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Role of infochemicals to enhance the efficacy of biocontrol agents in pest management

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Abstract

Infochemicals are chemicals that convey information in an interaction between two individuals evoking in receiver a behavioural or physiological response that is adaptive to one of interactants or both. Information conveying compounds, so-called infochemicals, are divided into two broad categories according to their use within and between species. Pheromones are substances that mediate interactions of individuals belonging to the same species. Allelochemicals, the second group of infochemicals, mediate interactions of individuals belonging to different species. Depending on the benefits for sender and receiver, they are categorized into allomones (beneficial for the sender), kairomones (beneficial for the receiver) and synomones (beneficial for sender and receiver). Kairomones are mainly involved in the host selection process including the habitat preferences and a series of consecutive behaviours that lead to the successful parasitisation of the host. These chemicals may originate from the host itself (e.g., cuticular compounds) or different stages of host (eggs, larvae, pupae, adult) host by-products (e.g., frass, exuviae, mandibular gland secretions, defense secretions etc.). In addition, parasitoids rely also on volatiles of the hosts food plant (synomones) induced by feeding or oviposition of the herbivore. Application of allelochemicals in pest control is impossible without knowledge of the behavior induced by the chemicals. Application of infochemicals have initiated many ideas in pest control: Enhancing searching efficiency of natural enemies, Bringing the natural enemies in a specific search mode, making novel or artificial host-prey species acceptable in a mass rearing, breeding plant cultivars that have an increased emission rate of natural enemy-attracting synomones. Chemicals are among the main information-conveying agents available to predatory arthropods. They play an essential role in almost all stages of prey searching and prey selection The idea of enhancing search efficiency through application of allelochemicals has been seriously tested in laboratory and field situations with *Trichogramma* spp. The 'push-pull' strategy, is based on practical use of allelochemicals, management of cereal stem borers in Africa have been successfully accomplished through push-pull strategy.

Keywords: Infochemicals, Insect Kairomones, Parasitization, Synomones

1. Introduction

Infochemicals are chemicals that convey information in an interaction between two individuals evoking in receiver a behavioural or physiological response that is adaptive to one of interactants or both. Vet and Dicke (1992) [41] defined infochemicals as achemicals that transmits information in an interaction between two individuals, inducing in the receiver a behavioural or physiological response. Information conveying compounds, so-called infochemicals, are divided into two broad categories (Fig. 1) according to their use within and between species (Nordlund and Lewis, 1976; Dicke and Sabelis, 1988) [25, 8].

Pheromones are substances that mediate interactions of individuals belonging to the same species. Most of them operate as releasers by causing immediate behavioural changes in the receiver (Wilson and Bossert, 1963) [42]. In contrast, primer pheromones induce physiological changes in the receiver, such as sexual maturation. However, some pheromones are known to have both a primer and releaser function (e.g. the honeybee queen pheromone) (Wyatt, 2003) [43]. According to their function, pheromones are subdivided into: territory marking pheromones, alarm pheromones, trail marking pheromones, aggregation pheromones and sex pheromones (Nordlund, 1981) [26]. Latter ones are widespread among insects released by males or females to induce behavioural responses directly or indirectly leading to mating (Powell, 1999) [29].

Allelochemicals, the second group of infochemicals mediate interactions of individuals belonging to different species.

Depending on the benefits for sender and receiver, they are categorised into allomones (beneficial for the sender), kairomones (beneficial for the receiver) and synomones (beneficial for sender and receiver) (Nordlund and Lewis, 1976; and Sabelis, 1990) [25, 9]. However, a given chemical can have several biological functions within a complex network of interactions and thus, the classification of infochemicals can rapidly become complicated. For example, sex pheromones of insects are often exploited by their natural enemies as foraging kairomones. Use of chemicals emanating from the host and its by-products which enhance the behavioural dynamics of entomophages increasing their effectiveness were advocated by Brown *et al.* (1970) [6], Lewis *et al.* (1975) [22] and Anantahkrishnan, (1991) [2]. Successful establishment, retention in target sites and manipulated behaviour of natural enemies are important components of a successful biological control programme.

