiochemicals which mediate interactions beneficial to organisms that detect them. The use of kairomones for biocontrol of insect pests has been of interest for several decades due to the fundamental importance of host-plant selection by phytophagous insects, as well as the potential of natural enemies to co-opt those processes in ensuring their own survival. Pest management efforts that enhance the effectiveness of natural enemies can reduce economic loss and negative effects of insect herbivory. However, biocontrol agents often are unable to manage the populations of insect pests satisfactorily, due to limited host-searching capacity and limited detection range of 'signals' from damaged host plants. Here, we discuss known successful examples of such semiochemicals, kairomones, and their ultimate potential for biological control.

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Contents

1. Introduction	00
2. Kairomones derived from host plants and their habitats	00
3. Kairomones derived from host insects	00
4. Synthetic saturated hydrocarbons as kairomone	00
5. Non-host-plant-derived kairomone	00
6. Effects of interspecific, intraspecific, and intra-population variability of host plants on entomophages	00
7. Field application of kairomone formulations	00
8. Conclusions	00
Acknowledgments	00
References	00

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1. Introduction

A kairomone is an interspecific semiochemical or a mixture of semiochemicals, produced by one species which induces responses advantageous to an individual of a different species perceiving the signal. Kairomones are important in biological control efforts due to the fundamental importance of semiochemicals in phytophagous

insect host-plant selection (Fig. 1) [1] and the potential for natural enemies to employ these as well as host insect odors in searching effectively for prey. It has been understood since the 1960s that herbivores in natural ecosystems are limited, not so much by food supply, but rather by natural enemies [2], i.e., by biological control. Because kairomones play an important role in limiting herbivore populations in natural ecosystems, especially in tropical areas [3], they may also have considerable utility for human management of insect crop pests.

Volatiles emitted from the host plants on which herbivores feed have been demonstrated in many studies to serve as kairomonal signals, attracting beneficial entomophages to the host plant, after which they employ other semiochemical and visual cues to search efficiently for different life stages of the plant pests. For example, parasitization by *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) on eggs of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) is high when the eggs are present on tomato rather than other crops [4]. Host insects also emit kairomones attractive to beneficial entomophages. Tricosane, present in wing scales of *H. zea* (Boddie) acts as a host-insect-derived kairomone attractive to *T. evanescens* Westwood, 1833 [5].

Entomophages utilize chemical cues for host habitat location, host location, and foraging activities as described in different sections below. Mixtures of cues from various sources in a crop or conservation habitat needing protection can elicit specific responses by natural enemies that result in their conservation and increased abundance. The sources of these kairomones can be natural host- and non-host plants, as well as commercial dispensers of long- and short-chain saturated hydrocarbons.

This report organizes and discusses information about major sources of kairomone and their scope in eliciting responses among entomophages for management of herbivores in crop eco-systems. The major topics of the report are diagrammed in Fig. 2. Herbivores directly benefit from host-plant biomass but can suffer negative effects from toxic host-plant secondary compounds. Herbivores can have direct positive effects on entomophages when providing biomass for sustenance, but can have indirect negative effects on

entomophages if they sequester secondary compounds that interfere with entomophage growth [6]. Entomophages have indirect positive effects on host plant biomass by reducing populations of herbivores. In addition, some kairomones that attract entomophages to host plants are attractive also to herbivores [7].

2. Kairomones derived from host plants and their habitats

Ecological and evolutionary studies have focused extensively on how entomophages locate host insects in plant habitats [8–10]. In multiple studies, the attractiveness of habitats with a diversity of crops and weed flora was increased by the mixtures of physical and chemical stimuli produced when the crops were stressed by herbivores. Parasitoids, in particular, have adapted to conditions of low host density by searching for herbivore-induced plant volatiles (HIPVs) [11,12] produced by infested host plants. Linalool-L and heptadecane detected from fruit extract of tomato cultivar have been reported by Tandon and Bakthavatsalam [4] to attract *T. chilonis* on the eggs of *H. armigera*. Leaf extracts of the same variety of tomato had different chemical compounds of α -phellandrene, α -pinene, *trans*-caryophyllene, (*Z*)- α -farnesene, *trans*- α -ocimene and selinene that were found to be attractive to *T. chilonis*. *Allium porrum* damaged by *Acrolepiopsis assectella* is known to produce sets of volatiles, including dipropyl disulfide and propyl propane, as well as thiosulfonate, propyl propane and thiosulfinate [13] that are attractive to *Diadromus pulchellus*. Allylisothiocyanate is abundant in volatiles of *Brassica nigra* damaged by *Brevicoryne brassicae*, which enhances the activity of *Diaeretiella rapae* [14] (Fig. 3A and B).

Attraction of two Scelionids, *Trissolcus bassalis* and *Telenomus podisi* was enhanced towards host legumes infested with *Nezara viridula* [15] and *Euschistus heros* [16], respectively. Pine trees infested with three-day-old egg masses of *Diprion pini* and elm infested with 3-h- to 5-d-old egg masses of *Xanthogaleruca luteola* attracted and arrested eulophid parasitoids, *Chrysonotomysia ruforum* and *Oomyzus gallerucae* [17,18], respectively. Tomato [19] as well as sorghum and pigeonpea [20] plants infested with

