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REVIEW ARTICLE

Pheromones in Aphids: A Review

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ABSTRACT: Aphids release an alarm pheromone on being attacked by predators to signal other members of the colony to evacuate and to make sure they do not become preys to natural enemies. This pheromone induces the individuals to produce winged offsprings which can fly away from the plant to avoid predators. The most common constituent in the alarm pheromone was found to be (E) – β – Farnesene. It is also found that these pheromones released by the Aphids can be a trail for attracting natural enemies towards colonies and hence causing self harm. As this pheromone can cause harm to the aphids themselves, it is of a great advantage to plants which produce (E) – β – Farnesene as one of the volatiles suspected to be a naturally resistant against Aphid infestations. Plants releasing this volatile are found to be protecting their sap against these aphid infestations as these pests are able to perceive these volatiles and avoid sucking the sap and disperse to avoid being attacked by enemies.

Keywords: Aphids, pheromones, (E) – β – farnesene, nepetalactol, nepetalactone

INTRODUCTION

Chemical signals and pheromones in particular play a very important role in agricultural pest management and help in improving the potential of various insecticides and drastically reduce the harmful effects on the environment (L. J. Wadhams. 1990). Aphids are polyphagous sucking pests which are capable of attacking various plants and causing severe damage. They suck the sap of the plants and produce toxic saliva over the plants leading to decrease in the plant's ability to conduct photosynthesis and also transmit plant viruses causing various diseases (Sarah H. Dewhirst *et al.,* 2010). They also produce excreta in the form of Honeydew which leads to growth of moulds in the host plants (Jia Fan *et al.,* 2015). Aphids are considered to be model organisms to study olfaction and chemical ecology. During higher temperatures they live in small groups and reproduce by parthenogenesis Mondor *et al.,* 2000). When aphids are attacked by natural enemies they produce an alarm pheromone after which they display behavior of producing winged forms that leave the plant or they just walk away to another plant with better nutrition due to predator pressure. This sticky secretion is produced by a pair of cornicles present on the dorsal surface of their body. This prevents their predators and parasitoids from feeding on them. This is also in indication for other members of the colony to move away from the host and get away from danger (Michael H. *et al.,* 2006). Some of the plants are also found to be producing volatiles having the same composition as that of the Aphid alarm pheromone which may be known to prevent these pests from settling on the plant and leads to a reduced nutrition intake by them which prevents their reproduction (Kunert *et al.,* 2010). This pheromone not only acts as a signal between aphid individuals but also acts as an interacting medium between aphids and plants and aphids and their natural enemies (Vandermoten *et al.,* 2012). On examination of various aphids species, studies suggest that 21 out of 23 species contain (E) – β – Farnesene in their pheromones (Huili Qiao *et al.,* 2009). The release of these alarm pheromone component may not only be beneficial to the aphids but also can be damaging because they will have to leave the host plant loosing out on food supply, increased risk of high mortality in individuals due to relocation and inviting predators to be attacked. To avoid these damages as much as possible the aphids may release the alarm pheromones only when physically attacked by the natural enemies and not when they detect predators indicating that they have a chance to preserve life and food (Christoph Joachim *et al.,* 2013).