Apart from pheromones, allelochemicals play a crucial role in the chemical communication of insects and induce highly diverse functions for the receiving organisms (Ruther and Steidle, 2002) [31]. In parasitic Hymenoptera, kairomones are mainly involved in the host selection process of females including the habitat preferences and a series of consecutive behaviours that lead to the successful parasitisation of the host (Vinson, 1998) [40]. In addition, parasitoids rely also on volatiles of the host food plant (synomones) induced by feeding or oviposition of the herbivore (Turlings and Wackers, 2004; Hilker and Meiners, 2006) [37, 13]. Volatile substances from plants (synomones) primarily enable the location of the host habitat and the host within the habitat, less volatile compounds are used by the parasitoids to recognise and finally accept the host (Godfray, 1994) [12]. These chemicals kairomones may originate from the host itself (e.g., cuticular compounds), its products (e.g., silk, faeces) or from organisms that live associatively with the host (e.g., bacteria, fungi, mites) (Vet and Dicke, 1992; Powell, 1999; Steidle and Loon, 2002) [41, 29, 32]. The response to chemical cues in the context of foraging is one of the important perspective to enhance the efficacy of biocontrol agents by utilizing these infochemicals (Vet *et al*., 1995) [39].

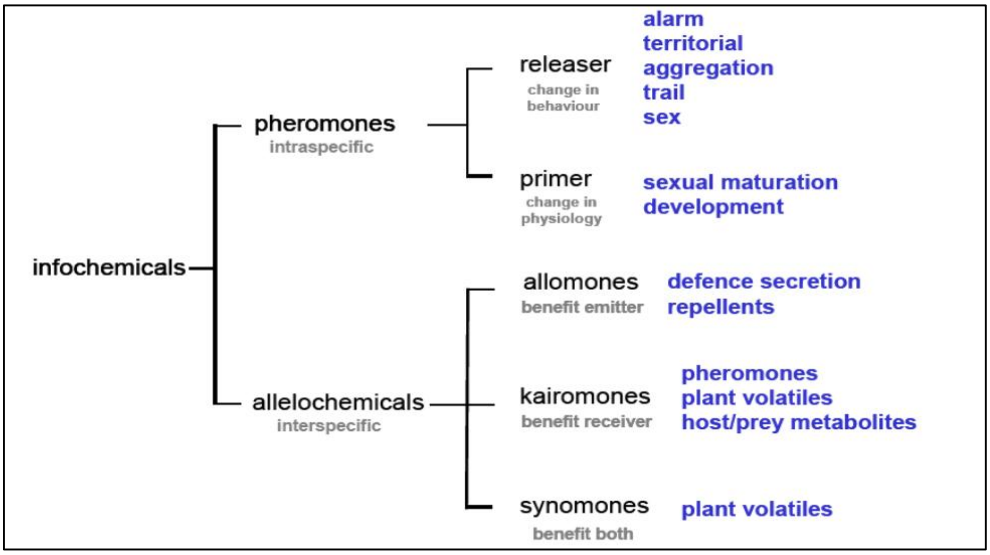

Fig 1: Showing classification of infochemicals.

Role of infochemicals in enhancing efficacy of biocontrol agents

Infochemicals typically enhance the efficacy of biocontrol agents by following ways:

- Enhancing searching efficiency of natural enemies
- Bringing the natural enemies in a specific searching mode
- making novel or artificial host-prey species acceptable in a mass rearing
- Using the response to the allelochemical as a criterion in the selection of natural enemies for biological control
- Breeding plant cultivars that have an increased emission rate of natural enemy-attracting synomones.

Allomones

Allomone may be defined as a chemical substance was proposed by Brown *et al.,* (1970) [6] to denote those substances which convey an advantage upon the emitter. Allomone is an allelochemical that evokes in the receiver a response i.e. adaptively favourable only to the emitter, not the receiver (Panda and Khush 1995) [27]. Moreover, allomone is any chemical substance produced and secreted into the environment by an organism of one species that evokes changes in the behaviour of a member of another species resulting in the advantage to the emitter species but not to the receiving organism of the other species. Allomones provide a usual kind of defensive measure manifested by plant species against the insect pest species or prey species against predator organisms. Sometimes species produce the sex pheromones of the organisms they exploit as prey or pollinators (such as bolas spiders and some orchids). Allomones act in number of ways (Table-1) as reported by Panda and Khush, 1995 [27].

Table 1: Effects of Allomones on the receiver organisms.