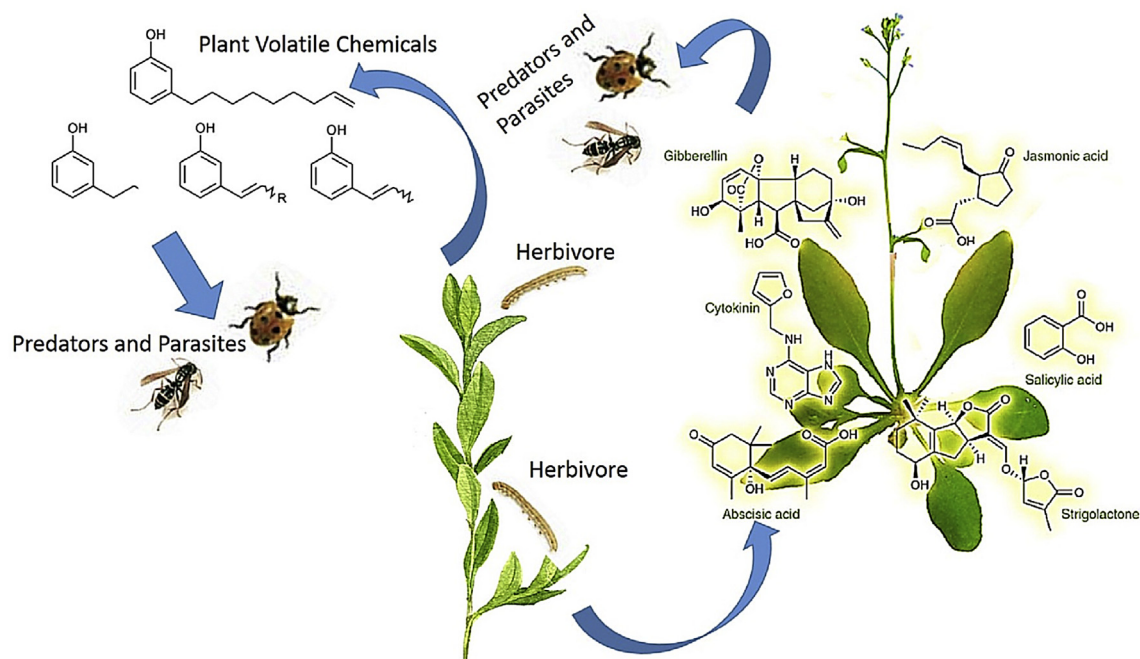


Fig. 1. Schematic representation of how plant response against the herbivore.

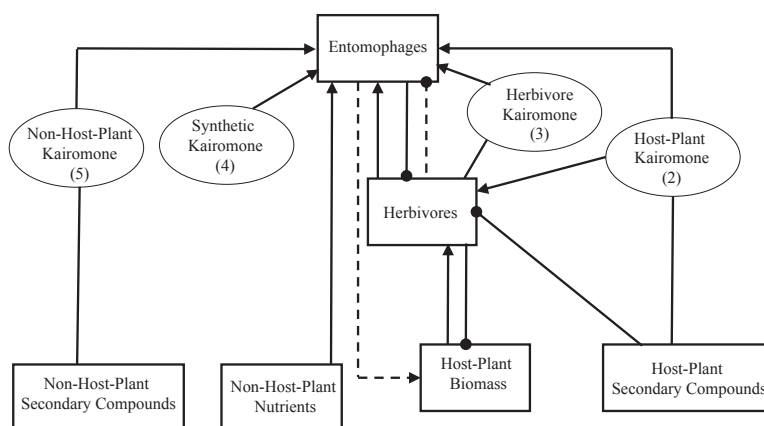


Fig. 2. Diagram of kairomone sources (designated by ovals) in field crop host plant-herbivore-entomophague interactions (designated by rectangles): Solid lines indicate direct effects and dashed lines, indirect effects. Arrows indicate positive effects and circle heads, negative effects. Numbers in parentheses designate sections of report where the kairomone types are discussed.

H. armigera, pepper infested with *H. assulta* [21] and cabbage infested with *Plutella xylostella* [22] arrested movement and increased the parasitism of *T. semifumatum* and *T. chilonis*. Brussel sprout leaves with 3-d-old egg clutches of *Pieris brassicae* [23], as well as maize extracts in combination with the synthetic host pheromone and host eggs of *Ostrinia nubilalis* [24], acted as arrestants to *T. brassicae/maidis* where the respective host insects were present. Attraction and increased parasitism of *T. pretiosum* were noticed when cotton and tomato were infested with *S. frugiperda* [25] and *H. zea* [26], respectively. The Mymarids like *Anagrus nilaparvatae* and *Anaphes iole* were reported to be attracted to rice infested with *Nilaparvata lugens* [27] and *Lygus hesperus* [28].

Herbivore-induced plant volatiles [29] were detected from long distances by parasitoids more efficiently than were host-derived kairomones [30] and the parasitoids preferred HIPVs produced by host plants, showing comparatively lower preference to blends of chemicals produced by genotypes of the same species [31–36]. Such preferences may be learned [37] from experience gained from previous visits to host plants and host insects for oviposition [38–40].

The diversity of vegetation in a particular eco-system has been positively correlated with abundance of natural enemies in several studies [41,42] while some other species showed more preference to monoculture habitat [43,44] or no response to diversified vegetation [45]. Strong preference and orientation of natural enemies has been reported towards the HIPVs when a particular crop is in monoculture rather the presence of non-host plants (weeds) in the vicinity [36,46,47]. Other studies demonstrated the interference on the location and selection of host insects and their habitats by natural enemies when unwanted volatiles from non-host plants are present and over-rule the most attractive volatiles produced by the plants in the same eco-system [48,49], coupled with impeding of free movement of natural enemies physically to locate the herbivore infested plants [50–53]. However, two parasitoids, *Diadegma semiclausum* and *Cotesia glomerata* were more abundant in mixed cropping than monoculture habitat [54,55] and such behavior is report to be modified by experience of females exposed to mixed cropping eco-system subsequently [55,56].

Parasitoids of phytophagous insects are known to orient to plants on which their hosts are found. They often use plant-derived chemicals that indicate or confirm the presence of the host [10]. Chemicals emanating from the plant itself may arrest parasitoids in the vicinity of their hosts, thus mediating successful host location and parasitization [57]. Host plant selection by the female

parasitoids involves a series of complex behavioral responses to a hierarchy of physical and/or chemical stimuli that lead them to their potential hosts [58]. Parasitoids respond to volatiles emanating from both undamaged [59] and damaged [60] plants. The nature of kairomonal responses depends on the insect pest, natural enemy, and the crop [61]. Complex tritrophic effects can occur, for example, when a pathogen manipulates a host plant to produce volatiles that attract a vector, but these volatiles also attract a parasitoid. Such effects have been reported by Yambhantanal et al. [62] in the case of a bacterial pathogen, *Candidatus Liberibacter asiaticus*, which induces citrus trees to release methyl salicylate that increases searching effectiveness of the vector, *Diaphorina citri* (Kuwayama), but also induces searching by *Tamarixia radiata* Waterston, which parasitizes *D. citri* nymphs.