PLANT VOLATILES AGAINST APHID INFESTATIONS

Volatiles mediate interactions occurring between the plants, aphids and the external environment. Plants have to capacity to show defense against various pathogens and pests by the ability to change their gene expression and metabolism rate (Martin de Vos *et al.,* 2010). Volatiles released by plants help in protection from pest infestations like that of aphids. As the constituents in the plant volatiles are found to be the same as the alarm pheromones produced by aphids, the plant is sought to be gaining a benefit from this due to a decrease in the aphid feeding and reproduction rates. This urges the aphids to produce more number of winged off springs which show behavior of leaving the host plant. This type of behaviour has been observed in Pea and Cotton species of aphids (Grit Kunert *et al.,* 2010). Studies by (Grit Kunert *et al.,* 2010) reveal that the continuous production of these volatiles from plants might not have a direct effect on these pests. It was found that some natural enemies of aphids may be attracted to these volatiles which may have a positive effect of controlling the infestations on aphid host plants. It is also well documented that plant volatiles like 2-Phenylethanol produced a response in the olfaction of aphid predators and parasitoids like lacewings which attract them towards the aphid host plants as a beneficiary act to get rid of infestations. Studying the olfactory responses between in the prey's host plant and the predators helps in development of efficient biological control in the field of agriculture to prevent invasive and harmful pests (Zhu *et al.,* 2005). Pyrethrum flowers are found to be attracting aphid predators like ladybugs by producing (E) – β – Farnesene indicating this pheromone helps predators find aphid preys and acts as a natural biological control. They exhibit defense mechanism from aphids by the production of these pheromones protecting the flowers which is the most important part of any plant (Jinjin Li *et al.,* 2019). Some species of wild potato are found to be metabolizing (E) – β – Farnesene as a volatile component due to which it acts as a natural resistance against aphid infestations (Huili Qiao *et al.,* 2009). Aphid parasitoid behavior of how they are attracted to their prey by chemical cues can be studied by using volatiles released by plants like mimicking pheromones produced by aphids like (E) – β – Farnesene (Alarm pheromone) and Nepetalactone (Sex Pheromones). Using these pheromones to attract these parasitoids can be used as a Bio-Control in Agriculture to stop aphid infestations on important economic plants (Ameixa *et al.,* 2011). In nature, plants follow a 'push and pull theory' where the volatiles push the aphid pests away and pull the natural enemies towards themselves for the environmental benefit. This helps in the study of aphid to plant, aphid to aphid, aphid to natural enemies and natural enemies to plant interactions (Jia Fan *et al.,* 2015).

PRODUCTION OF WINGED FORMS OF APHIDS

Studies demonstrated by (Grit Kunert *et al.,* 2005) show that when these aphids are exposed to artificial alarm pheromones just like the ones they produce naturally, this resulted in production of winged aphids in groups which was referred to as 'crowding'. Wild potato has found to be producing (E) – β – Farnesene which acts as a natural repellent against aphids. (Michael H. *et al.,* 2006) suggests that this phenomenon can be used to as a technique of crop protection from aphids by genetically modifying the crop to produce (E) – β – Farnesene. On exposure to (E) – β – Farnesene under laboratory conditions aphids were found to be producing good number of winged off-springs, but studies by (Hatano *et al.,* 2010) suggest that there was also a high proportion of winged individuals produced under field conditions. Sometimes production of winged morphs are also induced by the females if they are under some sort of stress like overcrowding of individuals on the host or non-availability of food on the host plant. In the case of Pea aphids, it was found that there is an increased production of winged individuals in large colonies due to more of physical contact among them which triggers the competition for food and space. Winged morphs are produced less in number in smaller colonies due to lower physical contact among individuals (Hatano *et al.,* 2010). Aphids in which the antennae were removed did not perceive (E) – β – Farnesene component of the alarm pheromone and did not produce wings to leave the host plant indicates that the pheromone signals could be perceived only by the olfactory system (Jia Fan *et al.,* 2015). Winged forms of Aphids also termed as 'alate' forms are not considered to be strong fliers but they can manage to fly to a good distance by drifting along with the wind. As aphids are pests that transmit plant viruses, some of them which are dependant on insect vectors for transmission can rely on these 'alate' forms of aphids which not only transmit diseases to other parts for the plant but also to different plants (Martin de Vos *et al.,* 2010).

A MUTUALISTIC RELATIONSHIP BETWEEN APHIDS AND ANTS

Aphids and ants are found to be engaging in a relationship of mutualism as ants get a continuous supply of honey dew, an excretion produced by aphids which is rich in carbohydrates and water and functions to be their good source of nutrition whereas in return aphids acquire protection and sanitation from the ants as they clean up all the trails of honey dew. Aphids show behavior of dispersal from the host plants by forming winged individuals when attacked by predators, but this may lead to loss of food supply to the ant colony. Hence the ants come up with various strategies to decrease their dispersal. These various strategies may include applying hormones on the aphids nymphs to prevent wing formation and to prevent them from flying away. The fire ants apply trial pheromones along the route that they take which leads them to the food source and this trail is maintained until the trail leading to the food source is not available anymore (Tian Xu *et al.,* 2021). (Verheggen *et al.,* 2012) suggested that ants have shown orientation and attraction towards the pheromones released by aphids which has been proved with olfactometer and choice assays while other volatiles did not show any response. Ants in association with aphids show behavioral responses on the abdomen of the aphids to generate increased release of honeydew and on exposure to the components present in the alarm pheromone of the aphids they prepare themselves to attack aphid predators as they provide protection to them. Ants are found to be locating their aphid partners for food by using low levels of the alarm pheromones produced by aphids when they are not attacked by predators. When aphids are attacked they tend to produce high amounts of alarm pheromone which urge the ants to show aggressive behavior intending to kill the aphids predators. On application of (E) – β – Farnesene, ants in mutualistic relationship with aphids are seen to be becoming very aggressive and attacking the aphid predators to protect them (Eduardo Hatano *et al.,* 2010). When aphids are attacked by predators they constantly release the alarm pheromone containing (E) – β – Farnesene which is perceived by the neighboring aphids in the colony and they disperse from the colony immediately as a result of threat but when the colony is attended by ants, the aphids do not disperse as they exhibit a mutual relationship and depend on the ants for protection (Acar *et al.,* 2001).