Allomones	Effects
Repellents	Orient insects away from the host plant
Locomotor excitants	Start or speed up movement of insects
Suppressants	Inhibit biting or piercing by insects
Deterents	Prevent feeding or oviposito n by insects
Digestibility reducers	Interfere with normal process of utilization of food

Kairomones

Allelochemicals that elicit a behaviour in the receiver organism and provide an advantage to the receiver oraganism only but not the emitter species are known as Kairomones (Dicke and Sabelis, 1988) [8]. Infochemicals have been reported to be secreted at various stages by the host organism viz. eggs, larvae, pupae, adult or host by-products (e.g., frass, exuviae) or mandibular gland secretions, defence secretions or intra-specific infochemicals (pheromones). Volatile secretions from the fecal matter observed from both larvae and adults of the elm leaf beetle (*Xanthogaleruka luteola*) were found to attract its egg parasitoid (*Oomyzus gallerucae*) (Meiners and Hilker, 1997). Many natural enemies have been found to utilise pheromones as kairomones. Synthetic sex pheromone [(*Z*)-16-methyl-9-heptadecenyl isobutyrate] of *Euproctis taiwana* was reported to attract the parasitoid (*Telenomus euproctidis*) as well as its male (*E. taiwana*) for reproduction (Lewis *et al.* 1982) [20]. Aggregation pheromone of the male bugs (*Podisus maculiventris*) was reported to be utilized by *Telenomus calvus* to come in host male's vicinity (Arakaki *et al*. 2000) [1]. Moreover, they also reported that sex pheromone [(Z)-16-methyl-9-heptadecenyl isobutyrate] of virgin tussock moths (*Euproctis taiwana*) as reported by earlier workers, allures *Telenomus euproctidis* which hides in the anal tuft until the female moth starts laying her egg clutch and parasitizes them. Egg parasitoid (*Trichogramma brassicae*) was first time reported to exploit antisex pheromones of its host i.e. cabbage butterfly (*Pieris brassicae*) (Fatouros *et al.* 2005) [11]. *Trichogramma ostriniae* expressed a positive response to odor released from gravid females of the Asian corn borer (*Ostrinia furnacalis*) which is its host (Bai *et al.* 2004). Also, on spraying plants with synthetic pheromones, egg parasitoids showed Arrestment and stimulate intensive searching behavior in these areas which increased the probability to encounter host eggs, resulting in higher parasitism rates.

Males of the leaf-footed plant bug (*Leptoglossus australis*) were reported to secrete aggregation pheromone (Aldrich, 1995) [3]. Egg parasitoid (*Gryon pennsylvanicum*) were found in the traps baited with male bugs only but never in traps with females bugs, which suggests the presence of a male-derived pheromone acting as a Kairomone for the wasps (Yasuda, 1998) [45]. *Trichogramma evanescens* was the first reported to show arrestment in response to chemical traces left by the grain moth *Sitotroga cerealella* (Laing 1937) [19]. The wing scales left by ovipositing *H. zea* or *Plodia interpunctella* moths were used as kairomones by *T. evanescens* was later confirmed by Lewis, *et al.* (1972) [21]. Further, wing scales of butterflies or moths chemical traces of walking bugs and marking pheromone of a fruit fly of adult hosts were found to provide a sufficient response to egg-larval parasitoids (Yong, *et al.* 2007, Salerno, *et al.* 2006) [44, 34]. *T. evanescens* showed Stimulation of parasitism by eliciting significant changes in orientations in response to hydrocarbons such as tricosane (biologically active cue) present in the wing scales of *H. zea* (Jones, *et al.* 1973) [15]. Also, host gender recognition cue for the egg parasitoids *T. basalis* was reported to be n-nonadecane, a cuticular hydrocarbon showing kairomonal activity on the egg parasitoid released by the tarsi and scutella of female bugs *N. viridula* (Colazza, *et al.* 2004) [7].

Field experiments were performed by Zhou, (2012) [46] in wheat exploiting infochemicals viz. (Z)-3-hexenol, (E)-β-farnesene, garlic extraction and Parrafin oil to control population density of cereal aphids and to promote the natural enemies of aphids *Metopolophium dirhodum* and *Sitobion avenae*. The population densities of cereal aphids and their natural enemies in wheat were significantly influenced by the use of infochemicals (Table-2).

Table-2: Total number of Aphids and their natural enemies recorded in wheat using 4 treatments of infochemicals.