High quantities of octadecanoic acid emitted from rice plants damaged by yellow stem borer may play a pivotal role in attracting *Trichogramma* spp. as well as in stimulating oviposition [63]. Volatile profiles of rice cultivars indicated the presence of 9,12,15 octadecatrienoic acid and 9-octadecenal, which may have played a positive role in the attraction of *T. chilonis* to specific cultivars while hexadecane, heptadecane, pentadecane and hexadecanoic acid were reported to be responsible for the attraction of *T. japonicum* [64]. A total of 16 compounds including alkane hydrocarbons, monoterpenes, sesquiterpenes, and diterpenes present in tomato fruit volatile and 19 compounds present in tomato leaf volatiles were reported to be responsible for high parasitization of *T. chilonis* on eggs of *H. armigera* [4] [Fig. 1].

Flowers often are highly attractive locations for egg laying by herbivores. Blends of chemicals present in flower extracts of highly susceptible genotypes may contribute also to attraction of natural enemies. Extra-floral nectaries in cotton, for example, appear to be important sources of kairomones for braconids, ichneumonids and trichogrammatids involved in the control of budworms and boll worms of cotton. These parasitoids are more abundant in cotton cultivars with extra-floral nectaries which act as an energy source, with sugars and varying types of amino acids, increasing the longevity of parasitoids [65]. *T. chilonis* showed increased parasitization of *H. armigera* eggs deposited on flowers and young squares in view of the nectar source. *Camponotus sonorensis* and *Microplitis croceipes* Cresson (Hymenoptera: Braconidae) lived longer, exhibited higher fecundity and showed increased vigor in nectaried cotton varieties than in varieties without nectaries, besides altering the physiological response of parasitoids [66]. Caryophyllene detected in the flowers and squares of Suvin, TCHB, MCU 7 and

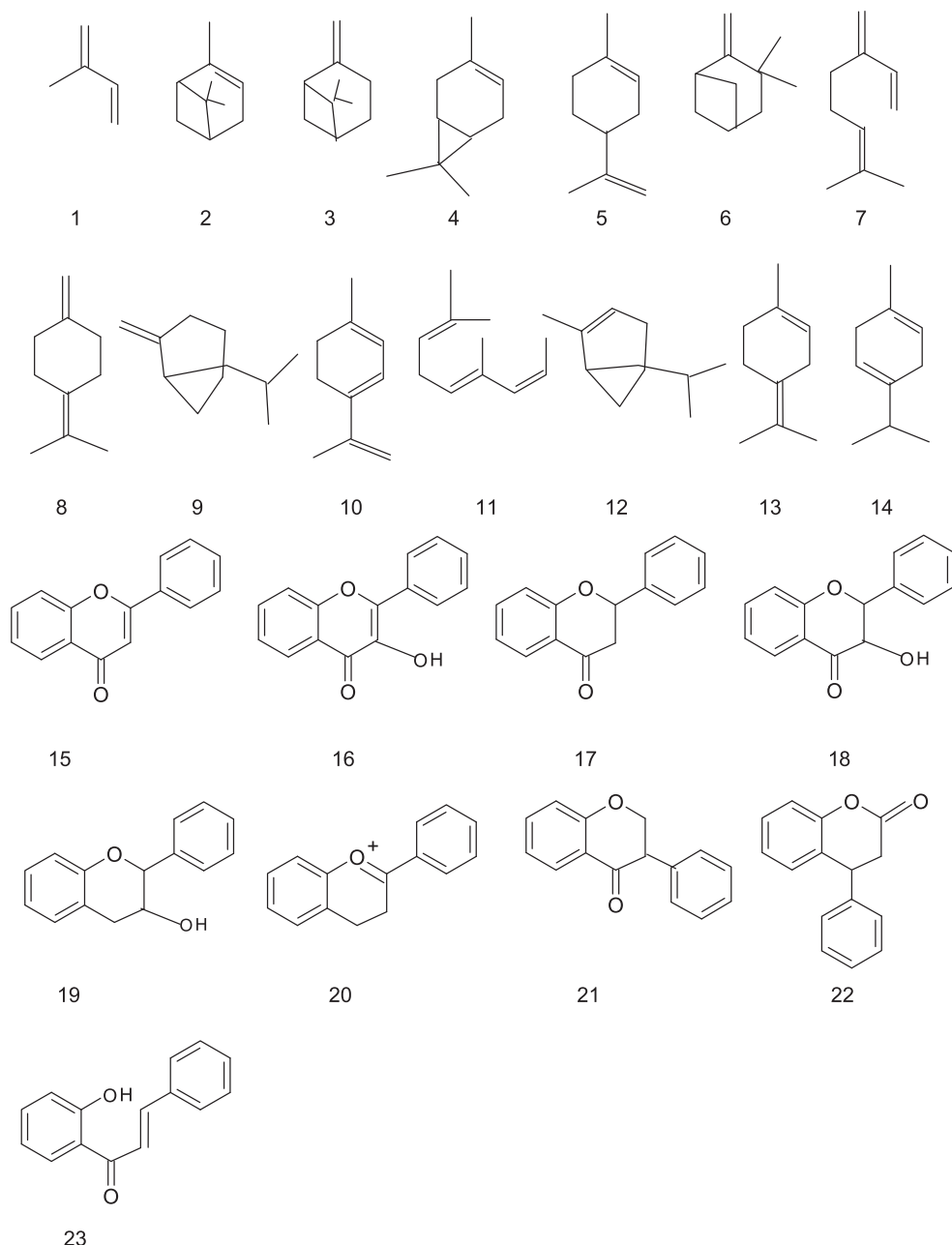


Fig. 3. Major chemical constitutions present in the kairomone.

A. Terpenes and Flavanoids

1. Isoprene 2. α -pinene 3. β -pinene 4. Δ^3 -carene 5. Limonene 6. Camphene 7. Myrcene 8. β -phellandrene 9. Sabinene 10. α -terpinene 11. Ocimene 12. Terpinolene 13. γ -terpinene 14. Flavones

B. Terpinoids

1. Geraniol 2. Eugenol 3. Citronellol 4. Linalool 5. Terpineol 6. Menthol 7. Menthone 8. Carvone 9. β -Pinene 10. Cineole 11. Carvacrol 12. Thymol 13. β -Caryophyllene.

C. Saturated hydrocarbons

1. Decane 2. Tridecane 3. Tetradecane 4. Pentadecane 5. Octadecane 6. Heneicosane 7. Eicosane, 8. Tricosane 9. Petacosane 10. Hexacosane 11. Octacosane 12. Nonadecane 13. Docosane, 14. Tetratriacontane 15. Hexatriacontane 16. Dotriacontane 17. Tritetracontane 18. Tetratriacontane, 19. Hexadecanoic acid.