SEX PHEROMONES AND OTHER PHEROMONES

Mature individuals on the colonies release sex pheromones which attract mates of conspecific species for sexual reproduction. Other pheromones they release are found to be called Aggregation pheromone. This is released when a single individual has landed on a new host plants and signals others indicating them about food availability (Dewhirst *et al.,* 2010). Aphid females produce sex pheromones to attract sexually mature males but predators and parasitoids like lacewings adults are also found to be getting attracted by these sex pheromones called Nepetalactol. Many aphid species belonging to the Family Aphidae produce sex pheromones that consist of a mixture of Nepetalactol and Nepetalactone belonging to the category of Iridoids (Cyclopentanoids) (Dewhirst *et al.,* 2008). Sexual female aphids produce Nepetalactol in their sex hormones which also function as Aggregation hormones which aid in accumulation of large population to ease the process of mating. This not only helps in females finding male mates but also allows them to look for various locations to produce their sexual female progeny (Park *et al.,* 2000). It is also observed that during summer and autumn season *oculata* species of lacewings are found to be attacking Soyabean aphids and are specifically located in the regions of their prey presence indicating that aphid pheromones are having a major role to play in attracting predators (Zhu *et al.,* 2005). Pheromones produced by herbivorous insects are detected by their various natural enemies and assist in prey localization and can be termed under the category of Kairomones (Christoph Joachim *et al.,* 2015). *P. humuli* species of male aphids are found to be responding to sex pheromones from a distance of three meters indicating they can locate their mates from a long distance. Electro-antennogram studies reveal that the primary Rhinaria in aphids (hairless region at the tip of the snout) detect a number of volatiles and sex pheromones at different positions of the antennae. In contrast to these studies the secondary Rhinaria are found to be detecting only sex pheromones in sexually mature females (Gynoparae) and males (Tom *et al.,* 2004).

Alarm pheromones produced by aphids having (E) – β – Farnesene can have both positive and negative effects. The production in of this in an overcrowded colony can help in dispersal of individuals but the constant release of this can invite trouble to aphids by attracting predators and natural enemies. Studies show that female hoverflies being one of the major predators for aphids lay eggs not depending upon the number of prey in the colonies but completely depend on the amount of evoking pheromone substances produced by the aphids and also the concentration of volatiles produced by the host plants (Almohamad *et al.,* 2008). (Verheggen *et al.,* 2008) demonstrates that the alarm pheromone produced by aphids can not only be trigger predator attacks but can also be released and accumulated in response to some odor signals released by other colony members in aphid juveniles during their developmental stages. When a colony experiences a potential threat by certain predator aphids they may have to adapt to such contagious responses as a small amount of pheromone released by very few aphids may not be enough to warn the entire colony. However when the *Acyrthosiphon pisum* species of aphids were exposed to alarm pheromone signals they showed a typical behavior of moving away and the results showed that they did not produce the excess of pheromone to warn the other colonies indicating that the contagious responses of (E) – β – Farnesene does not occur (Verheggen *et al.,* 2008). Lures containing aphid sex pheromone components like Nepetalactol and Nepetalactone were used for field evaluation to check for aphid abundance. Results indicated that though there was a variance in the aphid population there was a significant decrease their abundance due to attraction of parasitoids and natural predators causing a drop in their numbers. Thus utilizing the semio-chemicals derived from the host or prey can function as a good natural bio-control in avoiding pests on crops in field conditions (Yoshitaka Nakashima *et al.,* 2016).