Species	Parrafin oil (PO)	E-ß-farnesene(EBF)	Garlic extraction(GE)	(Z)-3-hexenol(ZH)	%
Aphids					
Metopolophium dirhodum	896	585	582	1112	89.5
Sutton avenue	138	35	54	148	10.5
Diversity and abundance of aphid species%	29	17.4	17.9	35.7	
Lady bird beetles 12.8 %					
Harmona axyndus	18	21	22	28	66.8
Coccinella septempunctata	9	9	8	3	21.8
Hippodamia variegata	1	1	0	1	2.3
Hoverflies 39.4%					
Episyrphus balteatus	69	108	85	76	82.6
Scaeva pyrastri	2	0	0	7	2.2
Lacewings 47.8%					
Chrysoperla carnea	95	128	152	121	100
Proprtion of natural enemies species %	**21**	**28**	**26.9**	**24.1**	

The main natural enemies of cereal aphids attracted were the lacewings (47.8%), the hoverflies (39.4%), and ladybird beetles (12.8%). Significantly higher abundances of hoverflies and lacewings were found in (E)-β-farnesene (EBF) and Garlic Extraction (GE release plots. Among the proportion of total predator species, the proportion was higher for (E)-β-farnesene (EBF), Garlic Extraction (GE) followed by (Z)-3-hexenol than control.

Usha, *et al.* (2006) [38] studied response of *Trichogramma japonicum* to cuticular extracts of adult, larval and larval frass of yellow stem borer (YSB) *Scripophaga incertulas*. Laboratory bioassays revealed that hexane extracts of the adult host body stimulate ovipositor probing of *T. japonicum*. Further, extracts of larval frass also stimulated parasitization (Fig. 2).

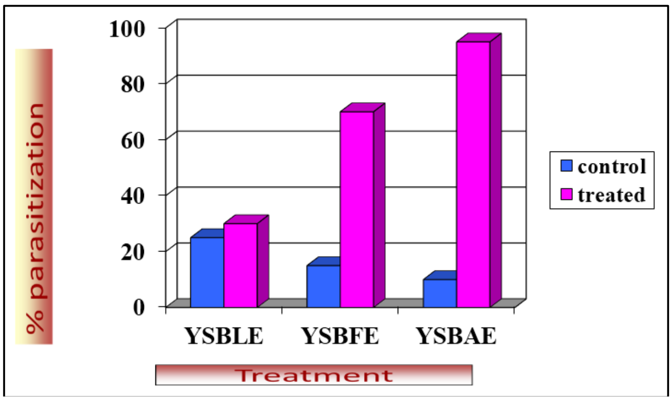

Fig 2: Influence of Extracts obtained from Rice Yellow Stem Borer on Egg Parasitization by *Trichogramma japonicum.*

In contrast, host larval cuticular extracts had no significant effect on parasitization rates. Analyses of the most active fractions by gas chromatography–mass spectrometry revealed that the extract contained saturated long chain alkanes and alkenes, docosane, tetracosane, pentacosane, and eicosane enhanced host egg parasitization (Table-3). Significant parasitization was observed with the treatment of adult extracts followed by larval frass extracts and no significant effect was noted with larval body extracts

Ananthakrishnan, *et al.* (1991) [2] studied effect of Kairomones on *H. armigera* (natural host) and *Corcyra cephalonica* (fractacious host) and their influence on parasitic potential of *Trichogramma chilonis.* They found that parasitization was significantly higher in *H. armigera* moth scale extract treated egg cards compared to control on treating egg cards with *H. armigera* and *C. cephalonica* moth scale.

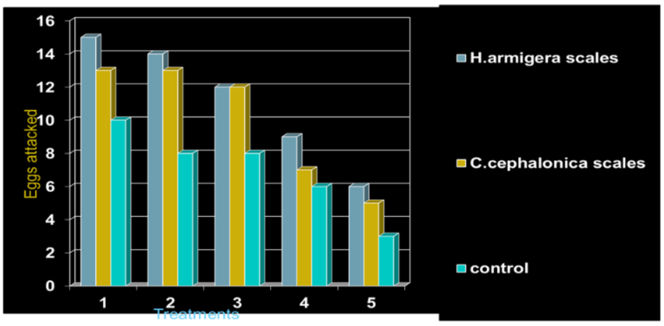

Fig 3: Influence of Extracts obtained *H. armigera and Corcyra cephalonica* on parasitic potential of *Trichogramma chilonis* with parasitoid age.