MCU 11, as well as octadecane, undecane and dodecane in LRA, and hexadecenoic acids in MCU 11 were reported to be attractive to *T. chilonis* [67].

3. Kairomones derived from host insects

Host insects have been reported to produce characteristic hydrocarbons, fatty acids and proteins which stimulate natural

enemies to intensify their search near the host [4,63,68]. Different semiochemicals are associated with various insect behaviors such as feeding, mating and egg laying. The use of such chemicals to increase the effectiveness of entomophages has been advocated by many researchers, including [69–72].

Scales from adult hosts elicit kairomonal activity in several parasitoid species. Lewis et al. [5] demonstrated that parasitization by *T. evanescens* was higher on eggs placed in areas where adults

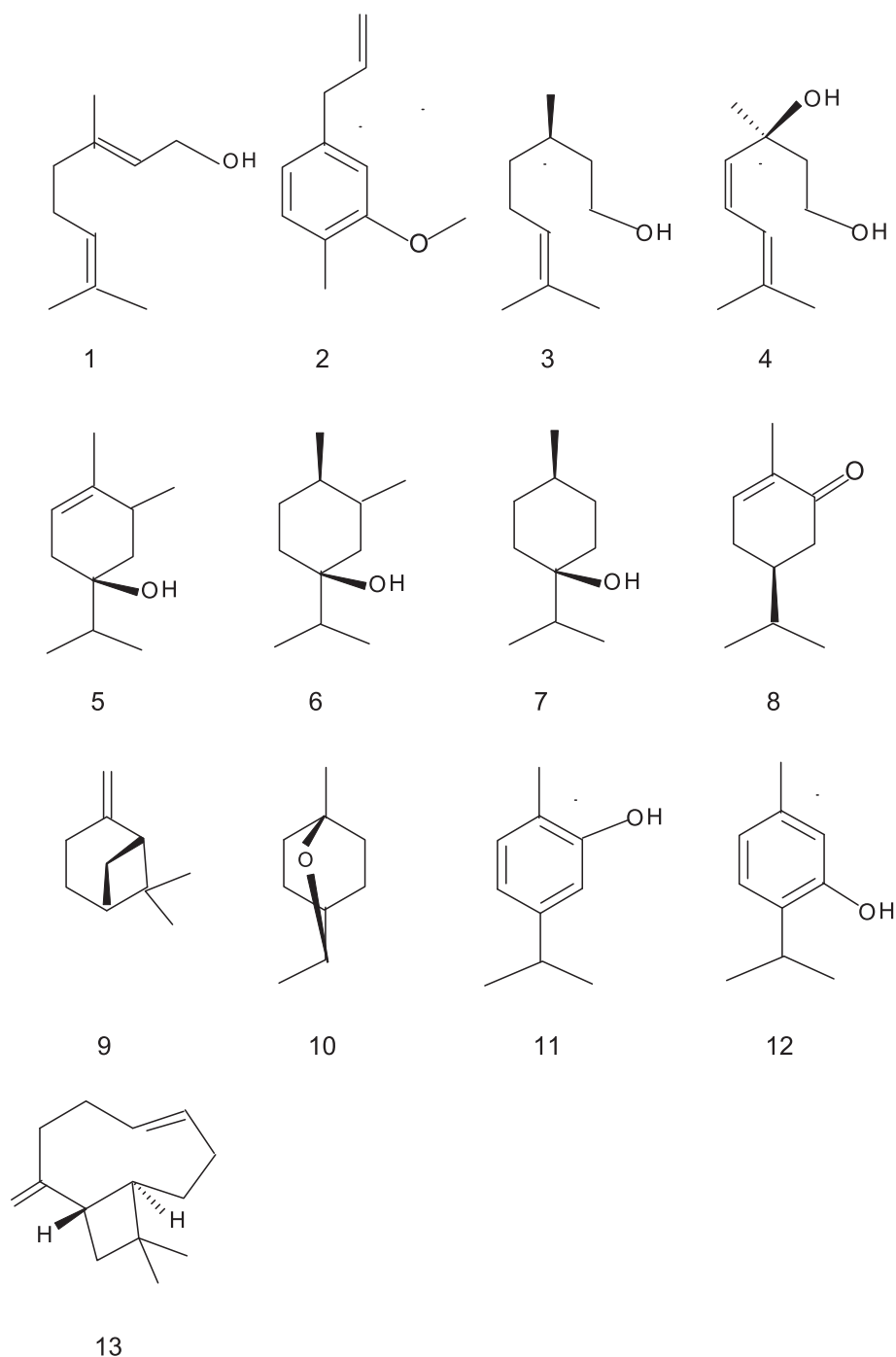


Fig. 3. (continued).

had left scales. Hexane washes of silk and frass galleries and larvae of *Opisina arenosella* (Lepidoptera: Crytophasidae) Walker elicited attractive responses from parasitoids *Goniozus nephantidis* (Muesebeck) (Hymenoptera: Bethyridae), *Brachymeria nephantidis* Gahan (Hymenoptera: Chalcididae) and *Elasmus nephantidis* Rohwer (Hymenoptera: Eulophidae), based on bioassays in which the numbers of parasitoids entering the kairomone arm were

greater than those entering the hexane arm in a Y-tube olfactometer [73]. Chemical analysis of kairomonal substances using GC-MS revealed the presence of 13-tetradecenal and myristic acid in the gallery washes in addition to dodecane, pentadecane, hexadecane, heptadecane, eicosane and tricosane. Larval washes contained the terpenoids, alpha-terpinene and alpha humulene [73]. In addition to volatile semiochemicals, non-volatile cues also mediate