Studies conducted by (Boo *et al.,* 2003) in the fields of Korea revealed that the lacewing species *Chrysopa cognata* being a major aphid natural predator was highly attracted to the aphid sex pheromone component Nepetalactol than the other component Nepetalactone. When both the component chemicals were mixed to check for responses, the number of *Chrysopa cognata* increased in the trap along with the increase in the concentration of Nepetalactol but the number of was never found to be higher than the count achieved when Nepetalactol was used alone (Boo *et al.,* 2003). Vials containing Aphid sex pheromone component was used as a technique to check for attracting aphid parasitoids in field conditions. These vials containing the pheromone components were placed at different distances from the aphid infested plants to analyze at what particular distance the parasitoids would get attracted to aphids. Traps placed next the infested plants or at a short distance from it showed a significant increase in the attacks on aphid colonies whereas the traps placed at a far distance showed no effect on the parasitoid attraction indicating that they could not perceive the pheromones at very long distances. Observations indicated that the placement of these vials having the pheromone components increased the attacks on aphids by natural enemies. These experiments gives a proof that the natural enemies of aphids are not just attracted by the pheromone trap but are found to be actively attacking the aphids around the spaces of the trap to mummify them (Glinwood *et al.,* 1998). Other than the major component (E) – β – Farnesene which is a sesquiterpene in the aphid alarm pheromone there are also many other components like Monoterpenes and analogs which have not been investigated as much as (E) – β – Farnesene. It was discovered that the combination of all these multiple components were attracting a large number of predators when compared to only a single component of (E) – β – Farnesene. The attractiveness of these predators also increased with increase in the concentrations of the multiple components (Yaoguo Qin *et. al.,* 2022).

In recent times, efforts have been made to conserve natural bio-control processes which involves enhancing the natural populations of aphid natural enemies to control infestations on economically important agricultural and horticultural crops. For locating their hosts, aphid natural enemies use the chemical information produced by their host. Infested plants with aphids were found to be inducing the neighboring un-infested plants to produce the same volatiles containing pheromones which could attract natural enemies. This was a behaviour shown by the infested plant to increase the signal potential to attract more predators. This behavior was physiologically induced by the infested plants when the rhizosphere of both the plants came in contact with each other when grown together in a same pot and the roots came in contact with each other (Wilf Powell *et al.,* 2003). Studies indicate that the attraction experienced by predators to the pheromones released by the hosts are not always uniform. The concentrations released completely depend on the type, intensity and the species that are involved in the attack. In the case of aphids, natural predators like ladybugs were found to be attracted to smaller concentrations of (E) – β – Farnesene and attacked the hosts very quickly when compared to lacewings which required higher concentrations (Joachim *et al.,* 2013). Lady beetles are considered to be one of the key factors used as bio-control to protect major crops from aphid infestations and also various other pests. Studies suggest that they can perceive (E) – β – Farnesene produced in the aphid alarm pheromone indicating that they have evolved along with a strong sensory system which can detect odors released by their prey. Lady beetles respond to various odors like these when they are in need of food, shelter and a host to reproduce. It is said that Lady beetles adults and larvae not only respond to olfactory signals but can also locate their host prey by recognising colours (EB Acar *et al.,* 2001). It was found that juvenile aphids tend to release large amounts of (E) – β – Farnesene in their alarm pheromones when compared to reproductively active adults as they reside in large clusters of colonies and are more likely to be predated when adults tend to move away from the host to different places. As the aphids develop there is surely in increase in the size of the droplets released by their cornicles but there is no increase in the concentration of (E) – β – Farnesene.

The adult aphids emit a lower concentration of (E) – β – Farnesene in their pheromone droplets when compared to the juveniles or pre-reproductive aphids. Reasons for this can be stated as pre-reproductive aphids are immature and can invest most of their metabolism into producing the alarm pheromone as they have low reproductive values. Another reason can be that younger aphids can be very easily killed by predators and natural enemies whereas adults are capable of leaving the host quickly by flying away or dropping off (Mondor *et al.,* 2000). Sometimes the amount of alarm pheromone emitted by the aphids may not be enough to alert all the individuals as the odor may get diluted along with the blowing wind. To overcome this the un-attacked aphids may also release more alarm pheromone in response to the signals received by the attacked individuals to double the amount and to also alert a large number of individuals from threat. This phenomenon still remains to be unknown as to whether they show such behavior or not. But amplification of the pheromones, instead of being beneficial may also turn out to be risky as they may invite more number of predators to the colony due to strong and concentrated emission (Eduardo Hatano *et al.,* 2008). Orchids come under the category of deceptive flowers which get the service of pollination by the pollinators but do not give the pollinators anything in return for the service provided. They often get their services done by the pollinators by deceiving them either by visual, olfactory or both.