Different compounds such as 1,2-Benzenedicarboxylic acid, Docosane, Hexatriacontane, Heptadecane, Tridecane 1-iodo, Pentacosane, tetracosane 2, 6, 10-dodecatrienal etc. were isolated and identified from the the extacts of two hosts using chromatography techniques Table-3. Hexatriaconitane showed maximum 96% parasitism while maximum retention time on eggs was noted with heptadecane (26.08 min) in natural host. However, pentacosane showed maximum 94% parasitization but retention time was recorded highest in hexadecane (24.84 min) in fractcious host.

Table 3: Compounds identified, retention time and eggs parasitized from *H. armigera* and *C. cephalonica* moth scales.

Kairomone Source	Retention time	Identified compound	% eggs parasitized
H. armigera	12.92	1,2-Benzenedicarboxylic acid	64
	14.77	Docosane	88
	20.58	Hexatriacontane	96
	26.08	Heptadecane	88
	18.72	Tridecane 1-iodo	89
	12.79	2, 6, 10-dodecatrienal	88
Corcyra cephalonica	16.91	Pentacosane	94
	20.54	Hexatriacontane	64
	22.33	Nonacosane	54
	24.84	Hexadecane	84

Shonouda, (1999) [33] studied effect of aphid-extract(source of host searching kairomones) on the behaviour of *Coccinella septempunctata* by applying the different concentrations AC1, AC2, AC3 and AC4 of aqueous extract from *A. fabae*, the predator C. septempunctata adult showed different responses.

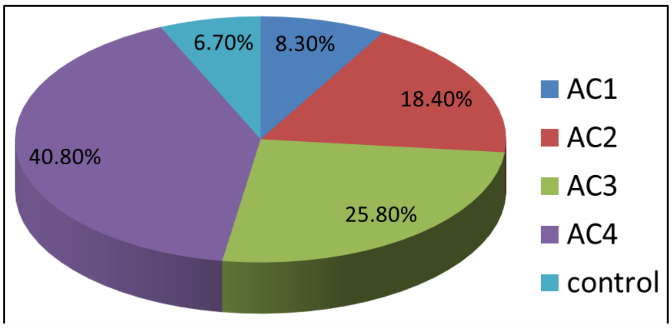

Fig 4: The percentage of number of *C. septempunctata* adult directed or attracted to the different concentration of Aphid extract (AC) in addition to control.

They observed that the percentages of attracted adults were more to each concentration of aphid extract 40.8 %, 25.8 %, 18.4 % and 8.3 %, as compared to control i.e. distilled water, which attracted only 6.7%. This confirmed that number of coccinellid adults attracted were directly proportional to the concentrations of the aphid extract (Fig.4). The reason for this phenomenon was presence of the chemical messengers (Kairomones) which stimulate and direct the predator coccinellid adults to the treated plants present in aqueous fractions of aphid extract.

Moreover, it was noted that adults showed vigorous change in moving behaviour at different concentrations of aphid extract as compared with the control. Also it was observed that the mean path length covered by coccinellid adults was greater than that with the control at the four concentrations of aphid extract (Fig. 5). Further, the overall trail distance covered by coccinellid adults under the influence of AC4, AC3 and AC2 were significantly higher than that in the control, while trail distance walked under influence of AC1 was insignificantly high when compared with control. Moreover, turning rate of coccinellid adults was affected significantly at different concentrations of aphid extract. It is evident clearly that different concentrations of aphid extract affects the searching behaviour of coccinellid adults such as the path length and the number of turns exhibited.

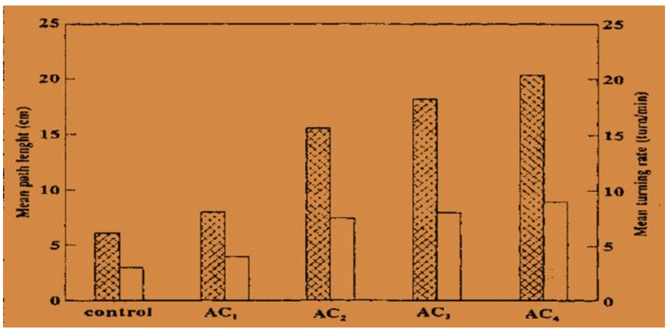

Fig 5: The mean path length (cm) and the mean turning rate (turns/min) exhibited by *C. septempunctata* under the effect of different concentration of aphid-Extract(Ac).