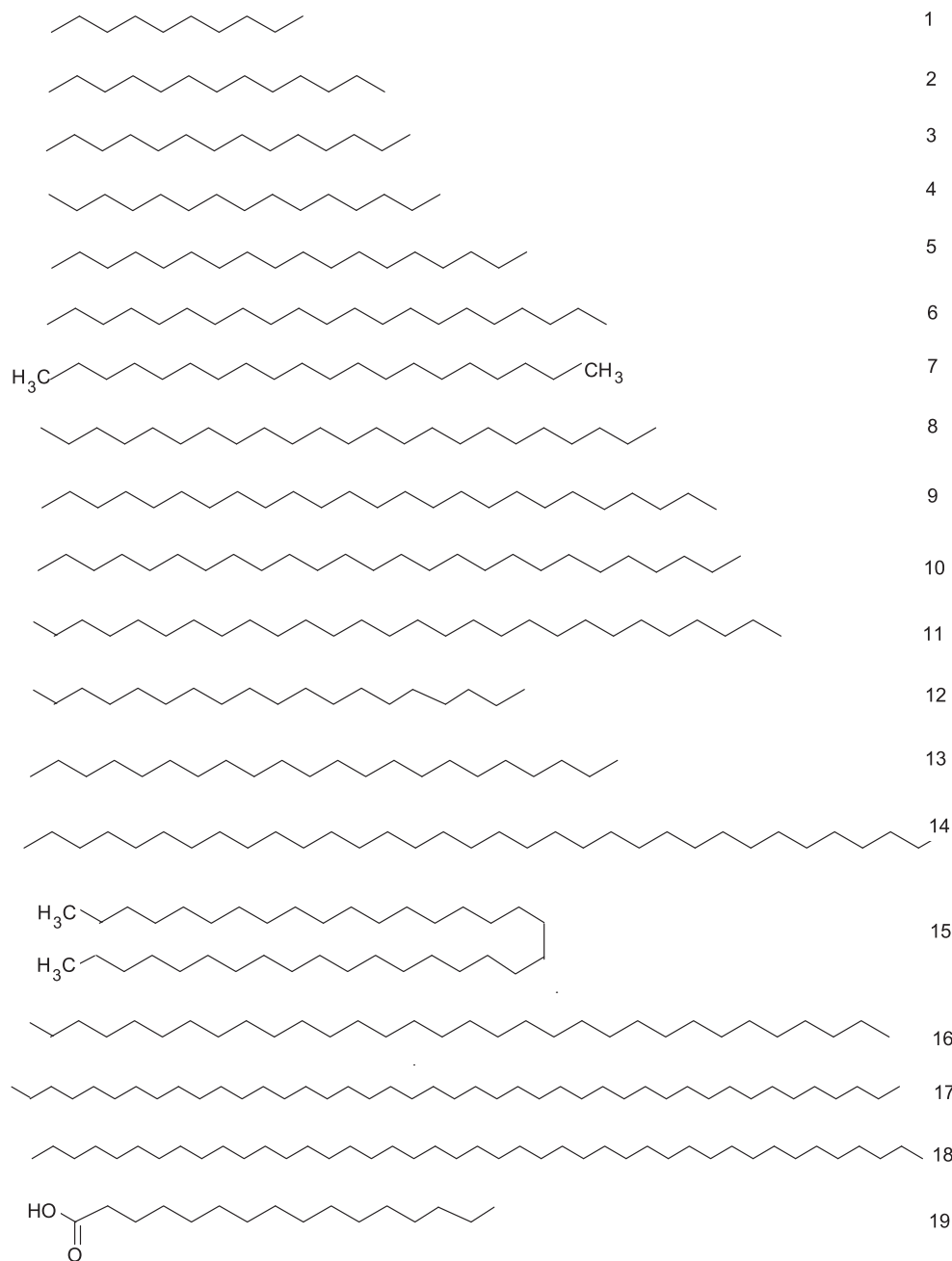


Fig. 3. (continued).

searching behavior of *Trichogramma* spp. Plants on which adult moths have been present may provide such cues for host location. Furthermore, egg deposition by herbivorous insects can induce changes of the plant that attract or arrest parasitoids [74,75].

It has been reported that host-searching stimulants for *T. evanescens* and *T. pretiosum* Riley are present in the wing scales, excretions and abdominal tips of female *H. zea*. A blend of aldehydes, hexadecanal, (*Z*)-7-hexadecenal, (*Z*)-9-hexadecenal, and (*Z*)-11-hexadecenal, increased rates of parasitization [76,77]. Airborne chemicals from egg masses and from virgin females of *O. nubilalis* (Hübner) (Lepidoptera: Crambidae) during calling activity stimulated intensive search behavior by *T. brassicae* Bez. [78] but mated females did not elicit responses. Scales and abdominal tip extracts

of *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) and *H. armigera* elicited attraction by *Chrysoperla zastrowi sillemi* (Esben-Peterson) in laboratory Y-tube bioassays [79]. More adults were attracted to acid-hydrolyzed L-tryptophan than to oxidized L-tryptophan [73]. Irradiated eggs of *H. armigera* and *Spodoptera litura* (Fab.) (Lepidoptera: Noctuidae) treated with whole body extract of *C. cephalonica* females were reported to elicit high levels of foraging by *T. chilonis* and *C. zastrowi sillemi* compared with hexane treated eggs [80–84].

Greater attraction by *T. chilonis* and *C. zastrowi sillemi* towards the whole-body extracts of female *C. cephalonica* than to male extracts may be due to the presence of larger amounts of attractive hydrocarbons in females [80]. Parthiban et al. [81] and

Maruthadurai et al. [85] reported that the parasitoid activity index of *T. brasiliensis*, *T. chilonis* and *T. exiguum* was high when they were exposed to female whole body extract of *C. cephalonica* and *H. armigera*, which contained a greater quantity of tricosane than male extract. Srivastava et al. [84] concluded that heneicosane and hexacosane present in the female whole body extract of *S. exigua* Hübner and *Chilo auricilius* (Dudgeon) (Lepidoptera: Crambidae) exerted significantly higher level of kairomonal effect on *T. chilonis*, as compared to other hydrocarbons. At the same time, female whole body extract of *S. litura* was more attractive to *T. chilonis* than male extract, as it contains greater quantities of docosane and heneicosane. Female whole body wash of *Earias vittella* containing heneicosane, tricosane, pentacosane, hexacosane, octacosane and nonacosane was reported to be attractive to *T. chilonis* [85]. Female whole body wash of *H. armigera* was also reported to be attractive to *T. chilonis* and *C. zastrowi sillemi* [86].

4. Synthetic saturated hydrocarbons as kairomone

The identification of kairomone volatiles from important crops is imperative for effective use of biological control in pest management due to heavy reliance of natural enemies on plant and prey semiochemicals for efficient performance as biological control agents. Various studies have reported these cues primarily were hydrocarbons [87,88]. For example, saturated long chain hydrocarbons, including pentadecane, heneicosane, tricosane, pentacosane and hexacosane extracted from whole body washes of female *H. armigera* and *C. cephalonica* have been reported to elicit kairomonal response in *T. brasiliensis* and *T. exiguum* [82,89–91] (Fig. 3C).