The terrestrial orchid species *Epipactis veratrifolia* emit fragrances which mimic the alarm pheromones produced by aphids attracting aphid natural enemies like hoverflies for pollination services. These hoverflies are considered to be beneficiary insects to the orchid flowers and show oviposition behavior of laying eggs which is also derived from the aphid produced kairomones. (E) – β – Farnesene is considered to be one of the major components of the aphid alarm pheromone but there are also other terpenoids which also conduct the action of alarm pheromones. A very common species of aphids in the Middle East called *M.Viciae* produces α- and β-pinene, and β-myrcene as a component in their alarm pheromones. The odor of these components were found to be very similar to the odor produced by the orchid flowers *Epipactis veratrifolia*. Studies suggest that orchid flowers do not mimic one particular species of aphid pheromones as they do not produce the exact amount and composition of pheromones produced by a specific species. This type of mimicry by the orchid flowers are completely justified as all the hoverfly species do not feed on one particular species of aphids (Johannes Stokl *et al.,* 2010). The pheromones produced in insects are considered to be in very small and trace amounts making it difficult to identify them, as they are also associated with various other substances. Gas Chromatography (GC) serves to be a highly efficient technique in the identification of various complex and natural substances but other additional techniques are also required along with it to isolate the biological products in the component. Small fractions of biological material obtained from the Gas Chromatography has been used for assay experiments to test the activity of insect antennae in the Electro-antennogram (EAG) (Wadhams *et al.,* 1990). As a defense mechanism Aphids have also shown a behavior of smearing the droplets released by their cornicles containing the alarm pheromone along the body of the predator which alerts the colony members of an approaching predator (Ezra G. Schwartzberg *et al.,* 2008). Aphids when reared in isolation under laboratory conditions produced less amount of alarm pheromones when compared to aphids reared along with other members. This behavior indicates that they prefer social environments and utilize the signals given by their neighbors to stimulate the pheromone production (Verheggen *et al.,* 2009). Genetically modifying plants with genes to produce volatiles similar to the Aphid alarm pheromone (E) – β – Farnesene is gaining importance in recent times as a good biocontrol agent to protect plants from infestations. This process has been successfully achieved by developing the hexaploid wheat cv. Cadenza. The volatiles released by this crop has shown successful results by preventing aphids from infesting and also attracts aphid natural enemies by the chemical odor (Bruce *et al.,* 2015).

ODORANT BINDING PROTEINS

The peripheral nervous system of insects consist of Odorant binding proteins (OBP) which regulate the antenna to detect various olfactory and gustatory senses (Qian Wang *et al.,* 2021). OBP help in perceiving different odors and aids in their discrimination (Huili Qiao *et al.,* 2009). They conduct chemo-sensation and chemical signals to identify volatiles on their host plant and also to locate their mates using sex pheromones (Qian Wang *et al.,* 2021). The hydrophobic volatile compounds in the environment are proposed to be transmitted to the insect olfactory system through these OBPs (Jia Fan *et al.,* 2017). OBPs transport the odor fragrances through the sensory neurons of the insect olfactory system. Their sensory receptors contain proteins of high concentrations but do not interact with each other in localized areas. Knocking down the genes involved in the OBP production showed that the Aphids were still being repelled by the production of (E) – β – Farnesene (Qian Wang *et al.,* 2021).

Among insects aphids specifically use their receptors in the primary and secondary Rhinaria present in the antennae to detect odors (Tom W. Pope *et al.,* 2004).

Studies indicate that OBP3 and OBP7 may be involved in the aphid olfaction for perceiving (E) – β – Farnesene in the alarm pheromone. *Rhopalosiphum padi* species of aphids were used to study the responses of olfaction for (E) – β – Farnesene and volatiles extracted from crushed aphids. Results indicated that *Rhopalosiphum padi* was repelled by both (E) – β – Farnesene and the volatiles extracted from the crushed aphids (Jia Fan *et al.,* 2017). Odorant receptors (ORs) are one of the sensitive chemosensory systems identified in aphids aiding in the perception of pheromones (Ruibin Zhang *et al.,* 2017). ORs are basically complexes that are present in the insect olfactory system consisting of a large number of odor specific receptors and odor specific co-receptors (Orco) (Fan *et al.,* 2015). An odorant receptor called ApisOR5 found to be expressing in the antennal segment of the aphids shows response to (E) – β – Farnesene when expressed along with Orca, an odorant receptor co-receptor. ApisOR5 is one of the receptors belonging to the large subfamily of odorant receptors (Zhang *et al.,* 2017).

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