Synomones

An infochemical of an organism that on emission evokes a behavioral or physiological response in the receiver, an individual of a different species, adaptively favorable to both receiver and emitter.

Chemical stimuli are an important source of information for arthropods and may convey information about the presence and quality of resources, competitors, and enemies. Arthropods that predate for herbivores exploit volatiles pertaining to herbivores. These cues have been reported to arise not from the prey (host) species, but from the prey's food plant, which releases chemical cues in reaction to herbivore injury also known as Host Induced Plant Volatiles (HIPV'S) or synamones. This chemical message generated from the plant reveals the identity and presence of herbivore organism which feeds on the plant (Dicke and Baldwin, 2010) [10]. Maize plants infested by Noctuid larvae (*Spodoptera frugiperda* and *S. exigua*) emit terpenoids and indole that attract a parasitic wasp, *Cotesia marginiventris*.

Leaves of plants have been found to release generally minute quantities of the volatile fractions of chemical compounds, but on injury by the herbivore insect the level of released chemicals sharply raises, these serves as a cue for the natural enemies (parasitic and predatory insects) of the insect pest which parasitize or feed on the herbivore organism. This three way link between producer (plant), herbivore (pest) and carnivore (predator) comprising of three tropic levels is commonly known as tritrophic interaction. Example for tritrophic interaction is known in cotton *Gossypium hirsutum*, the herbivorous insect *Helicoverpa zea* and parasitic wasp *Microplitis croceipes* (Fig.6) (Kaplan, 2012) [16]

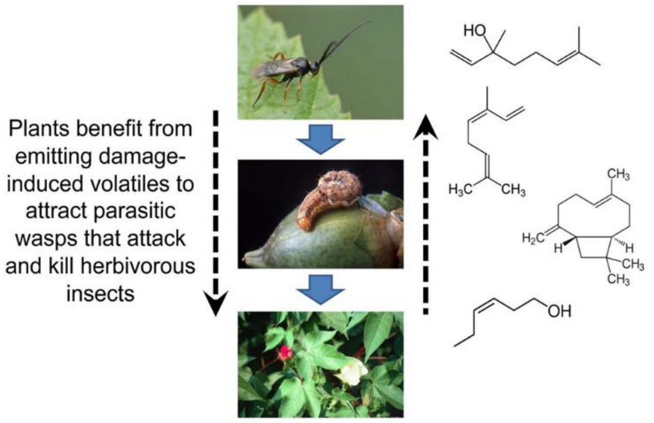

Fig 6: Interaction between cotton (*Gossypium hirsutum*), the herbivorous insect *Helicoverpa zea*, and parasitic wasp *Microplitis croceipes*.

Although plants release a variable range of chemical compounds that imparts defense or makes them susceptible to plant feeders, plant tissues release a varied range of volatile compounds in reaction to injury resulted from the herbivore attack which attracts the natural enemies. These chemical cues are important in order to differentiate among the normal uninfested and infested plants. A range of examples can be found which depict this interaction between injured plant, natural enemy and pest species. Predatory mites are attracted towards the volatiles released against Spider mites when they start damaging Apple and Lima beans, Hymenopteran parasitoids have been found to get attracted towards the corn and cotton plants against the caterpillar larvae of butterflies (Takabayashi and Dicke, 1996; Tumlinson *et al.*, 1993) [35, 36]. The released chemicals are known to be clearly distinct from those released from the un infested plants. A large number of chemical cues are released from leaf tissues which vary in composition, structure and properties from one another. A few chemicals such as linalool and (E)-b-ocimene (monoterpenes), (E,E)-a-farnesene and (E)-b-farnesene (sesquiterpenes), nonatriene and tridecatetraene (homoterpenes), indole and (Z)-3-hexenyl acetateare reported to be released from various plant species figure 7 (Paul and Tumlinson, 1999**)** [28].