The polyphagy of Trichogrammatids as control agents against lepidopteran pests of economically high valued crops makes them popular for field releases [92]. Foraging behavior of egg parasitoids is guided by a wide array of semiochemicals [93]. Octacosane, pentacosane and tricosane at 11,000 mg/l were found to enhance the parasitic activity of *T. chilonis* and *T. brasiliensis* on eggs of many lepidopteran species [94]. Whole female body extracts of *S. exigua* and *C. auricilius* containing tricosane, docosane, pentacosane, heneicosane and hexacosane exerted high levels of kairomonal activity on foraging activity of *T. chilonis* [84]. Tetratriacontane, nonadecane, tetradecane and dotriacontane were reported to elicit foraging activity of *T. chilonis* and *C. zastrowi sillemi* at 200–500 ppm on eggs of *C. cephalonica* [86]. Padmavathi and Paul [94] reported that tricosane, octacosane and docosane were found to enhance the activity and parasitic efficiency of *T. chilonis* while *T. exiguum* was attracted by pentacosane, hexacosane, pentadecane, hexatriacontane, tricosane and docosane [88,95–97]. Parthiban et al. [86] indicated that tetratriacontane was attractive to *T. chilonis* while tetratriacontane, nonadecane, tetradecane and dotriacontane were attractive to *C. zastrowi sillemi*.

Paul et al. [88,98] found that variation in the quantity and concentration of saturated hydrocarbons influenced the parasitization efficiency of trichogrammatids. The responses were concentration-dependent and foraging activity did not necessarily increase in response to increases of hydrocarbon concentrations past natural levels. The efficacy of pentacosane and docosane and dotriacontane to act as kairomone to *T. chilonis* and *C. zastrowi sillemi*, respectively declined when the concentration was increased from 200 to 500 ppm while the efficacy of nonadecane on *C. zastrowi sillemi* increased when the concentration rose from 200 to 500 ppm. Mathur et al. [95] reported that lower responses of trichogrammatids to octacosane relative to tricosane and pentacosane may result from its higher rate of depositing out of the air onto substrates.

5. Non-host-plant-derived kairomone

The stimuli influencing parasitoid searching, parasitization, or retention can originate from non-host plants also [63,89,99–102]. Occurrence of high diversities of plant species also may provide support for insect biological control at local and landscape levels [103–105]. Non-host plants can directly serve as food sources or provide other ecosystem resources for herbivorous arthropods and indirectly serve beneficial arthropods by providing food and shelter to their prey [106].

Intercropping, the cultivation of two or more species within the same field, is a common method to increase beneficial insect diversity within agro-ecosystems [107–110]. Intercropping affects pests by modifying microclimates, altering crop canopies, and influencing the pest population build-up through abiotic factors such as protection from wind, shading, sheltering, prevention of dispersal, etc. Biological factors that can be modified include releases of natural enemies, production of adverse chemical stimuli, and provision of alternate food sources [111–113]. Several intercropping systems are under study for the potential to reduce herbivore populations through habitat manipulation and provision of shelter, nectar, etc., to natural enemies [86,114–119]. For example, populations of *C. carnea* and spiders were found to be significantly higher on cotton intercropped with lucerne, cowpea and groundnut [120]. Cowpea was used as a short-duration pulse crop to attract aphids, thus increasing occurrence of coccinellids in groundnut [120]. Coccinellids were significantly more abundant in pigeonpea with sorghum or green gram or groundnut or maize systems [121,122]. A high diversity of predator and parasitoid species was recorded from intercropping systems like groundnut + maize and groundnut + pearl millet, wherein intercrop-supplied pollen and nectar provided supplementary feed to the natural enemies [104]. Use of lady beetles and lacewings as important predators in cotton intercropped with different pulse crops [123] has contributed to changes in cotton management procedures. The supplementary food resources increase the parasitoid fecundity, longevity [124] and also favor rapid colonization of generalist predators [125,126].

Non-host-plant allelochemicals have been reported to be attractive to natural enemies [86,127–131]. Combining deterrent chemical stimuli (push) with trap crops (pull) has been demonstrated as an effective means of biological control [132–134]. Flowering plant strips adjacent to main crop fields help support beneficial insect biodiversity in agricultural landscapes [135–137]. Attraction of *Tetrastichus schoenobii* Ferriere (Hymenoptera: Eulophidae), an egg parasitoid of *Scirpophaga incertulas* (Walker) (Lepidoptera: Crambidae), to flowers of bush mint, *Hyptis suaveolens* L., a common weed in rice fields was reported by Refs. [137,138]. Flower bud, flower, and leaf volatiles of *Tagetes erecta* L. were found to attract both *H. armigera* and its parasitoid [139,140]. Suppression of herbivore populations and reduction of damage was demonstrated in several intercropping systems, cotton + ladies finger (okra), maize + legumes, sorghum + cowpea, cotton + sunflower, groundnut + bajra (pearl millet), sesame + bajra, and cotton + cluster bean [86,118,119,141–146].

Increased populations of natural enemies has been reported in many intercropping systems. Growing sunflower as intercrop in cotton resulted in increased numbers of *C. carnea* [147]. Lin et al. [148] found increases in the attraction of lady beetles, lacewings, and spiders to cotton crops in China when they were intercropped with alfalfa. Padmavathi and Paul [94], in a review of changing trends in cotton pest management, noted that lady beetles and lacewings were important predators in cotton intercropped with different pulse crops. These supplementary food resources increased parasitoid fecundity and longevity [98] and also favored

rapid colonization by generalist predators [125,126]. Cluster bean and pearl millet have been found useful as intercrops [86,115,116,131,149]. Flower extracts of cluster bean were attractive to the natural enemies of *E. vittella* (Fab.) (Lepidoptera: Noctuidae) and *H. armigera* in okra [150]. Alkaloids, terpenes, flavonoids, and phenolic compounds in flowers of weed, *H. suaveolens* in rice ecosystem were reported attractive to *T. schoenobii*, an egg parasitoid of *S. incertulas* [137,138]. Flower bud, flower, and leaf extracts of *T. erecta* containing benzaldehyde, (S)-(-)-limonene, (R,S)-(\pm)-linalool, (E)-myroxide, (Z)- β -ocimene, phenylacetaldehyde, and (R)-(-)-piperitone were reported to attract *H. armigera* and its parasitoids [139,140,151,152].