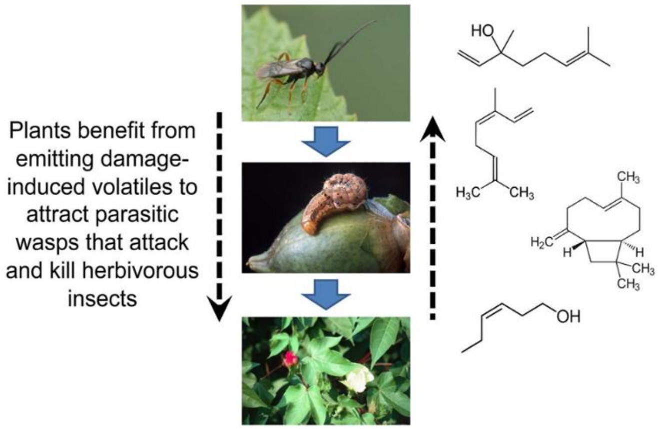

Fig 7: Metabolic pathway leading to volatile emission from herbivore damaged plants and exemplary structure of volatile compound.

Many workers are in notion that jasmonic acid is synthesised from linolenic acid by the octadecanoid signal for the natural enemies of pest. The volatile cues from the plants are released through stimulation of this octadecanoid/ jasmonate-signal complex as shown in figure-8, this is considered the main regulatory component in the transduction sequence that triggers synthesis and release of volatile compounds by plants. Also, insects secrete some elicitors such as volicitin, an octadecatrienoate at injury site which have found to enhance the release of emission levels of synomones from different plant species. There is still much to learn about the chemical interactions between plants and insect herbivores that lead to the synthesis and release of volatiles by the plants. Till date only one herbivore-specific volatile elicitor, volicitin has been identified.

The plants which are reported to produce volatile compounds such as synamones are notably similar in structure from insect damaged leaves and from leaves distal to the site of damage as evident from Table-6. The structural resemblance in the chemical emissions from various plants on insect feeding suggests the activation of a common set of biosynthetic pathways contributed by a wide range of plant families as shown in Table-6, and that the products are detectable to a broad spectrum of insect parasitoids and predators. The efficiency of host searching pests to discriminate and respond to such chemical cues and recognize them from background odors indicate that insect damaged plants emit volatile chemical compounds that are evidently distinct from those released in response to other kinds of injured or those emitted from uninjured plants. The plant's discrimination to distinguish between herbivore injury and a general injury response exclusively confirms the presence of elicitors linked with insect feeding that are absent from other types of leaf damage.

Table 6: Diverse plant species with shared volatile released in response to herbivory

Plant	Ocimene	Linalool	(E)-4,8-Dimethyl-1,3,7-Nonatriene	Farnesene	Tridecatetraene	Refrence
Apple	+		+	+	+	Takabayashi *et al.* 1994
Cucumber	+		+	+	+	Takabayashi *et al.* 1994
Lima beans	+	+	+		+	(Paul and Tumlinson 1997)
Cotton	+	+	+	+	+	Moraes *et al.* 1998
corn	+	+		+	+	Moraes *et al.* 1998
tobacco	+	+		+		Bolter *et al.*, 1997
Potato	+	+		+		Bolter *et al.* 1997

Meiners and Hilker (2000) [23] were the first to demonstrate that the field elm (*Ulmus minor*) releases volatiles (synamones) that attract the egg parasitoid *O. gallerucae* on oviposition by the elm leaf beetle *Xanthogaleruca luteola* which acts as a herbivore injury. Similar results were found in another tritrophic system where the eulophid egg parasitoid (*Chrysonotomyia ruforum*) is attracted by volatiles of Scots pine (*Pinus sylvestris*) induced by eggs of the sawfly *Diprion pini* (Hilker, *et al.* 2002; Mumm and Hilker, 2005) [14, 24]. Colazza, *et al*. (2004) [40] revealed that a generalist egg parasitoid, *Trissolcus basalis*, responds to plant synomones emitted by 2 different bean species (*Vicia fabae* and *Phaseolus vulgaris*) that are induced by the pentatomid bug *Nezara viridula.*

Practical application of infochemicals 'push-pull' strategy

Incorporation of infochemicals in integrated pest management programs is on its rise.

In Australia a strategy for insect pest management through infochemicals became popular and was popularly known as 'push-pull' strategy (Pyke, *et al.* 1987). The 'push-pull' strategy, anew emerging tactics for pest control programs, utilizes a joint use of behavior-modifying stimuli to exploit the to manipulate the dispersal and abundance of insect pests or natural enemies(bio control agents). In this strategy, the insect pests are diverted or repelled or deterred away from the main crop (push) by using chemical cues (infochemicals) such as(*E*)-ß-ocimene, α-terpinolene, ß-caryophyllene, humulene, and (*E*)-4,8-dimethyl-1,3,7-nonatriene that mask host appearance. The diverted pests at the same instant are attracted (pull), using highly apparent and attractive stimuli, to other areas such as traps or trap crops where they are concentrated, facilitating their control.