6. Effects of interspecific, intraspecific, and intra-population variability of host plants on entomophages

Parasitoids and predators of herbivores use cues released by host plants to find host habitats initially, and then use cues released by the herbivores to locate them on the host plant. As a result, interspecific, intra-specific and intra-population variability in host plants often plays a key role in whether entomophages are successful in finding prey. The host plants of insect pests are known to affect parasitoids directly or indirectly through tritrophic interactions [153]. Host plants invite natural enemies to reduce herbivore pressure and in several cases the female parasitoid responds to signals elicited from the host plant in response to pest damage in combination with signals from the herbivore [32,154]. For these reasons, the effectiveness of natural enemies for controlling insect pests varies across crops and different genotypes of the same crop [61,155,156].

Parasitization efficiency of *T. chilonis* on eggs of *H. armigera* under screen house conditions was reported to be higher on sunflower hybrid MSFH 17 (53.5%) than on hybrid KBSH 1 (38.0%) [4]. These glanded varieties release higher amounts of terpenoids compared with glandless varieties. Parasitoids such as *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) were attracted more to the glanded varieties of cotton than to glandless varieties [157]. Caryophyllene released by damaged *Vicia faba* (L.) attracted *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) egg parasitoids of *Nezara viridula* (L.) (Hemiptera: Pentatomidae) [158]. Linalool-L and heptadecane produced by fruits and leaves of hybrid tomato, Arka Ahuti, are reported to be responsible for high parasitization of *T. chilonis* on eggs of *H. armigera* in tomato ecosystems, while other compounds, α -phellandrene, α -pinene, *trans*-caryophyllene, (Z)- α -farnesene, *trans*- α -ocimene and selinene are known for their synomonal activity [4,159]. Among the genotypes of cotton, jayadhar and LRA- 5166 recorded higher electroantennogram (EAG) responses from the predator, *C. zastrowi sillemi* which may be due to the presence of high quantities of caryophyllene oxide, reported to be an important volatile compound released by *Chrysoperla* during egg laying [122].

Volatiles from different parts of cotton plants elicited increased attraction to different cultivars by *T. chilonis* and *C. sceleres* (Stephens) [160]. The most attractive volatiles included tetradecanoic acid, benzenepropanoic acid and hexadecanoic acid. Several researchers have reported the influence of different crop species on the relative dominance of parasitoids of *Heliothis* spp. in field conditions [161]. Mohite et al. [162] studied the parasitization of *H. armigera* eggs by *T. chilonis* on *Gossypium* spp. and reported that parasitization was 25% lower on *G. raimondii* Ulbr. than on *G. harknessii*.

The larval parasitoid, *Hyposoter ebenius* (Gravenhorst) (Hymenoptera: Ichneumonidae) showed greater preference for larvae of *Pieris brassicae* (L.) (Lepidoptera: Pieridae) when they were found on knoll-kohl (kohlrabi) than on cabbage, broccoli and cauliflower

[163]. The volatiles, 9, 12, 15 octadecatrienoic acid and 9-octadecenal present in rice cultivars of Kadamba, MTU-1010, KMT 148 and KCP-1, and hexadecane, heptadecane, pentadecane and hexadecanoic acid present in CTH-1, MTU 1010 and VTT-5204 were reported to attract *T. chilonis* and *T. japonicum* Ashmead to eggs of rice yellow stemborer and leaf folder, respectively [164]. The *H. armigera* larvae feeding on susceptible redgram genotypes, ICPL 87 and ICPL 97119 suffered significantly greater parasitization by *C. chloridae* Uchida (Hymenoptera: Ichneumonidae) than the other genotypes tested under no-choice, dual-choice and multi-choice conditions, suggesting that host genotype plays a significant role in the effectiveness of *C. chloridae* in parasitization of *H. armigera* larvae [165].

The activity and abundance of natural enemies varies across crops and different genotypes of the same crop [61,156]. The host genotype can influence parasitization by the natural enemies sometimes because of the effect of the morphological characteristics of the host genotype on herbivores [165]. The increased parasitization on herbivores on susceptible genotypes can also be influenced by survival of higher populations of herbivores on susceptible genotypes, lack of resistance to the herbivore, or production of greater amounts of the volatile compounds that attract the natural enemies for parasitization/predation [60]. Abundance of herbivores and their natural enemies can be affected by the host plant phenology and herbivore induced chemical profile of the genotypes [163]. It was suggested by Murali-Baskaran [166] that greater abundance of herbivores and their natural enemies on susceptible cultivar No. 55 of *Abelmoschus esculentus* (L.) Moench (okra), with lower abundance on resistant cultivars, resulted from secondary metabolites ingested by herbivores from the host genotype either directly affecting the foraging activity of natural enemies or indirectly affecting foraging through suboptimal prey.

Changes in biochemical composition of host plants in response to herbivory also influence the growth and survival of herbivores [167,168] which in turn influence the activity and abundance of natural enemies [169]. Sithanatham et al. [170] observed that parasitism of *H. armigera* larvae in chickpea was lower on resistant than susceptible genotypes. The rates of parasitism by *C. sonorensis* and *Cotesia congregata* (Say) (Hymenoptera: Braconidae) have been reported to be significantly lower on the resistant wild tomato, *Lycopersicon hirsutum* f. *glabratum* Humb.& Bonpl. but had little effect on parasitism by *C. marginiventris* (Cresson) (Hymenoptera: Braconidae) and *Cardiochiles nigriceps* Viereck (Hymenoptera: Braconidae) [171]. In chickpea, parasitism of *H. armigera* larvae by *C. chloridae* ranged from 8.33 to 28.00% [172] and varied considerably across genotypes [155]. Genotypic effects of pigeon pea were reported on the activity and abundance of *C. chloridae* natural enemies in pigeon pea against *H. armigera* by Hugar et al. [165].

It should be noted also that some parasitoid abundance differences result from host density effects. Bruce et al. [173] reported, for example, that as the incidence of a pest increases, the parasitoid activity also increases.

7. Field application of kairomone formulations

Determining structures of the chemical cues involved in kairomonal interactions can be difficult. Methodological problems include designing an appropriate bioassay. In a majority of studies, kairomones have been found to be complex mixtures [174]. This can make it difficult to synthetically produce enough kairomone for field applications. Several studies have shown that it is difficult to reconstitute mixtures that are as attractive as the original mixture [175]. In many cases, several of the mixture's components may evoke strong reactions, but these reactions are

not equal to the reaction to the natural mix [176]. This section discusses several examples where field applications were successful.