In Africa push pull strategy have been developed successfully by farmers for insect pest control, specifically for the control of stemborers on cereal crops. The push-pull strategy for maize stemborers in Africa comprises trapping stemborers on highly attractant trap plants (pull) such as Napier grass (*Pennisetum purpureum*), Sudan grass (*Sorghum vulgare sudanense*), while driving them away from the main crop using repellent intercrops (push) molasses grass (*Melinis minutiflora*), and desmodium (*Desmodium uncinatum* and *Desmodium intortum*). Moreover, Molasses grass when intercropped with maize, not only reduced infestation of the maize by stemborers, but also increased stemborer parasitism by a natural enemy, *Cotesia sesamiae* (Fig. 8).

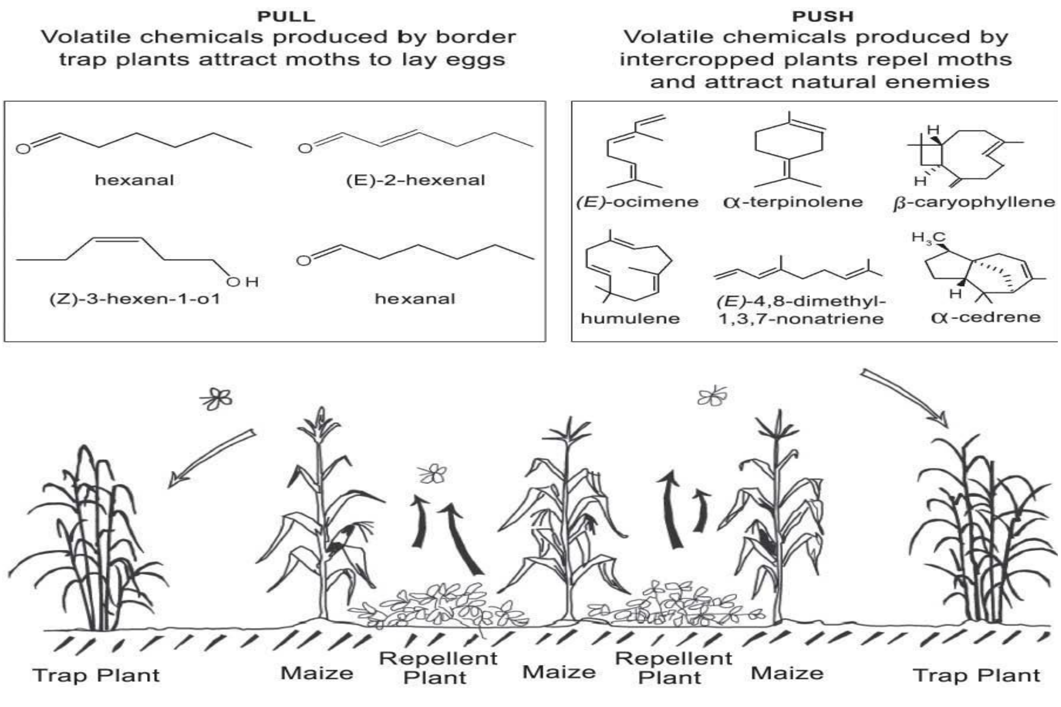

Fig 8: utilization of infochemicals in Push-pull strategy for maize stemborer parasitoids

Khan, *et al.*, (2008) compared the average maize yields in push–pull fields in 12 districts of western Kenya with the non push-pull fields in same districts. They found that the average maize yields were significantly higher as compared to the non push pull fields.

Conclusion

- Kairomones and Synomones play important role in recruitment of natural enemies.
- Infochemicals are increasingly being integrated with a range of methods producing new schemes.

- In addition to traditional approaches, research efforts should be continued to combine and develop new and innovative approaches including the manipulation of natural enemy behaviour through infochemicals.
- Armed with these tools, scientist may soon be able better to understand the role of infochemicals and apply this knowledge to improve biological control of herbivore pests.

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