Singh et al. [177] reported that spraying of artificial honeydews containing protein hydrolysates and sugar in small plots of Lucerne attracted adults of *C. carnea* from larger areas of untreated Lucerne than did plots sprayed with sucrose alone. Use of L-tryptophan was reported to increase the abundance of predatory chrysopids in olive and potato. Spraying of molasses and kairomones together on maize plants increased the rate of parasitization of larvae of *Sesamia cretica* Ledereer (Lepidoptera: Noctuidae) [178]. Gross et al. [57] reported increases in parasitization by *T. pretiosum* when the kairomones were sprayed along with tricosane at 395 mg/ha on soybean crops artificially infested with eggs of *H. zea* (Lepidoptera: Noctuidae). Hu and Chen [179] reported that spraying of kairomones extracted from the frass of *Cnaphalocrocis medinalis* (Guenee) (Lepidoptera: Crambidae) on rice plants in the field increased by 15–25% the parasitization of *C. medinalis* by *Apanteles cypris* Nixon (Hymenoptera: Braconidae). The performance of several parasitoids and predators was increased by kairomone at field conditions. Zaki et al. (1997) [178] reported that parasitism by *Meteorus rubens* (Nees Von Esenbeck) (Hymenoptera: Braconidae) on *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) increased when fields were sprayed with molasses (3%) and kairomone.

Acid-hydrolyzed L-tryptophan has been identified as an attractant to chrysopids [180] and a hydrochloride salt of tryptophan formed during hydrolysis was found to be attractive to *C. carnea*. Field trials on cotton, conducted during 2000–2002 revealed that the number of *C. carnea* eggs in the L-tryptophan treated plants was greater than in the untreated control. Also, larval chrysopids cue on volatiles from the scales of the prey insects for host location and feeding [79,127,181]. Larval kairomones consisting of scale extracts fortified with tricosane, along with eggs of *C. cephalonica* as the supplementary diet, combined with the adult kairomone, acid hydrolyzed L-tryptophan, were sprayed on cotton at three locations where higher numbers of eggs, larvae, pupae, or adults of *C. carnea* but fewer aphids, jassids, and bollworms were reported than in untreated fields [182].

Though several organic and inorganic materials are found to have kairomonal activity to different natural enemies in laboratory bioassays, their efficacy at the lowest concentrations often do not permit researchers to deliver them easily in the field. Suitable cost-effective formulations of kairomone need to be developed for delivery under field condition as has been accomplished for applications of pesticides. Nevertheless, successes with combinations of organic and inorganic materials have been reported. Paramasivam and Paul [183] formulated a kaolinite-clay-based kairomone with leaf extracts of flowering phase of maize and sunflower combined with washes of *C. partellus* (Swinhoe) (Lepidoptera: Crambidae) eggs and observed that the semiochemical dust formulation recorded highest parasitism by *T. chilonis* (47.13%) in tomato fields when compared to control (17.04%). Reitz et al. [184] reported that formulations of essential oils with kaolin successfully reduced populations of *Frankliniella* spp. and tomato spotted wilt on tomato. Rubber septa impregnated with a kairomone mixture comprising fresh hexane extract of *C. cephalonica* (1%) + hexacosane (0.3%) and *C. cephalonica* scale extract (1%) + nonacosane (0.3%) were tested in field studies of egg parasitization by *T. chilonis* and high rates of parasitization were recorded (77.25%) [185]. It was observed that rubber septa are better long-term dispensers for kairomones than paper strips, perhaps because rubber septa have better retention of kairomones and controlled release while paper strips release the cues quickly. Kant et al. [186] reported that cork and rubber septa gave higher catches of *H. armigera* than cigarette filters or filter. Similarly,

Ventura et al. [187] also reported that rubber septa dispensers impregnated with plant kairomone (Floral volatiles-1, 4-dimethoxybenzene) attracted more *Diabrotica speciosa* (Germare) (Coleoptera: Chrysomelidae) beetles than a control (dental wick). Knight and Light [188] developed a halobutyl rubber septa impregnated with ethyl (E-2)-2, 4, decadienone which successfully trapped codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae). Srivastava [189] recommended that tricosane at 250 mg/cm² and pentacosane and docosane either at 125 or 250 mg/cm² could be used for efficient attraction of *T. chilonis* in the field. Abagli et al. [190] found that pentacosane at 250 mg/cm² and hexacosane at 500 mg/cm² elicited highest response from *T. brasiliensis* and *T. exiguum*.

8. Conclusions

Consideration of the examples above suggests several conclusions about the future use of kairomones in biological control against crop pests. First, it is important to remember that the chemical profiles of plants supportive to natural enemies may vary from genotype to genotype within the species, and the ways in which they influence the tri-trophic interaction in a particular ecosystem need to be identified. This is important because plants use tritrophic interactions frequently as defenses against herbivores, but can fall prey to herbivores that make use of the same resources provided to the natural enemies.

Second, optimal release rates of non-host or synthetic kairomones have considerable potential to enhance the foraging efficiency of entomophages in integrated pest management programs, and may facilitate more rapid control of herbivores than through natural buildup of entomophage populations. Identification and demonstration of cost-effective, companion non-host plants may enable more effective use of inter-cropping, trap cropping, bund cropping, and weeds in many crop eco-systems. Further screening of non-host plants for their attractiveness to entomophages in programs of conservation biological control is likely to yield improved pest management efforts. Maintenance of such non-host plants in specific arrangements in main crop eco-systems can be attractive to natural and released populations of entomophages to enhance management of herbivores.

Biocontrol agents frequently are released without subsequent efforts to conserve the released populations. In the future, it is likely that entomologists will direct more efforts to provide diets and other support for the continued presence of natural enemies in the crop ecosystems.

Identification of previously unknown kairomones from female whole body washes of host insects could play a major role in future biological control programs. Sources of kairomones frequently contain multiple different cues in varying quantities. Such kairomones have been and continue to be identified through systematic laboratory and field experiments. The role of volatiles in attracting entomophages need to be elucidated in further studies, and the genes affecting production of these kairomones need to be identified to incorporate these traits in breeding programs. Field studies with proper dosages and economic analysis of the efficacy of the kairomones are necessary for proper recommendation of the product.

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